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Bears

— Their Biology and Management

Papers of the Fourth
International Conference on Bear Research
and Management

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PREFACE

International bear conferences have enjoyed a relatively brief but exceptionally productive history. It all started in 1968 when a small group of biologists gathered for several days of informal discussions in Whitehorse, Yukon Territory. By 1970, a rapid expansion of interest in bears led to the first formal conference in Calgary, Alberta. This was only the beginning, and in 1974 a truly international effort resulted in split sessions at Binghamton, New York, and Moscow, USSR. The fourth conference was held in Kalispell, Montana, a location where the ecology, management, and politics associated with grizzly bears had reached an emotional pitch during the previous year.

The most unique aspect of this series of conferences has been the amount and kinds of information presented. Few wildlife species have received the magnitude of attention that has been directed toward bear species during the past decade. Published proceedings are witness to this fact and serve as a record from which everyone interested can benefit. In fact, a point has been reached where synthesis and evaluation of general concepts may be in order prior to moving on. Beginnings of this are evident in many papers and even more so in associated discussions. Formulation and testing of hypotheses now appear to be within the grasp of nearly all who work with bears throughout the world.

International conferences have been and should rightfully continue to be the major definitive source of information on bears. Published proceedings provide a foundation from which a path for future research and management is projected. Quality and credibility of the papers have been enhanced by conscientious authors, critical reviewers, and scrutinizing editors. The effort is time-consuming, to say the least, but the values derived will persist far beyond our short time frames.

This conference was made possible by the interest and enthusiastic support of many hundreds, perhaps thousands, of people working with bears. Content reflects those interests and demonstrates that bears and their management are not passing fancies. Special acknowledgment is given to the agencies that provided financial support — National Park Service, Forest Service, Fish and Wildlife Service, and Bureau of Land Management. Beyond that, sincere thanks are extended to everyone who contributed, in whatever manner, to the conference.

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BIOLOGICAL CONSIDERATIONS IN THE DELINEATION OF CRITICAL HABITAT

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Abstract: Grizzly bears (*Ursus arctos*) require large areas to satisfy their needs for food, cover, and space. They thrive best where disturbance by man is minimal. It is not a coincidence that the two major grizzly bear populations in the lower 48 states exist in large wilderness systems closely associated with two large national parks and a relatively large game preserve. If management objectives for these areas do not change, and man-bear interactions can be kept low, viable grizzly bear populations can probably be maintained. Outside of parks and wilderness areas, the picture is less clear. Grizzly bears adapt to some habitat modifications. The extent of their adaptability to habitat modification or human interaction is largely unknown. Answers to many pertinent questions will be slow in coming. In the meantime, management policies based on common sense rather than on adversary reactions among agencies are the best insurance of the grizzlies' survival.

The necessity of declaring habitat critical to grizzly bears within the continguous 48 states raises 2 major questions: (1) How many grizzly bears do we want? (2) What are the environmental requirements for a viable population of grizzly bears? This paper attempts to deal with the latter.

The term *critical habitat* refers to specific habitats or habitat components that, if destroyed or adversely modified, would pose a threat to the survival of the population. Critical habitat is most easily explained and understood in reference to species that are more highly specialized than the grizzly bear or about which we are better informed. Winter ranges for ungulates and breeding areas for waterfowl, for example, are relatively easily defined, but analogous areas for grizzly bears are not recognized at this time.

We do have information about the types of habitat where grizzly bears are now found in the lower 48 states. Sumner and Craighead (1973), Mealey (1975), Craighead (1976), and Jonkel (1976) have all given good descriptions of grizzly bear habitat in Montana and Wyoming. Erickson (1975, 1976) has evaluated areas of apparent low bear density in the Lolo National Forest that have potential for grizzly bear management. Although bears inhabit these areas, we still are uncertain of their relationships with habitat components. Complicating our understanding is the bears' adaptability, which may adequately compensate for the lack of a given component in any one portion of their range.

Distribution of grizzly bears in North America indicates that they are extremely versatile. This indication is reinforced by the wide range of habitats utilized by any one population. The combination of omnivorous food habits, a nongregarious social structure, and a high degree of mobility enables grizzlies to utilize most of the resources an area has to offer. Since these capabilities evolved over thousands of years, it is axiomatic that both the capabilities and the opportunities to exercise them are important to survival.

FOOD REQUIREMENTS

Since the grizzly bear is an omnivore, its food habits can be highly variable. Most popular opinions on bear food habits originate either from spectacular events, such as predation, or from items easily recognized in scats, such as berries and pine nuts.

Animal matter is the most nutritionally complete food for the bear. The grizzly is usually not an efficient predator and must depend on special circumstances to obtain meat. Common but unreliable sources exist in spring when ungulates may be present as "winter-kills" or "walking carrion," in spring and summer when there are high population densities of rodents, during fish-spawning runs in early summer, and during fall hunting seasons when offal and crippled ungulates are available. Domestic livestock are eaten as carrion; sheep are taken occasionally as prey but cattle rarely so. Insects are actively sought and taken when opportunity permits.

Berries and pine nuts are popularly recognized as important bear foods. However, they are seasonal, and each species is subject to severe fluctuations in production. Roots, bulbs, and corms of some herbaceous plants provide a major proportion of the diet and are probably more reliable food sources than meat or fruits. Taken altogether, the plants that we know bears use are common but not abundant.

Succulent grasses, sedges, and forbs are eaten throughout the year. Many species are eaten, but the relative importance of individual species varies with locality. As a group, these foods are the most abundant and possibly the most important staple of the bear's diet.

A cursory look at the omnivorous habits of the grizzly bear might indicate that food is not likely to be a critical problem. With the exception of herbaceous materials, however, the grizzly bear depends on sporadic food sources. Even succulent herbaceous materials may be scarce during dry years. Since the grizzly bear does not use cured plant material, it must seek areas where succulent vegetation persists if other foods are not available. The bear has many options, but a variety of habitat types is essential to exercise these options during the course of a year.

COVER

All occupied grizzly bear habitat in the conterminous states is characterized by extensive timber cover as well as by open grasslands and meadows. Bear populations can thrive in open areas, as they do in the less settled portions of Alaska and Canada. Although the species apparently has no intrinsic need for extensive timber cover, populations living relatively close to settled areas may require the isolation. Whether required or not, bears spend most of their time in or near timbered areas. Although areas occupied by grizzly populations contain large openings, few bears are observed in them at any one time. Most day beds used by grizzly bears are found in timber stands, even at times when bears are commonly observed foraging in the open.

Denning sites may or may not be critical. Criaghead and Craighead (1972) suggested that bears prefer isolated northern exposures, but supplementary data indicate that other exposures and less isolated areas are used. All known den sites are in areas that normally receive heavy snowfall.

SPATIAL REQUIREMENTS

Several biological characteristics of bears indicate vast spatial requirements. Home ranges of individual bears are large. Sumner and Craighead (1973) stated that mature males may have home ranges exceeding 2,590 km^2. Current studies show that even a female with cubs-of-the-year may have a home range exceeding 518 km^2. Size of the range is probably influenced by sex, age, and reproductive status of the animal as well as by availability and distribution of foods and cover. Interspersion and diversity of habitat types probably have important influence on home range size, as does prior experience of individual bears. The home ranges of individuals overlap. Bears are highly mobile, and movements of 48-80 km in a few days are not rare.

The grizzly bear, under most circumstances, is not gregarious. While there is no evidence of territorialism, the hierarchy of social dominance suggests a low probability for sustaining high densities or the formation of large social groups, except at times in areas of exceptionally high food availability.

The reproductive rate of the grizzly is low. Craighead et al. (1974) calculated a female reproductive rate of 0.626 in Yellowstone National Park. Females may be 5 years of age or older before bringing forth their first young. At least 2 years and often 3 or more elapse between litters. Litter size may be from 1 to 4 but averages less than 2. It is unlikely that the reproductive rate appreciably exceeds 1.0.

Comparative isolation from human activity seems imperative, for it is generally agreed that bear-man confrontations pose a threat to the bear's survival equal to, or greater than, the threat created by probable habitat modifications.

The above factors — large home ranges, high mobility, nongregarious habits, low reproductive rates, and the need for isolation — all suggest large spatial needs for a viable grizzly population.

A further indication of space needs is the requirement of available alternative sources of food. Some major foods fluctuate between extremes of abundance. Bears must substitute for scarce items. A particularly favored site under periods of average or greater food supply may attract and serve several bears. During periods of food scarcity, bears probably take longer foraging treks that carry them beyond their "average" home ranges.

Most grizzly bear habitat in the conterminous states has been modified, either by physical alteration or intrusion by man. Since grizzly bears still survive in some areas, we assume that some human activities are tolerated. On the other hand, the drastic reduction in grizzly bear distribution in the 19th and 20th centuries indicates that many human activities are not compatible with bear survival and that man removed some grizzly bear populations. Delineation of critical habitat should include recognition of types and levels of human activities compatible with viable bear populations. In many cases, effects of activities are not known; and although they may not be completely restricted, they should be allowed with caution until their relationship to the bears is clarified.

Most types and levels of human activity presently occurring within occupied grizzly bear habitat are not known to be detrimental to the bear population if excessive man-caused mortality by shooting, trapping, or poisoning is excluded. However, any activity that superimposes more people and their property on grizzly bear range will increase the potential for human-bear interactions and may result in destruction of bears. This statement does not imply that man-caused bear mortality should be eliminated or that a policy to this effect is desirable. In fact, some man-caused mortality will probably be necessary to maintain grizzly bear population levels within acceptable socioeconomic limits. Such mortality is acceptable as long as it does not exceed the desired growth rate of the population.

Grizzly bear habitat presently provides many diversified recreational uses that need not be excluded if restricted to acceptable levels. These uses include hiking, backpacking, camping, hunting, fishing, picnicking, horseback riding, and snowmobiling. All can be tolerated at some time, within certain levels. However, means must be available to regulate numbers of participants in some or all of these activities for periods of time when risks of man-bear encounters are high.

The major physical modifications affecting bear habitat at this time are logging, fire, geothermal development, mining, livestock grazing, urban intrusion, commercial recreational development, and water impoundment. With the exception of fire and grazing, these activities promote new roads, which in turn increase the opportunities for bear-man confrontation.

Roads associated with logging and small mining operations are easily restricted from public access, involve relatively few people while in use, and can be permanently closed when the activities have ceased. Roads associated with most other uses, particularly urban development and commercial recreational development, are characterized by larger traffic volumes inconsistent with public restrictions.

Fire and logging modify extensive areas of habitat but usually only temporarily. Both have the potential for improving bear habitat. Water impoundment may be extensive and is destructive of terrestrial habitats.

Other activities modify or destroy relatively little habitat but have long-term or permanent effects. Too, off-site impacts from ancillary developments may be greater than on-site effects. As with water impoundment, their greatest impact may result from high levels of human use. In most cases, the resulting levels of bear-man interaction could be detrimental to bear populations.

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LEGAL ASPECTS OF CRITICAL HABITAT DETERMINATIONS

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Abstract: The Endangered Species Act of 1973 is the strongest legislation ever enacted to protect species faced with extinction. Section 7 of that Act requires all federal agencies to ensure that their actions do not jeopardize the continued existence of legally designated *endangered* or *threatened* species or result in destruction or modification of their critical habitats. *Critical habitats* are determined by the U.S. Fish and Wildlife service to delineate those areas of air, land, and water that are essential to the survival and recovery of listed species. Critical habitats are not refuges, *de facto* wilderness areas, or areas in which little or no activity can be undertaken. Rather, critical habitats are delineated so that federal agencies can be aware of the essential habitats of listed species and can take special care to plan and carry out their activities in ways that will not adversely impact endangered or threatened species or their habitats.

The Endangered Species Act of 1973 passed by the 93rd Congress and signed into law on 28 December 1973 is the strongest legislation ever enacted to conserve and preserve endangered and threatened animals and plants. Under the Act, the Secretary of the Interior is required to take certain actions to insure the survival of native and foreign fish, wildlife, and plants. He is directed by the Act to protect species that he determines are either in danger of extinction (endangered) or likely to become so in the foreseeable future (threatened). The Secretary has delegated his authorities under the Act to the U.S. Fish and Wildlife Service (FWS).

Protection is initiated by listing a species as either *endangered* or *threatened* throughout all or a portion of its range. Once listed as endangered, all prohibitions contained in Section 9 of the Act come into force. With certain exceptions, it becomes illegal to harass, hunt, pursue, or take any endangered species or engage in interstate or foreign commerce in such species.

A species may be listed as threatened rather than endangered if biological data indicate that the species is not on the brink of extinction but is likely to become so if certain environmental conditions or human practices are not modified. When a species is listed as threatened, as is the case with the grizzly bear (*Ursus arctos*), the Secretary is directed by the Act to establish appropriate regulations that will provide for protection and management based on the needs of the species.

Before discussing the legal aspects of critical habitat, the following background information on the listing of the grizzly bear may be appropriate. In February 1974, the Secretary of the Interior was petitioned by the Fund for Animals to list the grizzly bear in the lower 48 states as an endangered species. Based on the criteria in the Act for determining the classification, the evidence available to FWS did not support listing as endangered but did support listing as threatened. On 2 January 1975, the proposal to list the grizzly as threatened was published in the *Federal Register*, and on 28 July 1975, final regulations were published.

The regulations on the grizzly bear permit federal or state employees to take grizzlies for purposes of human safety and elimination of livestock depredations. Killing problem bears is permissible, but reasonable effort must first be made to live-capture and translocate them. Grizzlies may also be taken for scientific and research purposes. In addition, within the Bob Marshall Ecosystem of Montana, exclusive of Glacier National Park, bears may be hunted in accordance with Montana law. However, no more than 25 grizzlies can be killed in northwestern Montana for whatever reason — defense of human life, nuisance control, sport hunting, or other taking.

When species have been listed as endangered or threatened, Section 7 (*Interagency Cooperation*) provides further protection. Section 7 requires federal agencies, assisted by the Secretary of the Interior, to conduct programs for the conservation of listed species and to insure that activities authorized, funded, or engaged in by them neither jeopardize the continued existence of endangered or threatened species nor result in the destruction or modification of their habitats, which the Secretary, after appropriate consultation with the affected states, has determined to be critical. Section 7 does not apply to non-federal entities engaged in activities that do not involve or require federal authorization or funding.

The Fish and Wildlife Service has taken a number of steps to implement Section 7 of the Act. On 22 April 1975, FWS's concept of critical habitat was published in the *Federal Register*. This concept stated, in part, that critical habitat for any endangered or threatened species could be the entire habitat or any portion thereof, if and only if any constituent element is necessary to the normal needs or survival of that species. The following vital needs are relevant in determining critical habitat for a given species: (1) space for normal growth, movement, or territorial behavior; (2) nutritional requirements such as food, water, and minerals; (3) sites for breeding, reproduction, or rearing of offspring; (4) cover or shelter; and (5) other biological, physical, or behavioral requirements. The concept further stated that not all actions are detrimental to critical habitat. There may be many kinds of activities that can be carried on within the critical habitat of a species without causing a reduction in numbers or distribution or otherwise adversely affecting the species.

In April 1976, FWS provided the federal agencies with "Guidelines to Assist Federal Agencies in Complying with Secion 7 of the Endangered Species Act of 1973." The guidelines were developed by FWS in cooperation with the National Marine Fisheries Service (NMFS) of the Department of Commerce and with the assistance of an *ad hoc* interagency committee of representatives from 11 federal agencies. These guidelines are intended to assist the federal agencies in adjusting their internal procedures to meet the requirements of Section 7 and serve as a starting point for the development of Section 7 regulations. They were not published in the *Federal Register* and are not considered mandatory.

Contained in the Section 7 guidelines are "working" concepts that can be used to clarify key terms in Section 7, procedures for determining critical habitat, and the process used by FWS in providing consultation and assistance, as required by Section 7, to the other federal agencies.

The following "working" concepts clarify terms used in Section 7 in relation to critical habitat:

> "Critical Habitat" means any air, land, or water area including any elements thereof which the Secretary, through the Director, FWS, or NMFS, has determined is essential to the survival of wild populations of a listed species or its recovery to a point at which the measures provided pursuant to the Act are no longer necessary (hereinafter referred to as recovery). Determinations will be published in the *Federal Register*.
>
> "Destruction or (Adverse) Modification" means any act which would have a deleterious effect upon any of the constituent elements of Critical Habitat which are necessary to the survival of recovery of such species, and such effect is likely to result in a decline in the numbers of the species.
>
> (1) Constituent elements of Critical Habitat include, but are not limited to land, air, and water area, physical structure and topography, flora, fauna, climate, human activities, and the quality and chemical content of soil, water, and air.
>
> (2) The requirements for survival or recovery of listed species include space for normal growth, movement or territorial behavior; nutritional requirements such as food, water, minerals; sites for breeding, reproduction, or rearing of offspring; cover shelter; or other biological, physical, or behavioral requirements.

"The procedures for determining Critical Habitat are as follows:

(1) The Fish and Wildlife Service will seek consultation, as appropriate, with the affected States in which the species occurs.

(2) The Service will request biological information, assistance and recommendations from the affected Federal land-managing agencies prior to publishing the proposed determination in the Federal Register.

(3) The Fish and Wildlife Service will publish the proposed determination of Critical Habitat in the *Federal Register*, along with notifying the affected Federal land-managing agencies in writing, of the proposal and the reasons for it.

(4) The governors of the affected States will be notified in writing of the proposal and allowed 90 days in which to comment.

(5) A public comment period of at least 60 days will be provided at the time of publication.

(6) After review of comments and incorporation of appropriate changes to the proposal, a final determination of Critical Habitat will be published in the *Federal Register*."

Provisions are available for emergency determinations of critical habitat when impending federal actions would in all likelihood destroy habitat essential to the listed species. The emergency determination will remain in effect for 120 days during which regular procedures for determination of critical habitat should be completed.

The consultation and assistance process included in the Section 7 guidelines is intended to provide federal agencies with the opinions of FWS on biological subjects. Such opinions will address federal actions with respect to their probable impact, adverse or otherwise, on a listed species or its critical habitat. When FWS opinions are received, the federal agency involved will have the responsibility of deciding upon the course of action to take in light of its Section 7 obligations. It is not the prerogative of FWS to condemn these actions or to veto activities and programs adversely affecting listed species and their habitats.

On 26 January 1977, proposed Section 7 regulations were published in the *Federal Register* by the FWS. The proposed regulations are similar to the Section 7 guidelines, with some important exceptions. Instead of "working" concepts of key terms used in Section 7, definitions for "Critical Habit," "destruction or adverse modification," and "jeopardize the continued existence of" are included. Time limits are placed on FWS to respond to requests for consultation from federal agencies. FWS must complete the entire consultative process within 120 days unless special circumstances require a longer period of negotiation.

Of major concern to many people living in or near critical habitat areas and to the federal and state agencies having jurisdiction over these areas is what happens after such areas are determined to be critical habitat. This concern is particularly acute with respect to the FWS's proposal to determine critical habitat for the grizzly bear. Obviously, this concern stems from the stringent requirements of Section 7.

It must be reemphasized that Section 7 does not apply to state or private actions unless these actions require federal sanction. Section 7 clearly applies only to federal agencies, and only to the extent that a federal agency judges its actions to be in conflict with or contrary to the requirements of that section.

The Fish and Wildlife Service is obligated under the Endangered Species Act to specify for all federal agencies operating within the area of a listed species exactly which lands are essential to the species. Critical habitat delineation is intended to help federal agencies in the decision-making process. In this regard, it is similar to the National Environmental Policy Act (NEPA). The environmental impact evaluation process of NEPA is intended to provide federal agencies with information upon which decisions can be based. The function of critical habitat designation is to delineate the habitat necessary for the survival and recovery of a species. Without this information, federal agencies cannot determine whether their programs or actions are compatible with the requirements of Section 7.

The Fish and Wildlife Service does not have authority to tell another agency what it can or cannot do within the critical habitat of a listed species. FWS provides biological advice and opinions upon request, but the final decision rests with the federal agency contemplating the action.

Designation of critical habitat does not signify an inviolate sanctuary. It does not always demand a wilderness or a pristine, undisturbed area. It does not mean a refuge or federal acquisition of private lands to be used as such. For example, critical habitat determination for the grizzly, of and by itself, will not prohibit any kind of land use or activity in the area. The determination is simply an expressed recognition of the land, water, and air space that are essential to the normal needs and survival of the grizzly and other species. This determination is not restricted to key areas but includes sufficient habitat in which a species can survive and recover to the point where it can be removed from the list.

It is impossible for FWS to predict the decisions of another federal agency in regard to specific types of activities in critical habitat areas. These decisions will be made by the affected federal agency on a case-by-case or program-by-program basis. As stated, the Fish and Wildlife Service will, upon request, provide counsel and opinions on biological matters in a manner helpful to inquiring agencies, with documentation of the entire process.

The Fish and Wildlife Service holds the opinion that the designation of critical habitat will cause little or no disruption in anyone's daily life, livelihood, or recreational pursuits. We know that many people believe otherwise, but this belief is due in part to misunderstanding of the purpose of critical habitat determinations. Unfortunately, many rumors and highly emotional publicity have circulated on the matter. For example, it has been asserted that these determinations will curtail hunting of game animals on lands within the proposed critical habitat areas. This assertion is absolutely unfounded. The states are responsible for regulating hunting of game animals. Furthermore, Section 7 of the Endangered Species Act applies only to federal agencies and only to animals listed under the Act. Hunting of game on federal lands is normally carried out in accordance with state laws and regulations.

Many people have voiced concern that the economy of the region will be adversely impacted by the grizzly critical habitat determination. For example, some believe that timber harvesting will be curtailed. Decisions of the federal land-managing agencies cannot be predicted, of course, but it is believed that timber harvesting and other resource development can be undertaken in ways that will not jeopardize the grizzly. It may or may not require some changes in present practices.

The Fish and Wildlife Service is now in the process of determining critical habitat for the grizzly. Here, in brief, is a description of what we have accomplished and what remains to be done.

A draft proposal was sent to appropriate state and federal agencies in August 1976. It was developed after many meetings and discussions with state and federal representatives, and with private individuals and organizations knowledgeable in grizzly bear habitat needs. On the basis of comments received in the draft proposal, FWS published a proposed rulemaking in the *Federal Register* on 5 November 1976. The proposal presents the preliminary judgement of FWS as to which lands occupied by the grizzly are essential to its normal needs and survival in the lower 48 states. After publication of the proposal, a minimum period of 90 days (ending on 9 February 1977) was provided for comment. In addition, recommendations of the governors of Idaho, Montana, Washington, and Wyoming were solicited and public hearings were held in those states and in Washington, D.C.

Approximately 2 months will be required for review and evaluation of information received from the proposed rulemaking and testimony at the public hearings. Publication of a final determination of critical habitat for the grizzly bear will probably not take place before April or May 1977, and could take longer. At this stage, it is not possible to predict what the boundaries of the critical habitat will be. As the proposal now stands, the boundaries have been drawn to encompass all occupied habitat of the grizzly. Obvious problems arise with such gross delineation, but from a biological standpoint, it is difficult to treat a single component of any of the ecosystems apart from the others. A large, free-ranging animal such as the grizzly bear does not observe human administrative or political boundaries.

The Fish and Wildlife Service will ensure that a final determination of grizzly critical habitat is based on the best scientific evidence available. It should be pointed out that neither the listing of the grizzly as threatened nor the delineation of critical habitat are actions that are permanent. The rules and regulations can and will be modified at any time that sufficient evidence warrants a change.

CRITICAL HABITAT AND OTHER RESOURCE PROGRAMS IN RELATION TO GRIZZLY BEAR MANAGEMENT

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Abstract: The Endangered Species Act (1973) and the classification of the grizzly bear (*Ursus arctos*) as "Threatened" (1 September 1975) directed the Forest Service to delineate critical habitat of the grizzly bear. Critical habitat is any area necessary for the maintenance and survival of a species during any part of its life cycle. Evaluation of resource programs in terms of their actual and potential impacts on the grizzly within its critical habitat boundaries is required, based on a good understanding of grizzly habitat components. Coordination among biologists, sociologists, and economists is a prerequisite to comprehensive grizzly management. The Forest Service believes that integration of grizzly habitat needs and resource programs is possible but that the final decision on a goal statement is societal.

The Endangered Species Act of 1973 directs all federal departments and agencies to develop and maintain conservation programs for endangered and threatened species and to insure that other resource activities do not jeopardize the continued existence of such species or adversely modify or destroy critical habitat.

The Secretary of the Interior officially classified the grizzly bear as a threatened species on 1 September 1975. The Forest Service recognizes and endorses the need to identify and manage critical habitats for the grizzly bear. The determination of critical habitat must be based upon the best available biological information obtained through a deliberate and objective identification process. Since the production of various goods and services frequently entails competition among them, this nation cannot ignore the total productive potential of any of its lands. The people associated with the Critical Habitat and Land Management programs of the Forest Service must use their best professional judgement in deciding what and how much will be produced as well as where and when.

THE ESTABLISHMENT OF CRITICAL HABITAT FOR GRIZZLIES

General Definition

Critical habitat can be defined as that portion of a habitat essential to the maintenance and survival of a species during any part of its life cycle. The establishment of critical habitat is not the same as the creation of an inviolate sanctuary, wilderness area, or refuge by prohibiting any particular kind of land use or activity. Rather, within the critical habitat boundaries, federal agencies must evaluate their activities and programs in terms of the effect on the grizzly. Activities and programs having a negative effect on the grizzly's habitat are to be modified so as to have a neutral or a positive effect, or else be abandoned.

The Forest Service recognizes that some observers feel that no developmental activities can be tolerated by the grizzly. However, Geist (1971) contends that grizzly bears can coexist with man. However, he expresses concern over man's potential disturbance of habitat and the degree that man can remain a harmless part of the grizzly environment. An evaluation system must be developed that provides a fair picture of the environment and the effect that man's actions will have upon it.

An Evaluation System

Any good evaluation system must be based on research. A properly planned system should provide direction for habitat improvement. The wide variation over grizzly range makes it necessary to review each planned activity on each site. Components to be considered are:

1. Acreage affected
2. Duration of planned activity
3. Time of year
4. Grizzly seasonal habitat affected (early spring, summer, late fall, winter)
5. Expected recovery time of vegetation
6. Cumulative effects of many activities
7. Vegetative habitat types and elevations
8. Possible coordination prescription

The impact of other resource management programs and activities on grizzly bear habitat can range from negative to favorable, depending on their elements. The actual and potential impacts of all resource programs must be measured, evaluated, and documented with a good understanding of the components of grizzly bear habitat. In many cases an on-site evaluation will aid in adjusting and modifying programs to remove adverse elements. Some flexibility will exist in most situations; however, the first priority is the welfare of the grizzly.

Coordination Techniques

Wildlife biologists in the Yellowstone area are developing a wide range of coordination techniques. Some examples are:

1. Road and trail locations and closures
2. Logging treatments — clearcuts, overstory removal, thinning, postlogging treatments
3. Fire management — prescribed burns, wildfires, slash disposal
4. Livestock grazing — class of stock, season of use
5. Protection of nonforested areas — avalanche chutes, stream bottoms, burns, meadows, sidehill parks, subalpine ridgetops

Precisely what constitutes destruction or adverse modification of grizzly bear habitat is largely unknown. Restrictive interpretations could result in significant curtailment of many uses of national forest lands, ranging from timber management and domestic livestock grazing to energy development and recreational activities. Sociologists and economists must identify and quantify the socioeconomic impacts of proposed critical habitat designations.

Determination of population goals and acceptable population densities is a prerequisite to the allocation of land for critical grizzly habitat. There are land areas where grizzly bear recovery could be realized in harmony with established or proposed land uses, but there are some areas where other uses could not be permitted.

CONCLUSIONS

Since 1959, research has contributed to the basic knowledge about the grizzly bear. Craighead and Craighead (1972) conducted grizzly research from 1959 to 1970 in the Yellowstone National Park ecosystem. In 1974, the Yellowstone Interagency Grizzly Bear Project was initiated.

Research is now under way to learn more about the biology and ecology of grizzly populations and to determine what impact man may have on their habitat. Past research on the grizzly shows that it is possible to delineate critical habitat without including all the area the bear occupies. Research results do not support the assumption that all occupied habitat is *critical* to the welfare of the bear. Inclusion of all occupied habitat, as determined by sightings since 1930, is not a sound biological basis on which to build such an assumption. The fact is that grizzly populations are not presently uniform throughout their range.

The grizzly bear possesses the ability to adapt to new habitats that have undergone some modification. Food habits studies indicate that grizzlies are omnivorous, with a high dependence on forbs, grasses, and mesophytic shrubs, and that specific sites supply important grizzly foods necessary to the welfare of the species.

With its present data base, in addition to ongoing research, the Forest Service believes that habitat requirements of grizzly bears can be integrated with other resource programs without adversely modifying the bears' habitat. Habitat protection and maintenance cannot be achieved accidentally. Through creative, skillful planning it may be possible to improve grizzly habitat through other resource programs. The final decision on a management goal will be societal. It is the responsibility of man to predict and make explicit the spectrum of combinations, alternatives, and consequences inherent in such a decision.

SUMMARY

The public is expressing concern about the welfare of the grizzly bear. Scientific and lay communities are questioning management programs. This concern was stimulated by the bear's classification as "Threatened."

The critical habitat issue is now at center stage. Previous research has provided some basic information for identification of the elements of critical habitat. Current research and studies will refine these basic data. The agencies and the scientific community working with the grizzly bear and its habitat must cooperate in developing a positive management plan for this species.

The need for well-defined goals and objectives in grizzly bear management is evident. The public has every right to be involved in designing and developing these goals and is entitled to the Forest Service's best professional guidance in planning grizzly management for the future.

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THE BEAR BIBLIOGRAPHY PROJECT

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Abstract: Over 6,000 references on bears have been assembled, including published and unpublished materials. The FAMULUS programs are being used to produce and search files on brown and American black bears (*Ursus arctos* and *U. americanus*). As of July 1977, over 1,000 references on each of these two species had been computerized. Effective searches by subject (based on title), author, date, and keywords (for about 5 percent) are possible. Draft review copies were distributed. Announcements of general availability and search costs will be made as soon as feasible. Work is continuing, although additional support will be needed for maximum productivity.

The project objective is to produce an extensive, computerized bibliography on bears in order to reduce greatly the need for repetitive bibliographic searches. The U.S. National Park Service contracted this project through the Alaska Cooperative Park Studies Unit. National Park Service concerns dictated that the initial emphasis be placed on black bears and brown bears in North America, although we hope eventually to computerize citations on all species of bears on a worldwide basis. We expect to produce a set of files, stored in computer-readable format, which can be edited, searched, and printed out to suit the needs of many different workers. We will attempt to provide a clear specification statement covering the procedures for organizing and handling the material collected as well as an explicit statement of what has been searched and the search strategy.

The production of partial and even rather extensive bibliographies on bears is not new. We started the project with an extensive base of references that Dean had collected over a period of 20 years. The original file includes material from such bibliographies as that in Couturier's (1954) massive work, Hatler's (1964) supplement to Couturier, black bear bibliographies by Tigner and Gilbert (1960), Bray and Barnes (1967), and Eagar and Stafford (1974), several years' worth of ASCA profile results from the Institute for Scientific Information, Termatrex searches of the Review of Recent Literature produced by the American Society of Mammalogists for the entire period of their availability, and other structured searches.

We would like to acknowledge collectively the help of many members of the Bear Biology Association who responded to our request for assistance. Special thanks for very substantial contributions are due K. Lloyd and F. Bunnell, University of British Columbia; V. Cahalane, Clarksville, New York; J. Rothman, Hot Springs, Arkansas; W. Tietje and R. Ruff, University of Wisconsin; the Canadian Wildlife Service; and the U.S. National Park Service.

METHODS

Our current procedure is to collect as many references as possible, for both published and unpublished technical and semitechnical reports, and for popular publications (when the information in the latter seems to warrant inclusion). The initial search strategy includes all species and the world's literature insofar as possible. In general, the incorporation of the material into the computer will follow a scheme of priority that favors brown and black bears and North American information. Recent information receives greater attention than older information, and the priority of one paper over another is judged subjectively.

A system of programs called FAMULUS (Burton et al. 1969) is being used for the construction, editing, and manipulation of the files. The programs were developed by the U.S. Forest Service and have been used widely. They are currently available in versions that will run on IBM, CDC, and HIS computers (possibly others as well). We will not describe FAMULUS in detail. End users will be most interested in the capabilities of the programs SEARCH, PRINT (GALLEY), and PUNCH (OSSIFY). The SEARCH program permits individually constructed searches of either simple or complex design; logical combinations of "and," "or," and "not" are then possible, e.g., references simultaneously dealing with "brown bear" and "attacks" but not "Alaska" published after 1969. The PRINT and PUNCH programs provide convenient means of obtaining copies of either the entire file or selected parts of it. In particular, the PUNCH program will allow the transfer of card-image files from one computer to another.

FAMULUS handles the information associated with a reference in several fields which in our case have been specified for author, date of publication, title, publication or publisher, characteristics (such as number of references, language, source of hard copy if possible, date of inclusion in the file) and keywords; unspecified fields have also been reserved. Since the

EDIT program allows internal modifications and additions within citations, we are including some references in the computer file that have not yet been fully processed. Keywords will be added as rapidly as possible. FAMULUS allows searches on one or more specified fields; thus, even those papers without keywords may be searched on the basis of the words in the titles, the author field, and other fields.

Separate computer files are being made for the black bear, the brown bear, general bear information, and other species as one group. The latter collection will be split as the number of entries grows. Keywording is based on a thesaurus evolved at the University of Alaska several years ago as an outgrowth of the one used by the Fish and Wildlife Reference Service.

Originally the project was to include abstracts. Current interpretations of the recently changed copyright law suggest that we may not be able to use even author's abstracts from copyrighted periodicals or such sources as *Biological Abstracts*. We clearly will not be able to write many new abstracts. Doing a thorough job of keyword indexing will be much more rewarding.

All references encountered have been transcribed to a card file from which coding sheets are prepared. The data are then typed into a computer file and edited after proofing against the coding sheets. The file is then run through the FAMULUS EDIT program, adding the references and the associated information to what was already on the FAMULUS file. From this point, it may be searched and reproduced.

RESULTS

As of July 1977, our collection included about 4,500 citations for black and brown bears and about 1,100 references for other species. We are still a long way from having complete bibliographies for any of these species. As of July 1977, working computer files contained more than 1,100 references on the brown bear and over 1,000 on the black bear. Approximately 5 percent were assigned keywords (in some cases more than 40 per citation). Draft copies and a statement describing the search were distributed to more than 30 cooperators with hopes of generating useful criticism. In addition, authors with several references have been given an opportunity to proof our listings of their work.

An interactive search demonstration provided at the Kalispell meeting served to introduce the potential usefulness of the computerized files to the conferees. Users will ultimately be able to order individually tailored searches across files based on reasonably clearly specified boundaries; charges have not been worked out yet but should be moderate. Individuals wishing to operate the entire file on their own computer system can make arrangements to do so.

What is the project's future? We probably have knowledge of a substantial proportion of the generally known and published material, especially for North America. However, if this project is to be of maximum possible use, we need additional help. Individual workers can provide complete lists of their own papers and unpublished reports and advise us of material we may not otherwise locate. That sort of cooperation will measurably improve the quality of the end result. Since a bibliography is intended to ease the task of someone seeking information, completeness and accuracy are extremely important!

Once the file is ready for serious searching and/or reproduction, we expect to announce its availability and the associated costs. In addition to computer searches, there should be hard-copy editions available. After this initial job is done, there will have to be a continuing effort aimed at keeping the bibliographies current. However, a small annual effort on the part of each of those working with bears should reduce our individual requirements for extended time in the search phase of library work. It would be especially helpful if workers outside of North America could keep us up to date on their publications.

We are currently seeking financial support that will permit full-time rather than sporadic continuation, at least until keyword assignment of the present collection is completed.

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BEARS IN MODELS AND IN REALITY — IMPLICATIONS TO MANAGEMENT

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Abstract: The use of computer simulation models as an aid to understanding of biological data was demonstrated using a number of simulated bear populations. Data from black (*Ursus americanus*), brown (*U. arctos*), and polar bear (*U. maritimus*) populations were employed. Population models without feedback were used to compute mortality isoclines as a function of reproductive measures and to document the unreliability of age structure as an indicator of population growth form. A simple Leslie matrix projection was modified to include the effects of population density and hunting. The resulting models provided a consistent explanation for some of the sex and age ratios reported in the literature. The importance of spatial and temporal distributions of hunting pressure were documented, and management implications of hunting patterns, population biology, and dispersion of bears were summarized.

Of the enormous amount of detail known about bears, not all is amenable to simulation modeling; similarly, not all modeling techniques are appropriate to simulation of bear biology. Here we deal with the intersection of bears in models and reality. Our scope is broad taxonomically but narrow ecologically. We present analyses of black, brown, and polar bear populations but limit ourselves largely to the examination of population dynamics. Analyses are extended to encompass some relations with habitat through the influences of habitat on man as hunter. We limit our discussion largely to the simplest forms of models, those adapting the Leslie matrix formulation without feedback. Models incorporating more biological relationships of bears and thus more complexity are treated in Bunnell and Tait (1978). The approach involves (1) a brief review of the nature of models, including their advantages and disadvantages; (2) documentation of the usefulness and limitations of the basic form of population projection, the Leslie matrix; and (3) a summary of the implications of these analyses to research and management. The major emphasis is towards delimiting the intersection between bears in reality and in models, and thus towards finding ways in which models can facilitate our actions in the real world.

All models are simplified representations of reality and, in their broadest sense, include any set of simplifying assumptions or abstractions. The key to successful modeling lies in developing the appropriate abstraction and aggregation of the real system. This process of simplification has inherent advantages and disadvantages. The major advantages are straightforward — it is quicker, socially more expedient, and far less costly to explore the consequences of research or management activities in a model than in the real world. On the other hand, it may prove extremely difficult to determine whether the simplification adequately represents reality (Bunnell 1973, 1974). Because the process of abstraction or simplification attempts to grasp the essence of biological relationships, the ideas in ecological models, whatever their mathematical nature, are almost always nontrivial. One consequence is that the results of such simplification are not always intuitively obvious (see Fig. 2 for an example). A second consequence is that the concepts may not be amenable to rigorous analytical techniques. The implications are best explored by mimicking (simulating) the biological responses.

All models of population dynamics invoke the simple tautology that changes in population size are due to the net change in rates of immigration, emigration, deaths, and births. The models make assumptions about the rules that modify these rates. Rules for change are applied to a population at time t that produces the population size at time $t + 1$, to which the rules are again applied for as long as the projection continues.

$$\text{Population}_t \rightarrow \text{rules for change} \rightarrow \text{Population}_{t+1}$$

Clearly, the important factors are the assumptions made concerning the rates and the rules for changing these rates. Furthermore, the rules must be sufficiently general to apply to any interval of time. Rules we have invoked are discussed in association with specific models.

Many of the concepts explored in this paper evolved from discussion with C. Jonkel, A. Pearson, K. Scoullar, and I. Stirling. S. Buckingham prepared the figures. The development of models for bear populations was supported by a grant to F. L. Bunnell from the British Columbia Fish and Wildlife Branch as part of the Computer Assisted Resource Planning Program.

POPULATION MODELS WITHOUT FEEDBACK

Our theme is that even the most simple models can be used constructively to both bound and extend our understanding of bear population dynamics. First, we use a very simple, biologically incomplete model of population projection, the Leslie matrix (Appendix) to demonstrate the utility and limitations of a modeling approach. This simplest model applies constant sex- and age-specific survival rates to the number of bears in each age-class to generate the number of bears in the next oldest age-class in the next year of the projection. The number of cubs is calculated by applying constant age-specific natality rates to the number of female bears in each age-class. We treat the assumptions of such models explicitly. Explicit treatment can place boundaries on the population responses that are biologically possible and can *explain* seemingly counterintuitive observations, thus increasing our insight into the dynamics of bear populations.

Bounding the Biologically Possible

Following the rationale presented by Stirling et al. (1976), a near-absolute upper limit on the harvest rate can be generated by assuming that all mortality is due to hunting and that the mortality rate is constant for all age-classes. Cubs are assumed to die only if the mother is part of the kill. The mortality rate due to hunting is balanced against the natality rate essential to generate a stationary (nondeclining) population. The computed average mortality rate is thus the upper limit to the sustainable rate of harvest. Fig. 1 illustrates isoclines of the upper limit of maximum sustainable rates of harvest for populations with different average natality rates and different average ages of first reproduction. The natality rate is for reproductive females and is computed by dividing the average litter size by the interval between reproduction. Using this formulation, it is easy to compare populations of black, brown, and polar bears.

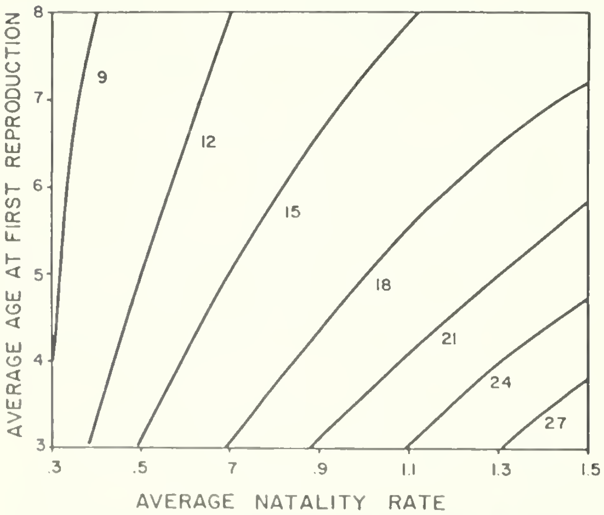

Fig. 1. Isoclines of maximum sustainable mortality (percent/year) as a function of average age at first reproduction and average natality rate (litter size/years between litters).

For example, a brown bear population in which females first breed at age 6.5, first reproduce at age 7, have an average litter size of 1.5, and breed every 3 years (natality rate = 1.5/3 = 0.5) can sustain no greater harvest than 10.7 percent per year. Similarly, a black bear population in which females conceive at age 2.5, reproduce at age 3, and produce a litter of 2.0 cubs every 2 years (natality rate = 1.0) can sustain an absolute maximum rate of harvest of 23 percent per year. Note that these values are for maximum sustainable *mortality*. If the brown bear population was experiencing a 6 percent mortality in addition to hunting mortality, the harvest rate could be no greater than 5 percent per year. Isoclines such as those in Fig. 1 can be developed for other population measures; their use lies in providing some limits to what is biologically possible.

Exploring Counterintuitive Observations

The life table dilemma. — Even the simplest models, by enforcing explicit treatment of the inherent assumptions, often produce counterintuitive results. Gross (1972) has demonstrated this point elegantly for simple models of maximum sustainable harvest that incorporate density-dependent feedback. The phenomenon, however, is general and applies to the simplest models of population dynamics — life tables and survivorship curves — employed in wildlife management. Consider as an example the 3 age structures presented in Fig. 2. Each curve has been plotted, in classical fashion, relative to a juvenile base of 1,000, and represents 3 consecutive years of the same projected population. Although the numbers depict a representative, unbiased sample, a manager confronted with such data could easily be deceived. One obvious interpretation is that the population suffered somewhat less mortality between years 1 and 2 and then experienced heavy juvenile mortality between years 2 and 3. In short, the data might suggest a potentially dangerous situation if conditions in year 3 persist.

In actuality the population is thriving. The changes experienced by the population are nearly the opposite of those inferred from the sample. Actual changes are

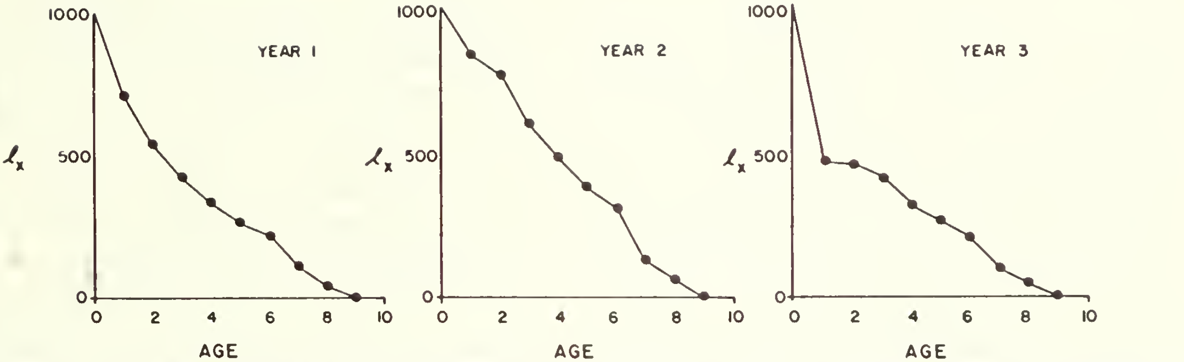

Fig. 2. Unbiased and representative samples of age structure from subsequent years in a hypothetical population. (The survivorship curves are from the population in Table 1).

summarized in Table 1 and result from the following modifications of rates of survival and natality:

Year 1 to 2:	decline in first-year survivorship from 0.7 to 0.6, with concomitant reduction from 0.5 to 0.33 in young/females of 2+ years of age.
Year 2 to 3:	first-year survivorship back to 0.7 from 0.6, and young/females back to 0.5 from 0.33.

The apparent high juvenile mortality is the result of the *relatively* large recruitment into the first-year age-class (Table 1).

Caughley (1974) addressed a simpler but analogous problem treating sex and age ratios in ungulates. He concluded that (1) what is occurring within a population is not intuitively evident from sex and age ratios, and (2) the growth form of a population *cannot* be determined from these ratios. The results of Fig. 2 imply a broader conclusion: In general it is *not* possible to infer from a single age structure or series of age structures what has happened in the past to generate the current structure of a population. Nor is it possible to predict what will happen over the next few years. It is not our intent to generate an aura of hopelessness, but to distinguish potentially futile exercises from useful ones.

Incongruent sex and age ratios. — There are several phenomena common to black, brown, and polar bear populations where simple models can reconcile seemingly incongruent observations. One broad area concerns differences in the sampled sex and age ratios of hunter kill and actual populations. We consider 2 phenomena: (1) In heavily hunted bear populations where selection by the hunter is predominantly for males, the sex ratio of the kill is close to parity. (2) A preponderance of males in the harvest generally implies a preponderance of females in the population. Both of these phenomena superficially appear to be counterintuitive.

Consider the first situation in which a heavily hunted population experiencing high selectivity for males shows an even sex ratio in the kill. Males may be 3-4 times as vulnerable as females to hunting, females with cubs may be legally protected, and still the sex ratio of

Table 1. Parameters and unbiased samples of these parameters for a changing population. (Unbiased sample is illustrated in Fig. 3.)

Age-class	Underlying parameters		Population numbers			Unbiased sample		
	Survivorship	Young/female	Year 1	Year 2	Year 3	Year 1	Year 2	Year 3
0- 1	0.70	0	100	70	98	100	100	100
1- 2	0.77	0.1	70	60	49	70	86	49
2- 3	0.80	0.5	54	54	46	54	77	47
3- 4	0.80	0.5	43	43	43	43	61	44
4- 5	0.80	0.5	34	34	34	34	49	34
5- 6	0.80	0.5	27	27	27	27	39	27
6- 7	0.50	0.5	22	22	22	22	31	22
7- 8	0.50	0.5	10	10	10	10	14	10
8- 9	0		5	5	5	5	7	5
9-10			0	0	0	0	0	0
Total			365	325	334	365	464	338

the total kill can (and most likely will) be close to even. Expressing the intuitive observation, Pearson (1975:75) noted that "Inasmuch as two out of every three mature female grizzlies should be protected from hunting because they are accompanied by cub(s) of the year or yearling young, there should be significantly fewer females than males harvested." In fact, the apparent incongruity is a natural and unavoidable consequence of heavy hunting.

Fig. 3a illustrates the age distribution of male and female bears in a heavily hunted population in which the males are about twice as vulnerable to hunting as females (i.e., the probability of an individual male bear being harvested is twice as great as the probability of an individual female being harvested). Prior to the hunting season, the first legally hunted age-class contains equal numbers of males and females. We assume that the sex ratio at birth is even and that natural mortality factors do not discriminate between young males and females. Because males are twice as vulnerable to hunting as females, twice as many males from the first hunted age-class appear in the harvest (Fig. 3b). Next year there will be fewer males than females in the next older age-class. Eventually the age-class of the males will be only half the size of the female age-class. The sex ratio of the harvest of that age-class will be even. The sex ratio of the harvest of all older age-classes will favor females because there will be few older males left to hunt. The total female harvest could thus equal the total male harvest and the first counterintuitive phenomenon is clarified.

A simpler rationale is to extend the concept of a heavily hunted population to assume that *all* mortality is due to hunting — every bear born eventually appears in the harvest. Since equal numbers of both sexes are assumed to be born, equal numbers must be harvested. This latter explanation, valid also for populations in which 1 sex is more vulnerable to hunting, obscures the underlying dynamics of the age distribution and the effects of changing sex ratios in the population.

Now, the second counterintuitive phenomenon mentioned is no longer counterintuitive. The population illustrated in Fig. 3a is predominantly female, with an even sex ratio in the kill. Males constitute a large portion of the harvest in the younger age-classes (Fig. 3b). In a population in which the harvest contains a greater proportion of males than in that illustrated in Fig. 3, conditions are similar except that some females are not harvested and die a natural death. Under such conditions, we would observe an even greater proportion of females to males in the population.

Fig. 3a,b was constructed from a simple Leslie matrix form of model, using parameters estimated from harvest data of a black bear population in North Carolina (Collins 1974). The population was assumed to be stationary and to be experiencing a constant rate of mortality due to hunting. Thus, the mortality estimate could be generated by regressing the log of the number of bears in the harvest on age. The age structure observed by Collins (1974) and the structure predicted by our estimation of mortality rates are summarized in Table 2. Mortality rates estimated by re-

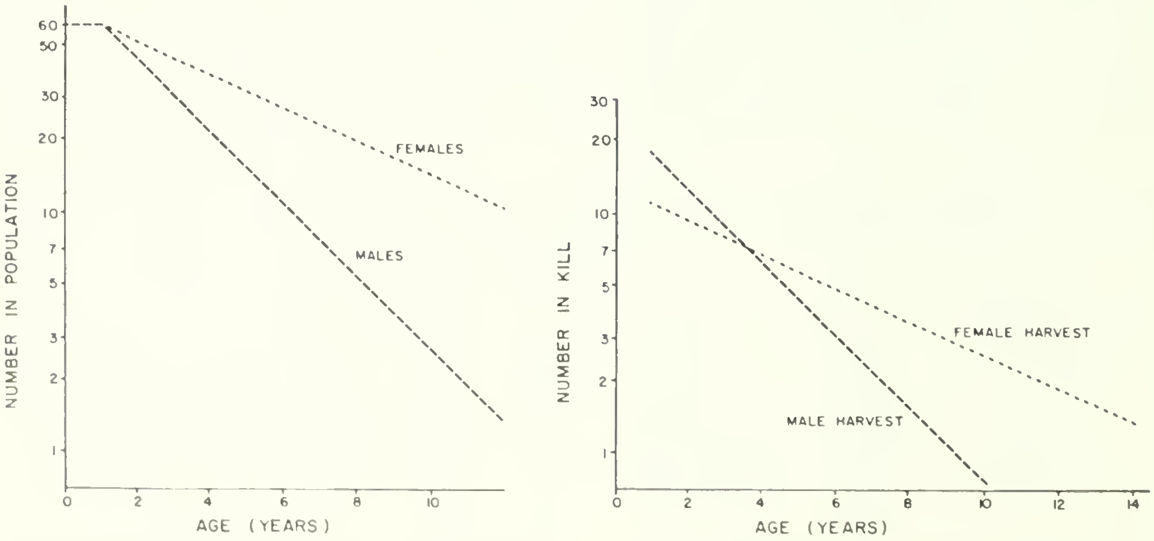

Fig. 3. Simulated age structures in the population (a) and kill (b) of a stationary bear population experiencing constant mortality due to a hunting.

gression are 30 percent per year for males and 15 percent per year for females. The regression model accounts for 80 percent of the variation in mortality rates of males and 76 percent of the variation in mortality rates of females.

Table 2. Observed and predicted age structures of black bears.

Age-class (years)	Numbers of males		Numbers of females	
	Observed[a]	Predicted[b]	observed[a]	predicted[c]
0.75	3	25	4	13
1.75	32	18	12	11
2.75	12	13	5	9
3.75	6	9	9	8
4.75	8	6	5	7
5.75	2	4	10	6
6.75	5	3	8	5
7.75	1	2	3	4
8.75	3	2	7	3
9.75	1	1	3	3
10.75	1	1	1	3
11.75		1	3	2
13.75	1	0		
14.75	1	0	1	1
15.75			1	1
17.75			1	1
21.75	1	0		
22.75	1	0		

[a] Observed values are from Collins (1974: Table 2).

[b] $Y = 32.7e^{-0.35\ \mathrm{age}}$; $r = 0.89$.

[c] $Y = 14.59e^{-0.16\ \mathrm{age}}$; $r = 0.87$.

There are 2 independent estimates of the relative vulnerability of males and females to hunting. The first estimate is simply the ratio of the number of males of the first harvested age-class to the number of females of the first harvested age-class, 32:12 or 2.7. The second estimate is given by the ratio of the average instantaneous mortality rates, assumed to be the sex-specific harvest rates. The instantaneous mortality rates (regression coefficients) are 0.35 for males and 0.16 for females, a ratio of 2.2. It thus appears that male black bears in North Carolina are about 2.0-2.5 times as vulnerable to hunting as are females.

The general pattern depicted in Fig. 3 is a recurrent theme in the literature of hunted bear populations. Harvests of brown bears on the Kodiak Islands, for example, had a sex ratio of 188 males to 100 females (Troyer 1961) whereas the sex ratio in the population was even for the younger age-classes and was 36 males to 100 females for bears 4 years old and older (Troyer and Hensel 1964). Erickson (1964) reported that although the verified sex ratio in black bear harvest data from Michigan was not significantly different from even, there were more male than female cubs shot and more female than male animals shot in older age-classes.

In Washington, Poelker and Hartwell (1973) noted that the average age of 135 known-age black bears was 3.7 years for males (maximum age, 14) and 6.6 years for females (maximum age, 27). They also reported a sex ratio of 100 males to 69 females in the 23,000 bear kills by sport hunters between 1967 and 1971. In their only sample of the population, as opposed to the kill, the sex ratio was 100 males to 138 females, not statistically different from even. On the basis of these observations, Poelker and Hartwell (1973) suggested a sex ratio of 100:100 for black bears in Washington, with a slight imbalance in favor of males. We conclude from our analyses and simple models that the sex ratio in the population is probably significantly biased in favor of females. The major assumption necessary to account for these observations is that hunter kill is a large portion of total mortality. The isoclines of Fig. 1 illustrate the maximum total mortality that populations can sustain and suggest that in many hunted populations, harvest does dominate the total mortality rate. The assumption has been addressed more explicitly for polar bears and grizzly bears by Stirling et al. (1976).

We conclude that the apparent incongruities between sex and age ratios of heavily harvested populations are natural and unavoidable consequences of the population dynamics of bears.

Exploring Alternative Hypotheses

We present 1 example to illustrate the manner in which the simplest models can be utilized to examine alternative hypotheses relevant to the same data. We have chosen the study of Pearson (1975) as our example because it contains sufficient data to provide a workable framework. The relevant data are life tables generated from kill data for male and female grizzlies in the Yukon Territory and the Mackenzie Mountains of the Northwest Territories during 1965-69. The sex ratio in the kill data is 146 males to 100 females. "After reaching sexual maturity the data show an initially elevated mortality rate, more pronounced in males than in females, and a fairly constant rate of 10-11 per cent in males and 15-16 per cent in females with the males having subsequently a greater longevity than the females" (Pearson 1975:62). Pearson noted further that to have a nondecreasing population, given the female age structure of the kill data and the low observed rates of natality (0.25 female yearling/mature female), the average mortality rate for females from their second to their seventh year of life could be no more than 7 percent per year. This value is less than half the estimated mortality rate of the mature females, 15-16 percent annually.

We play devil's advocate by first rejecting the conclusion that the rate of subadult mortality is only 7 percent, thus forcing a critical exploration of the underlying assumptions. The first assumption questioned was that the hunted population was stationary. A simple population model was "harvested" heavily, causing a decline in the computed population size. The only constraint was that the age distribution of the kill be the same as that observed by Pearson (1975). We found that with a constant harvest rate applied to all adult females, we could not change the subadult mortality rate of 7 percent more than about 2 percent without significantly changing the shape of the age distribution of the kill. Our inability to reject that assumption of a 7 percent subadult mortality rate even in a nonstationary population forced us to examine critically the other assumptions.

The problem, from the point of view of a modeler examining consistency of data, was that too few cubs were being recruited to the population because there were not enough adult females producing cubs. As a result, what few cubs could be recruited required a low mortality rate in order to generate sufficient adults. As Pearson (1975:60) pointed out, the use of kill data in analyses of life tables required "that every bear had an equal chance of being selected." If we assume that female grizzly bears have a declining vulnerability to hunting with age, or equivalently, that a female that escaped the hunt last year has a better than average chance of escaping the hunt the next year, then a number of incongruent observations can be reinterpreted.

Our new assumption is completely plausible biologically. We are assuming that some bears in a population, by virtue of their *behavior* or *location,* are more likely to be shot than others and that they retain this higher vulnerability until they are shot and die. If we then look at the average vulnerability in an age-class from year to year, we find that the average vulnerability decreases as the cohort ages.

One result of declining vulnerability to hunting with age is that the number of bears per age-class in the hunter sample will represent a progressively smaller proportion of the number of bears per age-class in the population, when increasingly older age-classes are considered. A life table generated from such kill data would diminish too rapidly in the older age-classes, and any mortality estimate would thus be too high. It is noteworthy that the estimated female mortality rate (15-16 percent) reported by Pearson (1975) is 50-60 percent higher than the estimated rate of male mortality (10-11 percent) despite the fact that there are 46 percent more males harvested than females. If hunting is a major source of mortality, males rather than females would be expected to have the higher mortality rate. A consequence of underestimating the number of older females in the population is an underestimate of potential cub recruitment and therefore a low apparent rate of subadult mortality.

Our change in assumption, that the average female has a declining rather than a constant vulnerability to hunting, provides an alternative and consistent interpretation of Pearson's data. We do not have to assume and rationalize a low rate of subadult mortality. Nor do we have the problem of a relatively high female mortality rate with a low female harvest. It should be noted that we have presented only an alternative hypothesis or interpretation. The explanation offered by Pearson is also consistent with the data. The 2 interpretations could most easily be distinguished by an estimate of the sex ratio of the live population. Our interpretation suggests that females would significantly outnumber males, whereas Pearson's interpretation suggests that males would outnumber females.

POPULATION MODELS WITH FEEDBACK

The Leslie matrix form of model treated in the preceding section contains a major weakness that makes it unsuitable for population projection and management planning at all but the most general level. Because the mortality rates and natality rates are constant, the simulated population will either grow exponentially to infinity, decline exponentially to zero, or remain exactly level. The natality and/or mortality rates must change either directly or indirectly with density before a viable or biologically reasonable population can be maintained. A more comprehensive discussion of models treating density dependence in bears is presented in Bunnell and Tait (1978). Here we treat spatial distribution and vulnerability.

We have seen that individual vulnerabilities of animals can produce the kinds of changes in the sex and age ratios of harvest that have been observed. We also suggested age-induced changes in vulnerability as an alternative explanation for patterns observed in some data. Here we explore in greater detail the concept of changing vulnerability of bears as it interacts with hunting.

The vulnerability of bears is the result of the interaction between man the hunter and bear the prey. An understanding of vulnerability thus requires an understanding of both human and bear behavior. Our first model of man as a hunter depicts man as an ambush predator. We do not mean that the hunter remains hidden and motionless but that during a hunt he remains within a limited area while the bear moves over a much larger area. This description approximates the nonresident's method of fall hunting used in the Yukon and elsewhere. Nonresidents generally hunt over short distances from outfitters' camps while the adult male bear is roaming over a home range of 287 km^2 (Pearson 1975). If we extend the model and consider a hunter randomly entering an area and waiting to encounter a bear, then the probability of the hunter-bear encounter is proportional to the area of the bear's home range.

We can modify the model to a second formulation by allowing the hunter sufficient mobility to move relatively quickly or frequently along a specific route — a road, river, or trail. The probability of encountering randomly distributed bears is then roughly proportional to the square root of the bears' home range. This second model would encompass incidental encounters with bears shot while moving along a road, hunting for black bears from charter boats in Prince William Sound (McIlroy 1972), and spring hunting for grizzly bears along navigable rivers in the Yukon (Pearson 1975). For black bears with their smaller home ranges, the model may approximate the encounter rate for hunters who move consistently along a trail. Both models suggest that the relative vulnerability of male and female bears to hunting should be related to the relative sizes of their home ranges.

When the second model (hunter following a fixed path) is used, the average relative vulnerability of male black bears to hunting is 2.4 times that of females (Table 3). The observed relative vulnerability of male to female black bears in North Carolina was 2.2-2.7 (Table 2). Because brown and black bears seem to maintain permanent home ranges (Jonkel and Cowan 1971, Pearson 1975), the model of man as hunter following a fixed route generates a declining average vulnerability with increasing age.

Fig. 4 illustrates a road (or river) that intersects the home ranges of 2 male grizzlies and 2 female grizzlies. The relative sizes and orientations of the home ranges are taken from Pearson (1975); the road is hypothetical. Grizzly female C is less vulnerable to hunting as a result of her relative isolation from the road. As the vulnerable bears (A, B, and D) are removed, they will

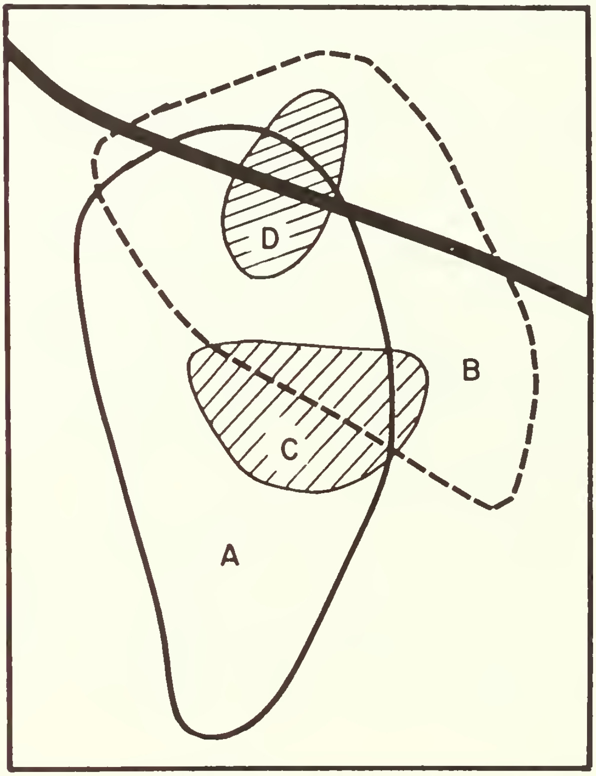

Fig. 4. Idealized home ranges of grizzly bears; A and B are males, C and D are females. Relative size and orientation of home ranges are from Pearson (1975); the solid band or road is hypothetical.

Table 3. Relative sizes of home ranges of male and female bears.

Bear species	Location	Average male home range (km^2)	Average female home range (km^2)	Male/female home range	Square root of male/female home range	Source
Black	Michigan	51.8	25.9	2.0	1.4	Erickson and Petrides (1964)[a]
Black	Montana	30.8	5.2	5.9	2.4	Jonkel and Cowan (1971)[a]
Black	Washington	85.0	5.3	16.0	4.0	Poelker and Hartwell (1973)[a]
Black	Idaho	112.1	34.3-48.9	2.3-3.3	1.5-1.8	Amstrup and Beecham (1976)
Average		-	-	6.7	2.4	
Brown	Yukon	287.0	86.0	3.3	1.8	Pearson (1975)

[a] Standardization to km^2 by Amstrup and Beecham (1976).

be replaced by young animals that will also be vulnerable. Female C, however, may live to an old age. The male bears, on the other hand, as a result of their larger home ranges, are less likely to have home ranges that do not come in contact with the activities of man. A decrease in average vulnerability with a decrease in density due to hunting may provide a density-dependent feedback that will encourage populations at low densities.

The above models of man as hunter are idealized approximations. As hunting pressures increase, or as hunters become more mobile relative to the bears, hunting will cover increasingly extensive areas and the effect of home range will diminish. At the extreme, one can envision the bears as being relatively stationary while man moves about. There would be no apparent differences associated with male and female bears, and the relative vulnerability would be 1. The only method of hunting reported by Poelker and Hartwell (1973) for black bears in Washington that had significantly more females than males in the kill was hunting with dogs. Use of dogs generates a pattern of hunting that had man moving over larger areas rather than along traditional paths. We suggest that the use of dogs reduces the relative vulnerability of male to female bears to hunting to approximately 1 and that the reported sex ratio (100 males to 127 females) in the kill reflects the sex ratio in the population.

Trapping, the only other form of hunting reported by Poelker and Hartwell (1973) that yielded a sex ratio significantly different from even, represents the other extreme model, man as a stationary hunter. The sex ratio of animals trapped was 100 males to 59 females and is consistent with the general difference in sizes of home ranges.

IMPLICATIONS TO MANAGEMENT

We have shown that even an elementary understanding of the population dynamics of bears, particularly as these are affected by man, incorporates some set of simplifying assumptions or model. All implications of even the simplest models are not intuitively obvious (Fig. 2). If management consists of acting knowledgeably on information, the manager must first organize and simplify relevant information into some model(s), then develop understanding of the model(s). By *gaming* or exhausting the implications of his assumptions, we feel that the manager can only improve on the quality of his decisions.

Some of the implications to management were presented in the preceding discussion. Others were not stated explicitly. For example, the nature of the density-dependent regulation suggests that control of black bear populations that concentrates on the more vulnerable male portion of the population may encourage population growth (Kemp 1976, Bunnell and Tait 1978). Acknowledging only this phenomenon suggests that control must be selective for females. A further implication that can be drawn from the discussion also concerns density-dependent response — the control must be operative at both high and low densities. In populations with a low reproductive rate, unrestricted hunting may permit no effective response at low densities. Quota systems will probably prove an insufficient regulatory device and limited-entry permits may be the only effective means of sustaining populations.

We can summarize many of the implications to management by treating a real-world example and by examining the intersection of the models presented and the data (reality). Consider the problem of managing the polar bear population in the area of James Bay and the Belcher Islands, described by Jonkel et al. (1976:6): " . . . the proposed annual quotas for the area . . . could be as high as 18% of the total population." From Fig. 1, the maximum sustainable rate of mortality for a polar bear population with an average litter size of 1.7 and age of first reproduction of 7 years is about 11 percent. Examination of the kill data by age and sex reveals that the average ages of female bears killed in James Bay and in the Belcher Islands are lower than the average ages of male bears. This trend is opposite to that illustrated in Fig. 3b, and suggests that females may be more vulnerable to hunting than are males. The kill taken by the Ontario Indians is predominantly female and reflects the sex-specific patterns of movement of female polar bears to their denning area in Ontario. The phenomenon is analogous to that illustrated in Fig. 4. From analyses such as those of Bunnell and Tait (1978), we know that slight overharvesting with a selection for females would produce no appreciable difference in the total population of adults nor in the success of hunters over the short term. The first few years of overharvest would affect the recruitment of the population with a lag of about 6 years before the total population of adults would reveal the impact. Lowered recruitment would not be evident in kill data. After about 6 years, the population would appear to decline rapidly. It is important to note that once the effect of overharvest became evident, it would take many years for countermeasures to reverse the trend.

We chose the example of Jonkel et al. (1976) not because their data have unique implications to management but because the example represents in a simple fashion the manner in which simple models can facilitate interpretation of data and consideration of management actions. Our plea is for increased examination of assumption by *any* means. We feel that simulation models can help to keep managers from joining that group of individuals so aptly described by St. Augustine as those who "saw the effect but not the cause."

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APPENDIX

Our "models without feedback" have been referred to as a Leslie model because the results could be duplicated by a Leslie-Lewis matrix, the assumptions embedded in our model and the Leslie-Lewis matrix are equivalent, and our results have the same characteristics as a Leslie-Lewis matrix — a constant growth rate and eventual stable age distribution. However, our modeling approach is not strictly that of Leslie (1945) in that we do not use a Leslie-Lewis matrix nor do we use matrix algebra to arrive at our solution. Our model simulates the following set of difference equations:

$$N_{x+1}(t+1) = S_x \times N_x(t)\; x = 0, 1, 2, \ldots, \text{upper age limit (maximum} = 30)$$

$$N_o(t+1) = {}_{all}\Sigma_x\, N_x(t+1) \times F_x$$

where

$N_x(t)$ = number of females aged x in year t,

S_x = proportion of females aged x that survive age x, and

F_x = average number of female offspring of a female of age x.

The upper limit on x is not allowed to exceed 30 and may be lower, depending on the particular survivorship schedule, S_x. As an example, the fecundity rate, F_x, used to represent a bear population with an average age of first reproduction of 5 years and an average natality rate of 0.9 cubs/year (0.45 females/sow) would be:

$F_x = 0 \qquad x = 0, 1, 2, 3, 4$

$F_x = 0.45 \qquad x = 5, 6, 7, \ldots$, upper age limit

By systematically choosing alternative values of S_x and simulating, one finds that with $S_x = 0.827$ for all ages (Fig. 1), the population size remains constant.

Density-dependent effects and hunter harvests were incorporated by appropriate time- or density-dependent modifications of S_x.

EXPLORATION OF OPTIMAL BACKCOUNTRY TRAVEL PATTERNS IN GRIZZLY BEAR HABITAT

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Abstract: Trade-offs among backcountry management objectives were explored for the northern half of Glacier National Park, Montana. Parametric linear programming was employed to quantify the trade-offs among 5 objectives, consisting of 3 measures of trail-related contact between grizzly bears (*Ursus arctos*) and humans (dangerous, nondangerous, total), a measure of solitude at the backcountry campsites, and the volume of backcountry overnight use. Contact indices were developed for these measures of contact for 3 time periods for each of 85 trail segments in the study area. Optimal patterns of backcountry overnight use were identified for various combinations of objectives within 2 management models. The first model minimizes all trail-related contacts between humans and grizzlies. The second model minimizes only dangerous contacts. Parametric linear programming is shown to be a powerful technique for dealing with multiobjective problems of the size and complexity considered in this study.

Researchers who have considered human use of grizzly bear habitat have suggested that management be directed towards controlling the volume and/or distribution of this use (Craighead and Craighead 1967, Herrero 1970a, Mundy and Flook 1973). Managers, however, have found it difficult to implement these management recommendations for several reasons. They have lacked the means to assess the number of contacts between humans and grizzlies likely to occur with alternative volumes and distributions of use. Moreover, the several goals typically pursued by management further complicate the task of evaluating the relative desirability of alternative use patterns.

Effective management of human use of grizzly habitat is important for several reasons. It not only serves to protect people from injury and death but also helps protect the bears. Grizzly populations are imperiled by the sentiment that periodically surfaces suggesting they be removed from national parks (Moment 1970). Grizzlies warrant special management attention, having been declared a threatened species in the continental United States (45 FR 31734-31736) under the Endangered Species Act of 1973 (PL 93-205).

Work conducted from 1974 through 1977 quantitatively assessed the trade-offs among management objectives relating to human use of grizzly habitat. In effect, the work has been an attempt to find optimal patterns of backcountry travel for various combinations of management objectives. Thus, the research empirically explored the suggestion that the distribution and/or volume of human use of grizzly habitat should be managed.

The type of information generated by this work is intended to be an input to backcountry management planning. The objective has been to enhance the manager's role as a decision maker by quantifying the trade-offs among management objectives so that more informed decisions can be made.

This research was aided by the efforts of University of California faculty members W. McKillop, S. Leopold, and S. Dreyfus, who provided valuable guidance. Data collection was facilitated through the efforts of Glacier employees C. Martinka, J. DeSanto, and K. Keller. R. Hinkins of the Lawrence Berkeley Laboratory assisted in the solution of the mathematical models. J. Bartolome reviewed the paper.

STUDY AREA

The study was conducted in Glacier National Park in Montana. The Going-to-the-Sun Road, which runs east-west, divides the park into 2 parts (Fig. 1). The study area was the backcountry north of the Going-to-the-Sun Road. This area comprises approximately 215,000 ha, or slightly more than half the total area of the park. The study area contains 39 designated backcountry campsites. Access to these campsites is facilitated by 22 trailheads and 461 km of backcountry trails (Fig. 2).

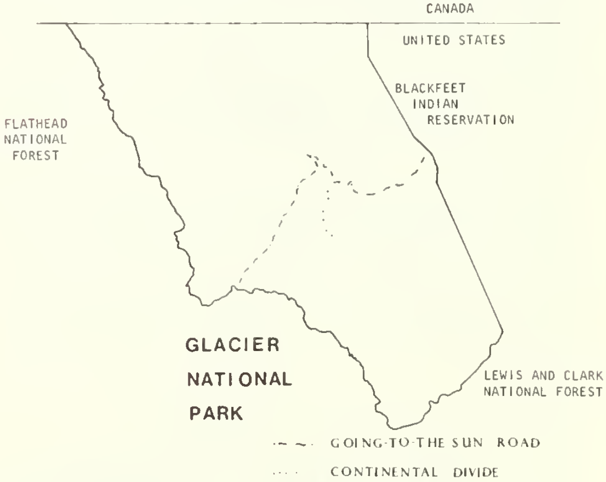

Fig. 1. Map of Glacier National Park and surrounding lands.

Martinka (1974a) has estimated that during the years

Fig. 2. Map of the trails, trailheads, and designated backcountry campsites in the study area.

1967-73, the size of the grizzly population in Glacier was stable, with a mean of 194 animals. The area inhabited by these bears has seen significant backcountry use in recent years. In 1975, 4,502 parties composed of 11,464 people camped overnight in Glacier's backcountry. The entire park had 8,206 party-nights of backcountry use, with more than three-fourths of it occurring in the study area.

There have been 3 fatalities caused by grizzlies in Glacier National Park. In 1967, 2 women died as a result of separate attacks by grizzlies in the backcountry. A third woman died after an encounter with a grizzly at a developed campground in 1976. In addition, grizzlies have caused a number of injuries of varying severity in recent years.

Glacier's backcountry is managed under a system of designated backcountry campsites and mandatory backcountry permits. The research has been carried out within this management framework, exploring the capabilities of the current system to accommodate human use of grizzly habitat more effectively.

CONTACT INDEX DEVELOPMENT

Effective management of the volume and distribution of human use requires knowledge of human-grizzly contact rates or probabilities specific to locations and time periods. Although there are several ways to estimate these values, data were available only from sightings of bears. It had been anticipated that estimates of human use on various trail segments by time period could be obtained. These estimates would have permitted conversion of the absolute number of grizzly contacts in an area during a time period into a contact rate. Thus, some of the biases known to be associated with observation data (Mundy and Flook 1973, National Academy of Sciences 1974, Singer 1976) could be eliminated. Obtaining reasonable-quality estimates of human use proved to be impossible, so the decision was made to use contact indices rather than contact rates.

Three contact indices were developed. The first related to dangerous contacts; the second dealt with nondangerous contacts. The third index pertained to all contacts between humans and grizzlies. These contacts included everything from direct physical contact to seeing a bear at a distance of a kilometer or more. For these purposes, dangerous and nondangerous contacts were considered to be both mutually exclusive and collectively exhaustive. Therefore, the total contact index was the sum of the danger and nondanger contact indices.

Indices were defined in terms of time periods. The backcountry use season was considered to extend from 1 June to 15 September and was divided into the early season (1 June-5 July), the midseason (6 July-10 August), and the late season (11 August-15 September).

Contact indices related factors associated with grizzly observations in the study area to data for the various trail segments. The focus on trails excluded consideration of off-trail travel and backcountry campsites. Off-trail travel is uncommon in the study area, and excluding it from consideration kept the problem to a manageable size. Contact indices were not calculated for campsites because campsite encounters with grizzlies can be more effectively handled through management actions directed toward camping practices and campsite locations than by manipulating the pattern of use.

Contact indices incorporated data from grizzly observations recorded in park files. For the years 1968-75, a total of 585 observations from the study area between 1 June and 15 September were located. Of these, 191 were observations of sows with young. The 585 observations included 598 adults and 362 additional grizzlies classified as cubs, yearlings, and 2-year-olds.

The observations were divided into the 3 time periods mentioned above to take into account the noted differential habitat use by grizzlies over the course of the season (Martinka 1972, Mundy and Flook 1973). The observations were further categorized by the habitat type and elevation zone in which each observation occurred. Five habitat types and 6 elevations zones were used. The 5 habitat types — alpine, forest, shrub, slide, and grassland — were those used by Martinka (1972) in his work on grizzlies in Glacier. The 6 elevation zones covered elevations in the study area ranging from approximately 945 to 3,200 m (Stuart 1977).

The percentage of the total number of observations in a time period was computed for each habitat type-elevation zone combination. Not all potential combinations existed in the study area, with only 20 having reported observations. The observations were further partitioned as to whether or not sows with young were involved. This distinction was based on the work of Herrero (1970a, 1970b, 1976), which showed that sows with young are disproportionately involved in aggressive contacts with humans. For each time period, similar calculations by habitat type-elevation zone were carried out for sows with young and for all other grizzlies.

Each of the 85 trail segments in the study area was systematically sampled at approximately 0.17-km intervals. Data were obtained for 2,682 sampling points. At each of these points, the following data were recorded: the length of unobstructed visibility on the trail in both directions, the habitat type(s) of the adjacent area, and a rating of the difficulty of off-trail travel in the vicinity of the trail. Combining elevation data from topographic maps with the habitat type data for each sampling point allowed estimation of the percentage of a trail segment in each combination of habitat type and elevation zone.

Rating the difficulty of off-trail travel and measuring trail visibility helped in assessing the likelihood that an encounter with a grizzly on a trail segment would, or would not, be dangerous. All else being equal, the chance of a dangerous encounter with a grizzly is much higher if a hiker meets the animal on the trail than if the grizzly is seen off the trail. In addition the more difficult the off-trail travel, the greater the likelihood that an encountered grizzly will be on the trail. A grizzly encountered on the trail, however, need not be considered dangerous if the hiker is aware of the grizzly soon enough to respond. An encounter is assumed to be dangerous any time a person is not aware of a grizzly until they are so close that the outcome will be determined by the bear.

The trail visibility data indicate that in many parts of the study area an unobstructed view of the trail is restricted to a short distance. Nearly 80 percent of the time, unobstructed trail visibility is limited to 30 m or less; over 90 percent of the time it is restricted to less than 61 m. Trail visibility is particularly important since Herrero (1976) indicated that injuries occurred when people were not aware of the grizzly's presence until a short distance separated them. This distance never exceeded 100 m and was often much less.

For each trail segment, computations were carried out to construct a danger contact index, a nondanger contact index, and a total contact index, for each time period. The danger contact index for a trail segment and time period was the weighted average of 2 values. Herrero (1976) reported that sows with young were involved in 80 percent of the major injuries attributable to grizzlies on the North American continent from 1970 through 1973. The danger contact index used the values 0.8 and 0.2 for these weights. The former was associated with the pattern of habitat use observed for sows with young, the latter for the pattern of habitat use for all other grizzlies.

The *sows with young* element of the danger contact index for a trail segment going from point *e* to point *f*, for time period *k*, was calculated as follows:

$$\mathrm{SWK}^k_{ef} = \frac{\sum_{i=1}^{5}\sum_{j=1}^{6}(S^k_{ij})(T_{ij})}{\sum_{i=1}^{5}\sum_{j=1}^{6}(S^k_{ij})^2}$$

where,

S^k_{ij} = the percentage of observations of sows with young during time period *k* recorded in habitat *i* and elevation zone *j*,

T_{ij} = the percentage of the trail segment estimated to be in habitat type *i* and elevation zone *j*.

Note that this element is constructed so that if a trail segment went through terrain and vegetation with the same pattern as that for observations of sows with young during that time period, its value would be *1*.

For the same trail segment and time period, the element for *all other grizzlies* was calculated as follows:

$$\mathrm{AOG}^k_{ef} = \frac{\sum_{i=1}^{5}\sum_{j=1}^{6}(O^k_{ij})(T_{ij})}{\sum_{i=1}^{5}\sum_{j=1}^{6}(O^k_{ij})^2}$$

where,

O^k_{ij} = the percentage of observations of all other grizzlies during time period *k* recorded in habitat type *i* and elevation zone *j*.

After computing these 2 elements, the value of the *danger contact index* for the trail segment from *e* to *f* during time period *k* was determined as follows:

$$DCI^k_{ef} = [(0.8)\ (SWY^k_{ef}) + (0.2)\ (AOG^k_{ef})]\ [(D)\ (V_{ef})(L)(B^k)]$$

where,

DCI^k_{ef} = the danger contact index for time period k for the trail segment from e to f,

D = the estimated proportion of the trail segment with a rating of average or greater for off-trail travel difficulty,

V_{ef} = the estimated proportion of the trail in the direction of travel with visibility restricted to 61 m or less,

L = length of the trail in miles,

B^k = the ratio of the mean number of grizzlies seen per day during time period k to the mean number of grizzlies seen per day during the entire season.

The *nondanger contact index* was calculated in a related manner. For the same trail segment (from e to f) and time period (k), the nondanger contact index calulations were as follows:

$$NDCI^k_{ef} = \frac{\sum_{i=1}^{5} \sum_{j=1}^{6} (A^k_{ij})\ (T_{ij})}{\sum_{i=1}^{5} \sum_{j=1}^{6} (A^k_{ij})^2}\ [(1 - (D)(V_{ef}))\ (L)(B^k)]$$

where the terms previously used are defined as above and

A^k_{ij} = the percentage of observations of all grizzlies during time period k recorded in habitat type i and elevation zone j.

In the danger contact index calculations, the product $[(D)(V_{ef})]$ is used as a proxy for the probability that a contact with a grizzly on a particular directed trail segment would be dangerous. Since dangerous and nondangerous contacts are considered mutually exclusive and collectively exhaustive, the term $[1 - (D)(V_{ef})]$ is employed in the nondanger contact index calculations.

For a trail segment and time period, the total contact index is the sum of the danger contact index and the nondanger contact index. In other words:

$$TCI^k_{ef} = DCI^k_{ef} + NDCI^k_{ef}\ .$$

MANAGEMENT MODELS

For any particular volume of use, the backcountry management problem is essentially to find the pattern of use, across the various time periods comprising the backcountry use season and throughout the backcountry within each time period, that best accomplishes the relevant management objectives. Hence, a variable in the management models is an overnight backcountry trip that can be taken during a given time period. The solution for a management model reveals the number of parties needed to undertake the backcountry trip during the time period represented by each variable, if an optimal pattern of use is to be achieved.

To find an optimal pattern of backcountry use, it was necessary to know all the backcountry trips possible in the study area. These trips represent various sequences of trail segments and campsites that meet a set of criteria. The most significant of these criteria are (1) that a trip involve camping only at designated backcountry campsites and (2) that each day's travel not exceed a maximum distance. Through the use of techniques from the field of network and graph theory, it was possible to identify all such theoretically possible trips (Stuart 1977).

A total of 2,116 trips were available for consideration by the models in determing optimal patterns of use. Due to the impassability of some trails at the beginning of the season, every trip cannot be undertaken in each time period. Only 833 of these trips can be undertaken in the early season of a typical year, but all 2,116 are feasible in both the midseason and the late season.

Each variable has a value for the danger contact index, the nondanger contact index, and the total contact index. These values are the sum of the index values for each trail segment traversed in the course of the trip and the time period implied by that variable.

Linear programming is the mathematical optimization technique employed in the management models. Solution of these models was carried out while parametrically varying one or more constraints, thus permitting identification of the trade-offs among various management objectives. The linear programs contained 5,065 variables and nearly 200 constraints.

Linear programming determines the optimal value for each variable in a model. This optimality is in terms of a linear objective function being maximized or minimized subject to linear equality and inequality constraints. For these management models, the variables are backcountry trips during specified time periods. The value of a variable is the number of parties recommended for the journey implied by that trip and time period. Constraints in the models limit the amount of overnight use at each backcountry campsite and the level of parking at each trailhead. Other contraints insure that any pattern of backcountry use identified will have additional desirable properties. These properties include reasonable distributions across the 3 time periods, among average daily travel distances, and among trips of various durations (Stuart 1977). Two alternative objective functions were used, giving rise to a pair of management models — Model 1 and Model 2. The difference between the models involves the implicit view a manager might have toward human-grizzly contacts.

Model 1 minimizes the value of the total contact index as its objective function. The underlying rationale for use of this model is that efforts should be made to prevent all contact between visitors and grizzly bears. A suggestion that prevention of all contacts ought to be the management objective for the National Park Service is in the literature (Craighead and Craighead 1967). In minimizing this objective function, the model minimizes the sum of the total contact index for each variable times the number of parties suggested for the trip during the time period represented by that variable. The value of the objective function for this model relates to the total number of trail-related contacts (of all kinds) between backpackers and grizzly bears that would arise over the course of the entire season.

Model 2 has as its objective minimization of the danger contact index. With use of this model, the goal is to prevent contacts with grizzlies in areas of the backcountry where the contacts are likely to be dangerous. This objective function relates to the total number of dangerous trail-related encounters between backpackers and grizzlies over the course of the season.

In generating values for constraints in the linear programs, 5 alternative definitions of backcountry campsite capacity were used. By comparing solutions for model runs that differ only with respect to the definition of campsite capacity, the implications of providing greater or lesser degrees of solitude at the backcountry campsites can be seen. This is an important feature of the models, since several researchers suggest that campsite solitude is an important element in a wilderness experience (Stankey 1973, Lucas 1973, 1974).

These 5 definitions of campsite capacity included the one actually used in the park. These actual capacities for the various campsites range from 1 to 10 parties per evening, with 3.9 the mean. The distribution of these values is presented in Table 1 under ACTUAL. Distributions of capacities under the other 4 definitions are also in Table 1. For each of these definitions, the capacity of a campsite is the minimum of the campsite's ACTUAL capacity and the integer value of the name of that capacity definition. Thus, each of the other 4 definitions is more restrictive than ACTUAL.

Table 1. Number of campsites with various maximum limits of nightly party use for alternative definitions of campsite capacity.

Capacity definition	Maximum number of parties per night										Mean capacity
	1	2	3	4	5	6	7	8	9	10	
ACTUAL	2	7	11	5	7	5	0	1	0	1	3.9
FOUR	2	7	11	19	-	-	-	-	-	-	3.2
THREE	2	7	30	-	-	-	-	-	-	-	2.7
TWO	2	37	-	-	-	-	-	-	-	-	1.9
ONE	39	-	-	-	-	-	-	-	-	-	1.0

RESULTS

The goal in Model 1 is to find the pattern of backcountry use that keeps the value of the total contact index as small as possible, for a given volume of use. One way of pursuing this goal would be to solve the model for one or several selected volumes of use, but the question of which volumes to use would then arise. By employing parametric linear programming, this aspect of the management problem can be treated in a more elegant and more comprehensive fashion. The linear programs were solved while parametrically varying the volume of use. In other words, for each capacity definition, an optimal pattern of use was identified for every volume of use (in party-nights) from zero to that level at which the backcountry is used to its capacity (Stuart 1977). A summary of these solutions is graphically presented in Fig. 3.

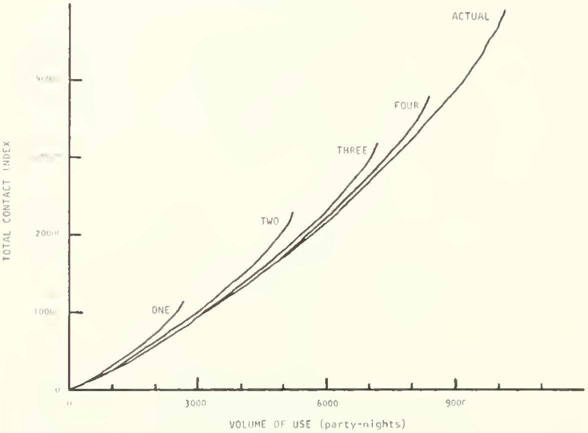

Fig. 3. Model 1 trade-off possibility frontiers for alternative campsite capacity definitions.

Fig. 3 presents 5 trade-off possibility frontiers, 1 for each of the 5 alternative definitions of campsite capacity. They show the trade-offs, given an optimal pattern of backcountry use, between the total contact index and the volume of use for each capacity definition. All points on these curves have a special property. The value of the total contact index associated with the volume of use for any point on a curve is the minimum attainable total contact index value for that campsite capacity definition and volume of use. There is, in addition, a specified pattern of use associated with each point on these curves (Stuart 1977).

This type of information can be employed by managers in several ways. For instance, for any volume of use, say 6,000 party-nights (in the range of recorded use in the study area during the 1975 season), the relationship between the total contact index and solitude at the backcountry campsites can be explored. For capacity definition ACTUAL, the total contact index value is 21,754. The more restrictive definition of FOUR raises the total contact index value to 22,252, an increase of 2.3 percent. Capacity definition THREE, even more restrictive, results in an index value of 23,379, 7.5 percent higher than that for ACTUAL.

In this way the manager is able to see the trade-offs between a measure of all trail-related contacts with grizzlies and a measure of solitude at the backcountry campsites, for all feasible volumes of use. The degree of solitude to provide and the level of contact between visitors and grizzlies to be endured is a judgement to be made by a manager. The data show how much of one objective the manager foregoes to achieve given levels on the other.

Information presented in this fashion also permits a quantitative assessment of the relationship between changes in the volume of use and the level of contacts with grizzlies. It has been suggested that increasing use levels are likely to bring higher levels of contact between people and grizzlies (Martinka 1974b, Merrill 1976). Here we see that even if these higher volumes of use are distributed optimally, a measure of total contacts is an increasing function of use. Now only does this measure of contacts increase with additional use, but it also increases more than proportionally. For example, at 6,000 party-nights of use with capacity definition ACTUAL, a 1 percent increase in use would produce a 1.35 percent increase in the total contact index. At 7,000 party-nights, a 1 percent use increase would raise the total contact index 1.38 percent.

Model 1 allows a manager to explore the trade-offs among 3 objectives in backcountry management: the volume of use, a measure of solitude at the campsites, and a measure of all trail-related encounters with grizzlies.

Model 2 explores the trade-off between the danger and nondanger contact indices for specified volumes of use and campsite capacity definitions. The results of solutions for this model can also be presented as trade-off possibility frontiers. Fig. 4 shows this relationship for 7,000 party-nights and the ACTUAL campsite capacities. This curve is again a set of points with valuable properties. Any point on the curve is simultaneously the lowest level of the danger contact index for that level of the nondanger contact index *and* the highest level of the nondanger contact index for that level of the danger contact index. Each point on the curve has associated with it a particular pattern of backcountry overnight use.

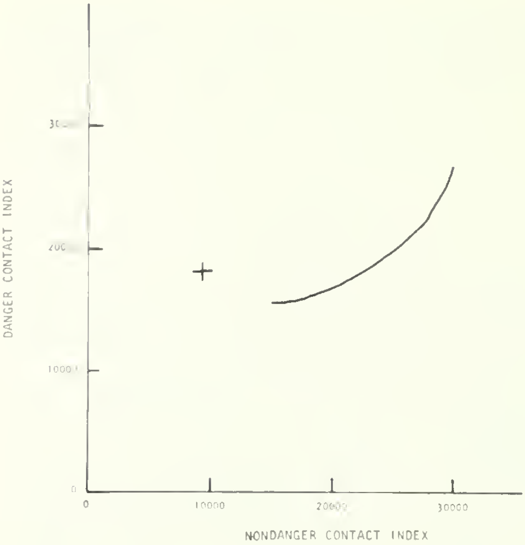

Fig. 4. Model 2 trade-off possibility frontier for campsite capacity definition THREE and a volume of use equal to 7,000 party-nights.

The point at the left of the curve is the minimum attainable value for the danger contact index. Other points on the curve are the minimum danger contact index values for progressively higher levels of the nondanger contact index. The problem was solved by parametrically varying the nondanger contact index over all pertinent values (Stuart 1977).

The + symbol in Fig. 4 represents the minimum feasible sum of the danger and nondanger contact indices, which is precisely the definition of the total contact index. The + is thus the minimum total contact index value found in Model 1. This illustrates that *if* a manager feels comfortable about distinguishing between dangerous and nondangerous contacts, substantial differences in the properties of optimal travel patterns result.

For the example presented in Fig. 4, the total contact index value from Model 1 is 26,932. This value is composed of a danger contact index value of 17,801 and a nondanger contact index value of 9,137 (differences are due to rounding in the original data). By minimizing the danger contact index in Model 2, its value was reduced to 15,552, a decrease of nearly 13 percent. The level of the associated nondanger contact index if 15,005, a 64 percent increase over the value from Model 1.

A manager need not prefer the point at the left end of the curve, the point for which the danger contact index is minimized. A manager might favor another point on the curve, tolerating a higher level of the danger contact index to achieve a higher level of the nondanger contact index. In more practical terms, a manager might choose a pattern of use that has a higher probability of people seeing grizzlies in nondangerous situations. The price for this decision, however, would be more chances of encounters with grizzlies in dangerous situations. As can be seen from the shape of the curve, the trade-off is reasonably attractive over a range but becomes progressively less attractive along the curve to the right. By examining these types of figures, a manager can see the trade-off between 2 management objectives (measures of dangerous and nondangerous contacts), holding constant the volume of use and campsite capacity definition.

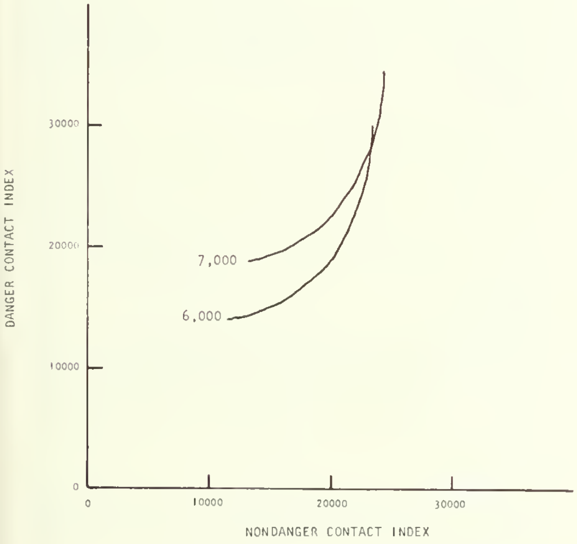

Fig. 5. Model 2 trade-off possibility frontiers for campsite capacity definition THREE and alternative volumes of use.

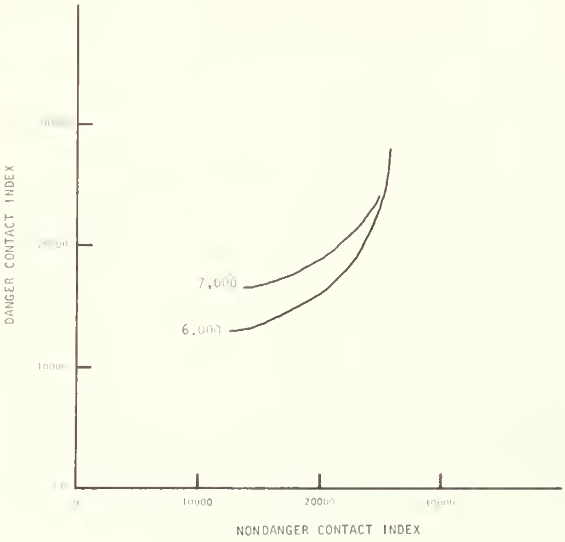

Fig. 6. Model 2 trade-off possibility frontiers for campsite capacity definition FOUR and alternative volumes of use.

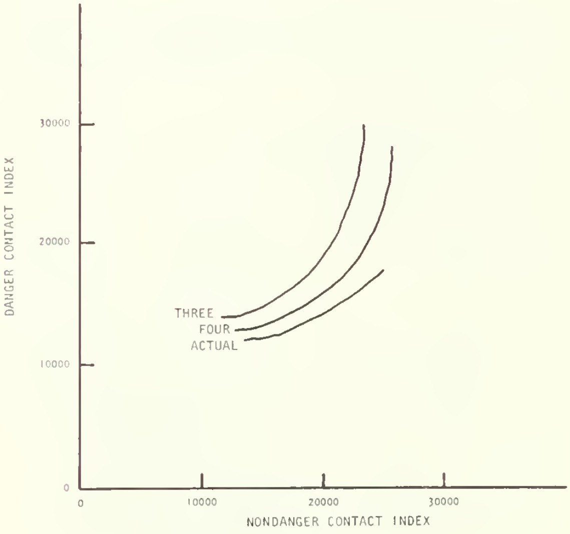

Fig. 7. Model 2 trade-off possibility frontiers for alternative campsite capacity definitions and a volume of use equal to 6,000 party-nights.

Even more valuable information can be displayed for the manager by plotting several related curves on the same axes, holding only 1 thing constant. Fig. 5 shows trade-off possibility frontiers for capacity definition THREE with alternative volumes of use (6,000 and 7,000 party-nights). Fig. 6 shows comparable results for capacity definition FOUR. Of course, there is no need to hold the capacity definition constant. Fig. 7 presents curves for alternative campsite capacity definitions for a constant volume of use (6,000 party-nights). In any of these multiple-curve figures for Model 2, a manager can explore the trade-offs among 3 objectives. By examining 2 or more related plots iteratively, trade-offs among 4 objectives can be evaluated.

DISCUSSION

The results presented above show some of the information that these management models can provide. Other information available includes the pattern of use by season for each trailhead, campsite, and trail segment. The change in the objective function that would result from altering the capacity of any campsite or trailhead is also determined. Modification of the models would permit consideration of such topics as the impact of changes in the trail network or in the set of designated backcountry campsites and evaluation of backcountry day use.

Contact rates that are specific to locations and time periods are clearly a critical element for models of this type. Use of contact indices had the advantage of exploring the feasibility of various mathematical management models as well as demonstrating the kinds of information these models can provide. The indices included in one fashion or another most factors that are suspected to be related to encounters between humans and grizzlies. Nevertheless, indices are no substitute for contact rates. Estimation of these rates would be a significant step forward in providing managers with information they could use in helping visitors plan their backcountry journeys. In this way, people can be advised of possible trips that would meet their objectives while simultaneously encouraging a pattern of use that poses fewer problems for the grizzlies.

The capacity to explore trade-offs among objectives would remove neither the opportunity nor the obligation for a manager to exercise professional judgement in considering alternative volumes and distributions of use. It would, however, allow necessary and difficult decisions to be made with much more relevant information than is currently available.

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A COMPUTERIZED SYSTEM FOR RECORDING AND RECALLING GRIZZLY BEAR REPORTS

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Abstract: Reports of grizzly bears (*Ursus arctos horribilis*) from throughout the Border Grizzly Area were collected, verified, coded, and stored in a computerized file called the base data bank. Each report included four primary categories of information — report type, date, location, and source of information. Depending upon complexity, additional data were either stored in the base data bank using secondary information categories or were recorded verbatim in a narrative file that was cross-referenced from the base data bank. Applications of the system and its further development are discussed.

Collection and storage of information concerning the occurrence, habitat use, and life cycle necessities of the grizzly bear have become particiularly important with the inception of the Endangered Species Act of 1973 and the subsequent listing of the grizzly bear as a threatened species in 1975. These circumstances have provided a formidable challenge to administrators and managers in the Border Grizzly Area (BGA) of Montana, Idaho, and Washington (Fig. 1). Although the grizzly bear requires large tracts of relatively undisturbed terrain, managers and governments must nonetheless guarantee (1) grizzly survival, (2) an increase in grizzly range and numbers, and (3) no detrimental changes in grizzly habitat. The range of the grizzly must therefore be identified and quantitatively analyzed to determine what constitutes detrimental modification or destruction of habitat. Simultaneously, population levels and changes, needs and habits of bears, and basic biological parameters of the border grizzlies must be determined. These are complex and extensive tasks for a long-lived adaptable species such as the grizzly bear.

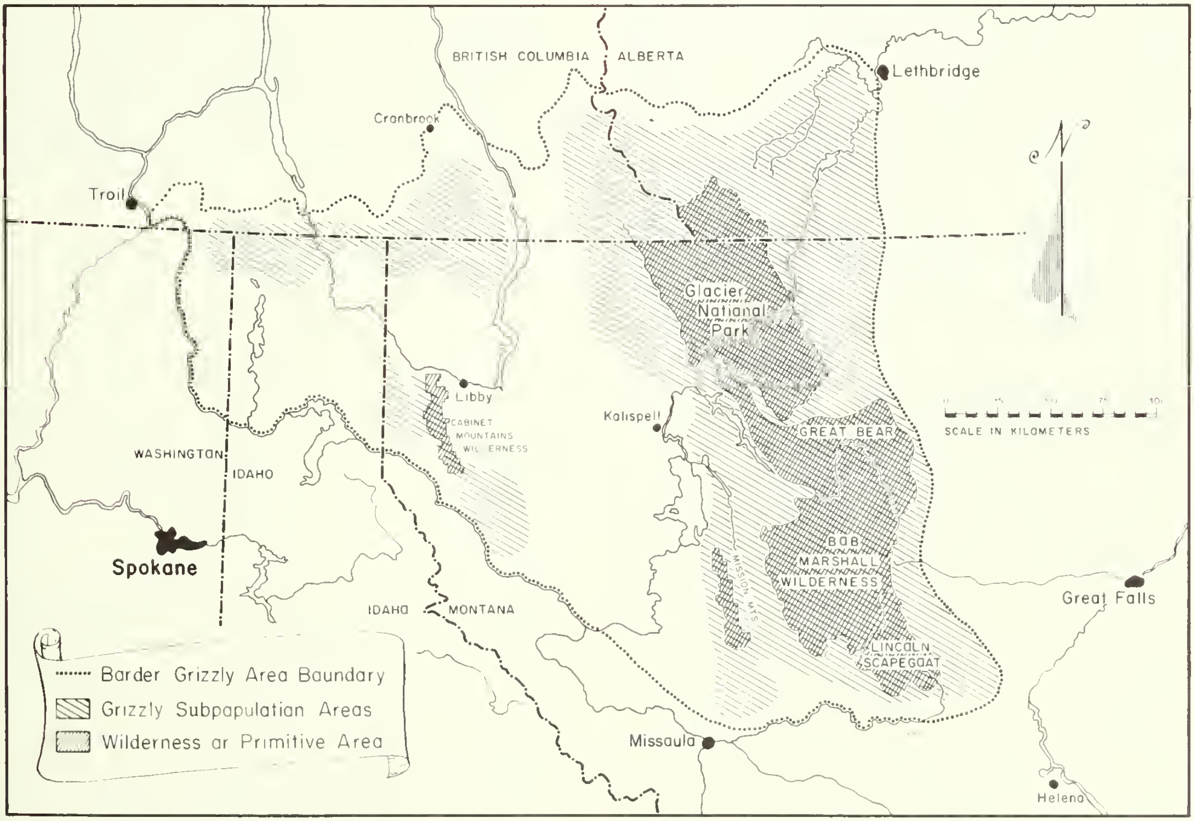

Fig. 1. The Border Grizzly Area.

Concurrently, the economic variability of the BGA is considered by many to be dependent upon the exploitation of timber, increased tourism, and intensive land development. These two broad goals — grizzlies and resource development — may simply be incompatible, but managers must search for solutions.

There has been an intense and increasing public demand for wise and immediate decisions concerning developments that might adversely affect the grizzly bear. Information on grizzly bears has always been difficult to collect and compile because the species is elusive and uncommon. Yet, reports of grizzlies were probably more often noted in historical journals than accounts of other animal species because they were a spectacular and unusual sight. Reliable old records, however, are scarce. Although reports are more available today, there is still a paucity of information.

Managers call upon biologists for direction and information when decisions regarding wildlife have to be made, but it often happens that biological research is not supported until the need for answers has already developed. The resulting sense of urgency can often prompt premature or unwise decisions. This paradox is even more acute in the case of the grizzly bear where industrial, environmental, and political factions are all deeply involved. Decisions, therefore, have not been easy for wildlife managers responsible for the bear population or for land managers responsible for the bear's habitat. A considerable amount of base-line information has been collected by private citizens and agency personnel, but its usefulness has been limited because it has not been readily available on an interagency basis nor is it complete for different users. Both problems could be remedied if standard information were collected and stored in a readily available data bank.

This paper presents a computerized system for recording and recalling grizzly bear reports. The Border Grizzly Project and Glacier National Park are collecting and recording reports from diverse sources to provide base-line information about grizzly bear occurrence, habitat selection, and population trends. Once historical or current reports have been judged for reliability and recorded systematically, this information file can be rapidly searched and summarized to help resolve questions about land management and recreational use and safety.

We wish to express our thanks to those people who have worked for years at recording information about wildlife and at solving the problems of organizing and storing records. We thank C. J. Martinka, C. Jonkel, and W. M. Colony for support, encouragement, and direction; M. Meagher and S. Fullerton for input and comment; T. Dundas and G. Rogers for their work on coordinate systems and maps; and N. McMurray and S. Kiser for patience, comments, and hours of labor.

METHODS

Grizzly reports today can be just as valuable as historic reports. Although it is important that each report be documented and readily accessible, reports are still being gathered in a piecemeal fashion, without documentation or follow-up, and important details are often lacking. Because of the vastness of the BGA, the Border Grizzly Project, in conjunction with Glacier National Park, developed a computerized system to record and store reports of grizzly bears from throughout the area. This system is designed to serve both managers and researchers at the field level. It can be used to answer immediate questions or to assist research and management planners.

The system works from a file of information called the base data bank that is composed of individual grizzly bear reports. Each report includes four primary categories of information — report type, date, location, and source of information. (The report type may be of a kill, sighting, track, scat, den, daybed, dig, marking, depredation, and other less frequent reports.) Additional data such as the bear's physical characteristics, its activity, or a description of its environment can be recorded in secondary information categories. Table 1 lists the types of information that can be included in the computerized file system. All information stored in the base data bank is coded in order to save storage space and to facilitate searches. Coded information can be located, tallied, and decoded for easy reading. A user can obtain a list of all reports fitting a particular search request by specifying a range of values to be sought for one or many categories of data. For example, if a re-

Table 1. Summary of types of information that can be included in the base data bank, Border Grizzly Project and Glacier National Park.

Information category	
Primary	Secondary (incomplete list)
Report type	Group size
Date	Group composition
Location	Food
Source	Elevation
	Habitat type

source manager requested legal locations of all observed grizzly bears or their sign, for a given area, during a particular season, over a certain time span, he might specify the North Fork of the Flathead River, fall, 1973-77. The printout would list (by legal location and report type) only those reports fitting the designated limits.

Most of the detailed information included in reports can be incorporated into the base data bank by using the secondary information categories, but some reports include complex explanations that cannot be easily coded. In such cases, the information is recorded verbatim in a separate narrative file and referenced from the base data bank. Narrative information, too, can be recalled and printed on request, although it cannot be searched as comprehensively and economically as the base data bank. The coding system is designed to be comprehensive enough that only rarely would the original written report have to be consulted. Once the system is established, it can be searched, updated, and otherwise maintained from a remote terminal requiring only a telephone line for access. All programs have been written in FORTRAN IV. Computer programs that search the base data bank have been completed and are being tested. Programs for decoding base data, cross-referencing narrative data, and searching within a geographic area are written but not yet tested.

An auxiliary report-mapping capability provides another dimension of data analysis. Maps can be produced by the Montana Department of Community Affairs, Helena, to display any data set. This versatile service requires only the location coordinates of each report (preferably Universal Transverse Mercator coordinates) in order to map data summaries. Because color and symbol may be varied for each point, two variables can be readily displayed on a single map. For example, grizzly bear reports can be mapped to indicate season and report type by using a different symbol for each season and a different color for each type of report. Overlays can be produced for a base map of any scale. For any area within Montana, detailed base maps can be generated as well. For areas outside Montana, base maps cannot be produced, but data can be plotted given a reference point, scale and grid, or coordinate system. All locations in the current base data bank are recorded by one of three standard coordinate systems: Government Land Office, geodetic (latitude/longitude), or Universal Transverse Mercator (UTM). Coordinates can be converted by computer from one system to another. For mapping, reports must be recorded by the geodetic or UTM system.

DISCUSSION

This system is based on human involvement. It is a compilation of reports from people who discover and report grizzlies or their sign. The data bank depends first upon humans and grizzlies (or grizzly sign) occurring in the same place at the same time, and second, the conscientious effort by the individual to record the information. People today are well-traveled and widely dispersed, but unless their reports can be collected, verified, and entered into a standardized and widely available system, our knowledge of grizzly bear range and needs is hardly more advanced than during the pre-1900 era. The usefulness of this system depends upon the active participation of governmental agencies in providing detailed reports of grizzlies and in making full use of the system. Glacier National Park and the Border Grizzly Project plan to refine and maintain the system to the degree that finances allow, but the active role of other agencies is strongly encouraged for the realization of the system's full potential.

What are some of the potential applications of this system? Although the system cannot provide answers, once a question is posed, it *can* provide base-line information and a starting point. Federal agencies would find this system valuable in developing land management plans on areas designated as grizzly bear habitat. Summaries of grizzly bear information would be very useful from specific areas that require dynamic trail and human-use management or have pending timber sales, special use and grazing permits, exploration and development plans for energy reserves, and recreational and industrial construction and maintenance activities — to name just a few. State agencies and private citizens who are recipients of federal funds also find that they are legally responsible to uphold the intent of the Endangered Species Act. Specifically, utility siting leases and subdivision approval are involved. Known grizzly bear seasonal use and traditional travel corridors within an area must be considered in such developments, and in these instances the computer system could supply the requisite information. Management of and research on the grizzly bear itself might be facilitated if this system were utilized.

In addition to the base data bank and the narrative file, separate computer files are also being developed for specialized purposes such as storing telemetry information, den site information, and capture data. For even broader application, the system could easily be adapted to accommodate storage of data on other animal species. All files could utilize the codes already developed for the base data bank. It is hoped that this project can be coordinated with agencies having similar systems or similar needs, and to direct further development to answer as many needs as possible. To realize the system's full capabilities, mutual contributions of information to the data bank and cooperative use of the system are vital. Fully supported and used, the system will help us maintain and use reports of grizzly bears for wise management of this threatened species and its remaining habitat.

BIOCHEMICAL VARIATION IN THE BLACK BEAR

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Abstract: A total of 35 presumably distinct biochemical loci were analyzed in black bears (*Ursus americanus*) from Alaska, California, Maine, Montana, Tennessee, and Virginia by using starch-gel electrophoresis. Limited spatial subdivision of gene frequency was observed in Tennessee. Overall heterozygosity levels are lower in black bears than would generally be expected for mammalian species. Levels of interpopulation genetic similarity are extremely high for a species with such wide distribution, in contrast to the observed morphological variation.

Recent efforts have been made to evaluate the potential and encourage the use of information on the genetic structure of wildlife populations (Berry 1971, Morgan et al. 1974, Smith et al. 1976). Gene frequencies change through time and space (Krebs et al. 1973, Redfield 1973, Utter et al. 1974, Berry and Peters 1976, Manlove et al. 1976) and these changes may be functionally associated with demographic changes (Smith et al. 1976). Levels of genetic variability need to be assayed to evaluate the potential use of genetic data in the formulation of a comprehensive management program. Our objective is to document levels of biochemical variability in the black bear from various populations throughout its range.

Certain ecological and historical factors affect levels of biochemical variation (Selander 1976, Soulé 1976) and confound the interpretation but not necessarily the application of genetic data. Low levels of biochemical variation could be due to drift or founder effect, but both of these factors imply small population numbers at some time in the past. For example, Bonnell and Selander (1974) have explained low biochemical variability in northern elephant seals (*Mirounga angustirostris*) by suggesting a bottleneck effect of reduced numbers resulting from their interactions with humans. Although this argument is certainly tenable, the ecological effects of low environmental variability on a large animal with high vagility might also explain the reduced variation. Animals with a large body size, great mobility, and a high level of homestatic control may be expected to exhibit low levels of genetic variability (Selander and Kaufman 1973). For a population experiencing the environment as fine-grained (i.e., apparently homogeneous), the optimum evolutionary strategy will often be a single phenotype adapted to the conditions in the environment that are most frequently encountered (Levins 1968). Valentine (1976) has predicted the occurrence of relatively low genetic variability in large migratory carnivores of the temperate zone since, by perceiving the environment as relatively fine-grained, they should have alleles whose products function under a variety of conditions.

Studies of biochemical variability in mammal populations have emphasized small mammal species, and few studies exist for large carnivores. Larsen (personal communication) found no evidence of genetic variation in polar bears (*Ursus maritimus*), and Yang (personal communication) found low levels of variation in brown bears (*U. arctos*). Because of the potential use of protein polymorphisms for population studies and the lack of adequate data to verify theoretical generalizations, the assessment of genetic variation in large wildlife species such as black bears is of particular interest.

The laboratory aspects of this research were supported in part by contract (AT 38-1-819) between the U.S. Energy Research and Development Administration and the University of Georgia. S. Yang, Museum of Vertebrate Zoology, University of California at Berkeley, graciously provided the supplementary data from California. D. Beeman, Graduate Program in Ecology, University of Tennessee, assisted in sample preparation. We particularly appreciate the cooperation of R. Hugie, Maine Department of Inland Fisheries and Wildlife, University of Main; C. Jonkel, School of Forestry, University of Montana; R. Modafferi, Alaska State Department of Fish and Game, Anchorage; and J. Raybourne, Staunton, Virginia, who took time and effort from the course of their own research to provide samples for this study.

METHODS

The black bears included in this survey were from populations in 6 states and represented diverse habitats across the species range. Blood samples were collected by investigators conducting research on bears in Alaska (Prince William Sound), California (Yosemite National Park), Maine, Montana, Tennessee (Great Smoky Mountains National Park), and Virginia.

Whole blood was collected from bears in the field and separated into red cell and plasma components by centrifugation. Except for the samples from California, these tissues were sent to the Savannah River Ecology Laboratory, where they were frozen and stored at −70 C until analysis. The California collection was comprised of relatively fresh samples including liver and kidney tissue, which were analyzed in the laboratory of S. Yang at the University of California at Berkeley. Plasma and hemolysate were electrophoretically analyzed for bears from California, Montana, and Tennessee; only plasma was analyzed for bears from Alaska, Maine, and Virginia.

Samples were subjected to horizontal starch-gel electrophoresis and protein banding patterns resolved with standard histochemical staining methods as described by Selander et al. (1971) and Manlove et al. (1976). Numbers of enzymatic and general proteins that were successfully resolved varied among populations and among samples within populations, depending on the kind (hemolysate or plasma) and condition of material available. These proteins are listed in Table 1 along with buffer systems used during electrophoresis. Sixteen additional proteins not listed in Table 1 were resolved from the California samples. These include adenosine deaminase, alcohol dehydrogenase, esterase-3, globulin, aspartate amino transferase-1 and -2, α-glycerophosphate dehydrogenase, gluconate dehyd-

Table 1. Summary of electrophoretic data for proteins assayed from plasma and hemolysate in black bears. The proportion of individuals in a population heterozygous at a given locus is given in parentheses for polymorphic loci. The proportion of loci that are polymorphic and average heterozygosity per individual are given at the end of the table for each population.

			Number of alleles and heterozygosity(h)					
Proteins or enzymes	Tissue	Buffers[a]	Alaska N=12	Calif. N=52	Maine N=26	Mont. N=35	Tenn. N=64	Va. N=44
Albumin (ALB)	Plasma	Lithium hydroxide (LiOH)	1	1	1	1	1	1
Esterase-1 (ES-1)	Plasma	LiOH	1	1	-	1	1	1
Estherase-2 (ES-2)	Plasma	LiOH	1	2 (0.273)	-	-	-	1
Esterase-3 (ES-3)	Hemolysate	Tris-maleate (Tm)	-	1	-	1	1	-
Tetrazolium oxidase-1 (TO-1)	Hemolysate	Tris-hydrochloric acid (T-HCl)	-	1	-	-	-	-
Tetrazolium oxidase-2 (TO-2)	Hemolysate	T-HCl	1	2 (0.214)	-	1	1	1
Lactate dehydrogenase-1 (LDH-1)	Hemolysate	T-HCl	-	1	-	1	1	-
Lactate dehydrogenase-2 (LDH-2)	Hemolysate	T-HCl	-	1	-	1	2 (0.206)	-
Malate dehydrogenase-1 (MDH-1)	Hemolysate	Tm	-	1	-	1	1	-
Malate dehydrogenase-2 (MDH-2)	Hemolysate	Tm	-	1	-	1	1	-
Malic enzyme (ME)	Hemolysate	Tm + NADP	-	-	-	1	-	-
6-phosphogluconate dehydrogenase (6-PGD)	Hemolysate	Tm + NADP	-	1	-	1	2 (0.016)	-
Phosphoglucomutase-1 (PGM-1)	Hemolysate	LiOH	-	1	-	-	-	-
Phosphoglucomutase-2 (PGM-2)	Hemolysate	LiOH	-	1	-	1	1	-
Glucose phosphate isomerase (GPI)	Hemolysate	LiOH	-	2 (0.045)	1 (0.156)	2	1	1
Peptidase-1 (PEPT-1)[b]	Hemolysate	Tm	-	1	-	-	1	-
Peptidase-2 (PEPT-2)[b]	Hemolysate	Tm	-	1	-	-	1	-
Plasma protein B (PPB)[c]	Plasma	LiOH	1	-	1	1	1	1
Transferrin (TF)	Plasma	LiOH	1	1	1	1	1	1
Number of loci			6	17 (33)[d]	4	14	15	6
Percentage of polymorphic loci (P)			-	0.176 (0.121)[d]	-	0.077	0.133	-
Mean individual heterozygosity ($\overline{H}$)			-	0.031 (0.016)[d]	-	0.013	0.015	-

[a] See Selander et al. (1971) or Manlove et al. (1976) for recipes (except peptidase) and pH values for buffers; NADP = nicotinamide adenine dinucleotide phosphate.

[b] Stain recipe: 30 mg L-leucyl-L-alanine, 10 mg *Bothrops* snake venom, 20 mg peroxidase, and 10 mg o-dianisidine di-HCl in 50 ml 0.2 M tris-hydrochloric acid buffer (pH=8.0).

[c] May be identical to PT-1 for California samples listed in the text.

[d] Includes 16 additional proteins surveyed in California samples as listed in the text.

rogenase, hemoglobin, isocitrate dehydrogenase-1 and -2, leucine amino peptidase-1 and -2, mannose phosphate isomerase, protein-1, and sorbitol dehydrogenase.

The proportion of polymorphic loci (P) and average heterozygosity per individual ($\overline{H}$) in a population were calculated for bears from Montana, Tennessee, and California by using the data for proteins listed in Table 1. Comparisons were made of populations from all localities (excluding California) to verify allelic identity across populations. The term *population* as used above refers to all samples from an area or state and is not necessarily meant to be definitive of a biologically functional population. In designating allelic differences for polymorphic loci, superscripts "*a*" and "*b*" indicate the relative migration distances of the phenotypes associated with each allele; "*a*" is the faster-migrating or more electronegative form.

RESULTS

The proportion of polymorphic loci (P) and the average individual heterozygosity ($\overline{H}$) values are given at the end of Table 1. Of the 19 proteins listed in Table 1, 6 were polymorphic, each exhibiting 2 electrophoretic alleles. Although bears from California and Tennessee were polymorphic at more than 1 locus, only 1 locus (GPI) was polymorphic in more than 1 population.

Identical mobilities were observed across populations for all loci fixed for a single allele and when polymorphism occurred, the common allele was the same as that fixed in other populations. For example, LDH-2 had 2 alleles in the Tennessee population (Table 1). The common allele, *Ldh*-2^b was 0.18. The *Ldh*-2^a allele was fixed in the Montana population.

Gene frequencies for the other 5 polymorphic loci were *ES*-2^a and -2^b, 0.45 and 0.55, respectively (California); *To*-2^a and -2^b, 0.32 and 0.68 (California); *Gpi*^{a} and *Gpi*^{b}, 0.02 and 0.98 (California), 0.11 and 0.89 (Montana); 6-*Pgd*^{a} and 6-*Pgd*^{b}, 0.01 and 0.99 (Tennessee). Heterozygosity values for these loci are also given in Table 1. Of the additional 16 proteins surveyed in California bears, 1 (protein-1) was polymorphic, having 2 alleles, *Pt*-1^a and *Pt*-1^b, with frequencies of 0.11 and 0.89, respectively.

The number and distribution of samples from the Great Smoky Mountains National Park permitted an analysis of genetic subdivision among these bears. Allele frequencies at the LDH-2 locus in bears from 6 sample areas (3 separate watersheds) were significantly different among areas ($X^2 = 20.91, P < 0.05$). Part of this subdivision was due to a high frequency (0.47) of the *Ldh*-2^b allele (including 5 homozygotes) in the Rabbit Creek area. This allele is relatively rare elsewhere and its possible association with a family unit along Rabbit Creek is supported by data from activity monitoring and field observations.

DISCUSSION

From the standpoint of using protein polymorphisms as genetic markers on a broad scale to supplement demographic studies of black bear populations, the prospects are not particularly encouraging. There are, however, a few isolated polymorphisms that could be useful for obtaining indices of genetic subdivision and inbreeding and for following patterns of dispersal and gene flow among populations. The localized distribution of the *Ldh*-2^b allele among bears in the Smoky Mountains provides a rough index to genetic subdivision of the population(s).

Where allelic variants are spatially concentrated, an opportunity exists to incorporate an index of gene flow into other measures of dispersal. Such information could be very useful for interpreting results from population studies of many wildlife species, including bears. Knowledge of the extent of spatial genetic subdivision among populations may be of value in defining management units (Manlove et al. 1977). Spatial subdivision and short-term genetic changes in time are documented for populations of a variety of species (Smith et al. 1976), and the dynamic nature of the genetic structure of wildlife populations should be an important concern in developing management strategies.

Evaluations of results of P and $\overline{H}$ values from Yosemite bears (Table 1) implies that both of these estimates for the Montana and Tennessee populations would be lower if based on more protein systems. However, these values are lower than those generally observed in mainland populations of other mammals. $\overline{H}$ values for 200 mainland populations of 47 mammal species given by Smith et al. (1978) range from 0 to 0.155 ($\bar{x} = 0.042$). $\overline{H}$ values below 0.02 are primarily restricted to species with relatively local distribution or to island populations. Levels of genetic variability in bear populations are toward the lower end of the range for mammals. Since estimates of variability are currently available for only a few large mammals, the significance of low levels of protein polymorphism in black bears remains speculative. Valentine (1976) has suggested that food resource specialists should maintain relatively low levels of genetic variability. As food generalists, bears do not support this speculation. Unpublished data for populations of elk (*Cervus canadensis*) from Montana and caribou (*Rangifer tarandus*) from Alaska, along with the previously cited studies of bears and elephant seals, conform to Selander and Kaufman's (1973) prediction that large, mobile animals tend to have lower levels of genetic variability than small, less mobile animals. In apparent contrast to this generality, however, are white-tailed deer (*Odocoileus virginianus*), with $\bar{H}$ values exceeding 12 percent in some populations (Smith et al. 1976), which are among the highest values observed in mammals. Even if body size and mobility affect levels of genetic variation, the relationship is certainly confounded by other environmental and demographic effects. Since fluctuations in number can have a measurable effect on genetic variation (Soulé), an adequate explanation of this measure cannot ignore some account of the population's recent history. It is apparent from laboratory and field studies of small mammals that levels of genetic variability are directly related to absolute densities and reproductive success (Smith et al. 1975). This relationship could have profound implications for managing wildlife populations when genetics data can be systematically incorporated into demographic studies.

Since comparisons on the same gels were not made of Yosemite bears with other populations, their allelic identity to the other populations is not certain. We expect, however, that most if not all loci in the sample would be fixed for alleles common in the other populations across a large geographic area. Electrophoretically detectable genetic uniformity across the black bear's range is greater than that generally found in small mammals. Biochemical similarity among black bear populations also appears to contrast with observed phenotype variation in morphology across the species range (e.g., variation in body size and coat color). We must recognize the fact that broad-scale generalizations of the causes and consequences of genetic variation are inadequate to explain either the subtle differences in genetic structure among populations or the trends observed in major taxonomic or trophic groups without concurrent knowledge of local environmental, demographic, and historical effects.

This study of black bears should be considered preliminary. With increasing concern for managing optimum bear densities in refuges with limited suitable habitat, some knowledge of the genetic consequences of manipulating habitat quality, population structure, and densities may be important for planning and evaluating the success of a management program. Also, although much data have been accumulated to describe individual movement patterns in populations of many wildlife species, including black bears, we know very little about the extent of effective dispersal (i.e., gene flow) in and among populations. The use of electrophoretic protein variants as genetic markers to complement data on movement and breeding behavior provides an excellent way of beginning to deal with this problem. Future studies of biochemical variation in black bears should attempt to increase the sample size of the populations surveyed and should focus on detectable polymorphisms and genetic indices that will provide data on changes in genetic structure in time and space to supplement concurrent studies of activity patterns, demography, and breeding structure.

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FURTHER EVIDENCE FOR HIBERNATION OF BEARS

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Abstract: Typical mammalian hibernators overwinter with low metabolism (0.01 normal), heart rate (7 bpm), and body temperature (5 C). There is some evidence that bears hibernate like typical small (50-500 g) mammalian hibernators. It is known that bears remain in winter dens for 4-7 months with very little movement and without food, water, urination, or defecation; they show a large reduction in heart rate and a small reduction in core temperature. To gain further evidence, we compared the unique EKG of typical hibernators with the EKG of bears with respect to season, activity, and dormancy. In this study, the EKG of 3 species of bears and of *Marmota* hibernators was recorded by implanted radio-capsule while they were in winter dens. The EKG of awake typical small hibernators is characterized by a reduced relaxation (QT) interval. It was determined that the 3 species of bears, when awake, also have a reduced relaxation interval (bears 0.14-0.23 second; marmota-species 0.07-0.14 second; man 0.39 second). This finding was interpreted as further evidence that bears are hibernators. Additional findings were that (1) the faster the heart rate of hibernators, the shorter is the relaxation interval; and (2) at a constant heart rate, the relaxation interval of both bears and typical hibernators when nondormant, changes from winter to summer.

In the previous symposia on the biology of bears, we presented evidence that 3 species of bears undergo a form of dormancy that in several respects is more profound than the dormancy of typical, classical hibernators such as woodchucks (*Marmota monax*) (Folk 1967, 1968; Folk et al. 1970, 1972, 1976). These 3 species of bears (black, *Ursus americanus;* grizzly, *U. arctos;* polar, *U. maritimus*) are independent of food and water and do not defecate or urinate for 3-5 months, and probably as long as 7 months in northern Alaska. These observations were confirmed by Nelson et al. (1973) and Craighead et al. (1976). The body temperature of bears does not drop in dormancy to the extent observed in small hibernators. Such a sharp decline would be biologically disadvantageous to bears because several days would be required for their body temperature to rise spontaneously at a time of emergency. However, Craighead et al. (1976) showed a drop from the usual core temperature of 37 C to 31.8 C, and Rausch (1961) found a drop to 33.0 C. Other physiological depression also occurs: the cardiovascular function of all 3 species of bears changes slowly over a period of approximately 1 month in the fall; their sleeping heart rate in summer ranges from 40 to 50 beats per minute (bpm); yet in dormancy during extreme weather, they frequently have a heart rate as low as 8-10 bpm. These findings have been detailed in the preceding 5 references from our laboratory.

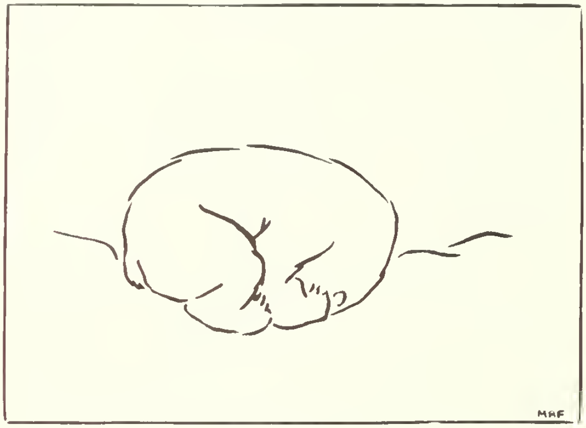

Fig. 1. Drawing of a hibernating black bear observed intermittently during its dormancy period of several months.

During winter dormancy, some bears have been observed to assume the dormancy position of small hibernators. The body is rolled into a tight ball with nose near tail and forehead pressed against the ground. We frequently observed one black bear in this position when he was maintained at an air temperature of −1 C for an entire winter (Fig. 1). He sometimes raised his head but was not observed to leave his nest in the corner of the cage all winter. If this behavior is the rule, we must ask why muscles do not become cramped and bones do not show degenerative osteoporosis.

In one biochemical characteristic — high serum magnesium during dormancy — the black bear, at least, is like typical hibernators. High serum magnesium is not found in non-hibernator mammals when they sleep nor under any circumstances when in health.

In this paper, we consider the relaxation interval of the EKG as a taxonomic clue to a common physiological characteristic, to determine whether the behavior of the hearts of bears (when not in winter dens) was more like that of man or like that of the classic hibernators. Each heartbeat is composed electrically of 3 spikes referred to as *P*, *R*, and *T* waves (Fig. 2). Hibernators are known to have a very short interval between the second spike (R wave) and the third spike (T wave) (Dawe and Morrison 1955). The T wave represents the relaxation of the heart and the preceding 2 waves (P and R) represent contrac-

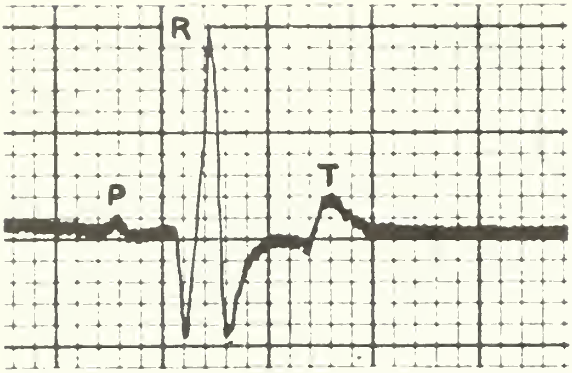

Fig. 2. A single heartbeat of a polar bear, recorded by radiotelemetry. Note the three spikes referred to as P, R, and T.

tion, and therefore we say that the relaxation interval of hibernators is relatively fast.

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METHODS

Three species of bears were given winter dens at the Naval Arctic Research Laboratory (Point Barrow, Alaska) or at the River Laboratory of the Arctic Aeromedical Laboratory (Fairbanks, Alaska). Small physiological radio-capsules were implanted in the abdominal cavities of these bears by methods described in earlier papers (Folk 1964, Shook and Folk 1965, Folk and Copping 1973). The method of recording was described in the same publications. Specifically, recording paper was turned on for 30 seconds every 30 minutes for periods sometimes lasting for 2 months. Signals from the radio-capsules were recorded by heat stylus. On occasion, the record was unsatisfactory because of electrical noise from the atmosphere or the ground, but on most occasions, heart rates at least could be easily read. On about 25 percent of the records, the complete EKG, or at least the R and T wave, could be read. The short interval between the R and the T waves, mentioned above, is referred to as the *QT interval;* the term *relaxation interval,* although used, is an oversimplification, because a small part of the contraction of the ventricle is actually included within this interval.

We used the same radio-capsules and the same technique to study 6 marmots (*Marmota caligata*) and 1 woodchuck. Because these species are in the same genus, we refer to them collectively as *marmota-species*. The woodchuck was in a natural burrow (Folk 1976). Comparisons between non-hibernators and hibernators would best be made with human subjects since many thousands of measurements of QT intervals have been made on human subjects and the values are to be found in numerous citations concerned with the EKG.

A standardized procedure was used for measuring each interval: 10 QT intervals were always measured. If there were only 10 bpm, all QT intervals were measured. If there were 20 bpm, every other heartbeat was used. If the heartbeat was rapid, with a rate as high as 100 bpm, only the first half of the record was used (50 beats), the middle 20 beats were selected from these 50, and every other beat was measured. Breathing has an effect upon heart rate, but we believe that this effect was randomly distributed through our sample by the standardized procedure used.

Our comparisons among animals were made with absolute values of the QT interval usually at the same heart rate, or at the comparable sleeping heart rate, of the species. Use of a ratio of QT interval to the total interval between heartbeats proved unsatisfactory because the QT interval is relatively constant and only varies systematically and slightly with a change of heart rate, but the total interval between heartbeats is extremely variable, due partly to respiration.

Clearly readable records were obtained from 1 polar bear in summer and winter, 1 black bear in summer and winter, 1 additional black bear in winter, and 2 grizzly bears in summer and winter.

RESULTS

To compare relaxation intervals of non-hibernators with those of hibernators, one must determine whether there are differences in the relaxation interval (1) among man (A), bears (B), and marmota-species (C) during summer sleep; (2) among these species during summer activity (D, E, F); (3) between summer sleep and summer activity within each species; (4) between summer sleep and winter sleep (H, I) within each species; (5) between summer and winter activity (J, K) within each species; and (6) between winter sleep and hibernation (L, M) within each species.

These same questions are expressed in tabular form as:

	Summer sleep	Summer activity	Winter sleep	Winter activity	Hibernation
Man	A	D	--	--	--
Bears	B	E	H	J	L
Marmota-species	C	F	I	K	M

We compared: (1) A, B, and C (Table 1);
(2) D, E, and F (Table 2);

(3) A with D, B-E, C-F (Table 2);
(4) B with H, C-I (Table 3);
(5) E with J, F-K (Table 4); and
(6) H with L, I-M (Table 1).

In round figures, the relaxation interval in summer sleep of man is about 0.4 second, that of the grizzly bear about 0.2 second, and those of the polar bear, the woodchuck, and the marmot are about 0.1 second (Table 1).

Table 1. Mean QT intervals ± SE for summer sleeping and winter hibernation heart rates. Recorded by implanted radio-capsules.

		Summer sleep		Winter hibernation	
Species	*N*	QT interval (seconds)	Heart rate (bpm)	QT interval (seconds)	Heart rate (bpm)
Man	7	0.39±0.03	54	-	-
Grizzly bear	2	0.226±0.057	46±2	0.474±0.111	19±7
Black bear	2	-	-	0.448±0.033	22±4
Polar bear	1	0.141±0.003	48	-	-
Woodchuck	1	0.065±0.005	92	0.163±0.005	10
Mamot	6	0.144±0.031	90±8	0.170±0.015	12

Evidently the EKG patterns of bears and marmota-species are similar during summer sleep. This similarity holds during activity in summer (Table 2).

Table 2. Mean QT intervals ± SE for summer sleeping and summer active heart rates. Recorded by implanted radio-capsules.

		Summer sleep		Summer active	
Species	*N*	QT interval (seconds)	Heart rate (bpm)	QT interval (seconds)	Heart rate (bpm)
Man	7	0.39±0.03	54	0.33	90
Grizzly bear	2	0.226±0.057	46±2	0.204±0.036	90
Black bear	2	-	-	0.205±0.012	94
Polar bear	1	0.141±0.003	48	0.132±0.012	92
Woodchuck	1	0.065±0.005	92	0.057±0.005	150
Marmot	6	0.144±0.031	92±6	0.132±0.028	152±4

We next considered the question of winter activity; much of the time in winter, both bears and marmota-species are alert and normothermic, between bouts of hibernation. We found that when these animals were not dormant, the relaxation interval within species was longer in winter at the same sleeping (not hibernating) heart rate than in summer (Table 3). This finding prompted us to compare heart rates of bears and marmota-species during summer activity with rates during winter activity (Table 4). There was an increase of approximately 43 percent in the relaxation interval at a high heart rate of winter over summer. This increase is especially evident in a graphic analysis (Fig. 3); the graph of summer heart rates is significantly different for both woodchuck and arctic marmot. The results for bears are not quite as striking (Fig. 4); for grizzly bear no. I, the relaxation intervals were very different at low and high heart rates. For grizzly bear no. II, in one of the

Table 3. Mean QT intervals ± SE and low heart rates during sleep in two seasons at the same heart rates. Recorded by implanted radio-capsules.

Species	*N*	Summer sleep QT interval (seconds)	Low heart rates (bpm)	Winter QT intervals (seconds)
Grizzly bear	2	0.226±0.057	40±10	0.340±0.006
Black bear	2	-	39±5	0.329±0.015
Polar bear	1	0.141±0.003	48	0.351±0.024
Woodchuck	1	0.065±0.005	90	0.084±0.007
Marmot	6	0.144±0.031	90±10	0.174±0.058

Table 4. Mean QT intervals ± SE and high heart rates during activity in two seasons at the same heart rates. Recorded by implanted radio-capsules.

Species	*N*	Summer active QT interval (seconds)	High heart rates (bpm)	Winter active QT interval (seconds)
Grizzly bear	2	0.204±0.036	80±4	0.304±0.031
Black bear	2	0.205±0.012	72	0.278±0.013
Polar bear	1	0.132±0.012	92	0.153±0.013
Woodchuck	1	0.057±0.005	150	0.078±0.006
Marmot	6	0.132±0.028	150±10	0.136±0.029

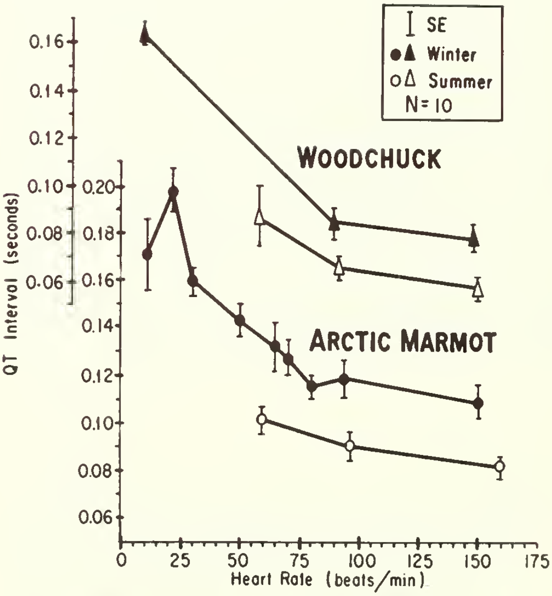

Fig. 3. QT intervals at different heart rates of 2 marmota-species (2 woodchuck, 1 marmot) in winter and summer. Heart rates lower than 30 bpm represent hibernation. Each point represents a mean of 10 heartbeats.

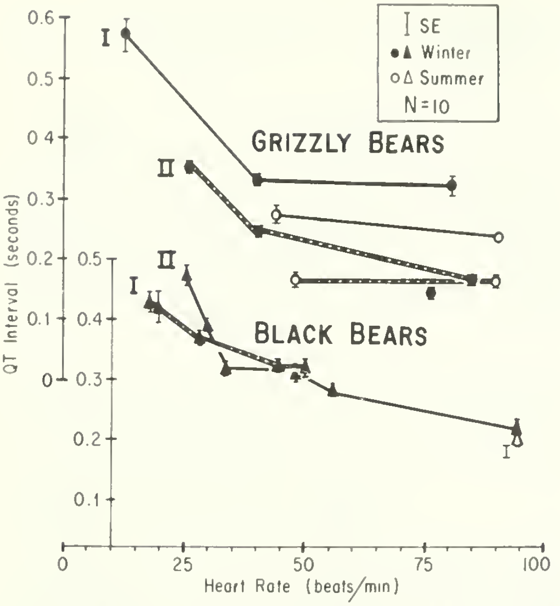

Fig. 4. QT intervals at different heart rates of 2 species of bears (2 grizzly, 2 black) in winter and summer. Heart rates lower than 40 bpm represent hibernation. Each point represents a mean of 10 heartbeats.

two cases the relaxation interval was different. Information for the black bears was inadequate to determine this point.

Disregarding the effect of summer and winter, the slope in Figs. 3 and 4 also demonstrates that the relaxation interval shortens with higher heart rates, as shown in Table 2. The graphs are best interpreted for marmota-species by considering only the heartbeats higher than 25 bpm (non-hibernating), and for bears, heartbeats above 40 bpm. For example, there was a 9 percent drop in the relaxation interval for the marmot when, in summer, its heart rate increased from 92 bpm to 152 bpm (Tabel 3). The heart is very cold during hibernation and so the relaxation interval is lengthened during that period (Table 1).

DISCUSSION

During summer sleep, the relaxation interval of bears (0.18 second) was about one-half that of man (0.39 second) and was approximately the same as that of marmota-species (0.11 second). Thus, this aspect of the physiology of bears is in accord with the more common types of hibernators.

An unexpected finding was that in both bears and marmota-species, the heart behaves very differently in winter even when the animal is not in hibernation. There is a conspicuous shortening of the relaxation interval in summer or a lenthening in winter. Another phenomenon is that in both bears and marmota-species, there is approximately a 45 percent change in the relaxation interval as these animals become more active and have an increased heart rate. Finally, it should be pointed out that the relaxation interval is prolonged in the cold heart during hibernation.

To summarize, Folk et al. (1976) suggested that bears could be considered better hibernators than the classic, small hibernators because only the bears are independent of food, water, defecation, and urination for many months. Comparisons of cardiac function, presented here, also place bears with hibernators. We conclude that we need no longer hesitate over such terms as "winter denning," "winter dormancy," "winter sleep," or "winter lethargy." After 10 years of experience with bears in winter dens, two groups of investigators (not only in our laboratory but also in that of R. Nelson at the Mayo Clinic) have agreed that bears assume a physiological state in winter that is best designated as "hibernation."

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SEX, AGE, AND SEASONAL DIFFERENCES IN THE BLOOD PROFILE OF BLACK BEARS CAPTURED IN NORTHEASTERN PENNSYLVANIA[1]

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Abstract: Sixty-six blood samples were collected from 44 livetrapped black bears (*Ursus americanus*) for 23 blood chemistry and hematology determinations. Statistical factorial experiments for analysis of variance revealed significant ($P < 0.25$) individual variability for 19 of 23 blood characteristics. Male bears had significantly ($P < 0.05$) higher serum calcium, mean corpuscular hemoglobin (MCH), and mean corpuscular hemoglobin concentrations (MCHC) than females. Cholesterol and MCH increased significantly with age; total protein and globulin were both significantly higher in adults than in yearlings or cubs, and total bilirubin in cubs and yearlings was significantly higher than in adults. Predenning samples (1 July-31 December) had significantly higher glucose, packed cell volume (PCV), and mean corpuscular volume (MCV) but lower MCHC than postdenning (1 January-30 June) samples. Leukocyte differentials were comparable to findings by others. Of 48 serum samples submitted for brucellosis and 1 suspicious and 1 positive reaction were observed for leptospirosis; a female cub had 50 percent or more cell agglutination at a 1:1,600 dilution for *Leptospira pomona*. Examination of approximately 250 blood smears resulted in no observations of blood parasites.

Fundamental to an understanding of the effects of various factors on the health and welfare of a species is the establishment of base-line data for physiological parameters such as blood chemistry and hematology. The potential of blood analysis for determining effects of disease, immobilization, nutrition, stress, habitat quality, and population density on individuals or populations has been demonstrated or suggested for several species (Packer 1968, Franzmann and Thorne 1970, Franzmann 1971, Seal et al. 1972a, Presidente et al. 1973, Seal et al. 1975). Some blood values for black bears have been reported; however, most data have been for captive animals or have involved small sample sizes (Svihla et al. 1955; Jacobs 1957; Youatt and Erickson 1958; King et al. 1960; Erickson and Youatt 1961; Hock 1966; Seal et al. 1967; Brown et al. 1968, 1971; Halikas and Bowers 1972; Halloran and Pearson 1972; Pearson and Halloran 1972; Nelson et al. 1973; Eubanks et al. 1976).

The purpose of the present study was to establish base-line physiological data for continuing black bear research in northeastern Pennsylvania and to investigate possible effects of sex, age, or season on these data.

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METHODS

Wild black bears were captured with trailer-mounted culvert traps (Erickson 1957) and Aldrich foot snares (Bacus 1964). Captured animals were immobilized with M-99 (Etorphine, American Cyanamid Company, Agriculture Division, Princeton, N.J.) (Wallach et al. 1967). Blood samples were obtained from a femoral artery or vein in 3 15-cc clot tubes and 1 10-cc tube containing ethylenediamine tetraacetate (dipotassium) (EDTA) anticoagulant, with a B-D Vacutainer Aspirating Syringe (Becton, Dickinson, and Company, Rutherford, N.J.). Clotted samples were usually centrifuged within 1 hour of collection, with a standard clinical centrifuge for 10 mintues, to obtain the serum.

Blood chemistry and hematology analyses were contracted to Automated Analytical Laboratories, Ventura, California, which provided air mailers and serum vials containing stabilizers for enzymes and glucose. We selected the Multi-26 Health Screening Panel; using this program, each sample (3 cc of serum and 2 cc of whole blood) provided information on 23 blood chemistry and hematology parameters.

Eight thin blood smears for leukocyte differential counts and erythrocyte morphologies were prepared from each whole blood sample, usually within 1 hour of collection. Four smears were mailed to the Animal Diagnostic Laboratory at The Pennsylvania State University for staining with Wright's and Giemsa's stains, and the remainder were stored unstained. Leukocyte differentials were determined by examining a minimum of 200 cells and reporting the results as percentage composition.

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To establish base-line data, we used single samples from each bear to calculate mean, standard error of the means, and maximum-minimum values for each parameter.

To determine possible influences of sex, age, and season, and to obtain an indication of the sensitivity of blood analysis, factorial experiments for analysis of variance were performed on single samples from each bear. Multiple samples from individuals recaptured 1 or more times were included in the analysis if they were collected during the same season and year. Analysis was based on the model

$$Y(IJKL) = S(I) + T(J) + R(K) + ST(IJ) + SR(IK) + TR(JK) + STR(IJK) + B(IJKL) + E$$

where

S = sex,
T = season (1 = predenning, 1 July-31 December, and 2 = postdenning, 1 January-30 June),
R = age (1 = cubs, 2 = yearlings, and 3 = adults and unknowns),
B = individual variability, and
E = random error term.

The model states that the blood parameter being considered, $Y(IJKL)$, is a function of the Ith sex, the Jth season, the Kth age, and the Lth individual.

Multiple samples were first tested for significant ($P < 0.25$) individual variability. If significance was indicated, analysis was based on the above model; if no significance was indicated, analysis was based on the model

$$Y = S + T + R + ST + SR + TR + STR + E.$$

We further tested parameters demonstrating significant ($P < 0.05$) age effects, using the Student-Newman-Keuls' multiple range test to determine differences between age groups.

Arc sine transformations were performed on all percentage and ratio data, including albumin/globulin (A/G) ratios, packed cell volume (PCV), and mean corpuscular hemoglobin concentrations (MCHC), before analysis of variance was performed.

Seasonal categories were selected on the basis of date distribution. No animals were captured during December through February or during July and most of August. The traditional division into 4 seasons was therefore impractical and predenning and postdenning classifications were used.

Blood samples were also taken from 2 captive male black bears, retained at The Pennsylvania State University, for comparison with wild bears.

Although a study of disease in black bears was not a primary consideration of our overall study, the availability of extra sera and blood smears afforded an opportunity to conduct a limited disease study. Frozen sera were submitted to the Animal Diagnostic Laboratory, The Pennsylvania State University, for brucellosis and leptospirosis screening. Sera were screened for brucellosis by plate agglutination card tests. Reagents used in the screening were supplied by the Animal Health Division of the U.S. Department of Agriculture.

Leptospirosis determinations were by plate agglutination using killed *Leptospira* antigens from Fort Dodge Laboratories, Fort Dodge, Iowa. The sera were tested for the following leptospiral species antigens: *pomona, grippotyphosa, hardjo, autumnalis, icterohaemorrhagiae, wolfii, canicola, ballum, australis,* and *hyos*. Sera demonstrating positive or suspicious results were shipped to Veterinary Services Laboratory, Ames, Iowa, for testing by the agglutination lysis method with live antigens.

Blood smears used for leukocyte differential counts were also completely scanned for microfilariae, nematode larvae, and intracellular parasites.

RESULTS AND DISCUSSION

Sixty-six blood samples were obtained from 44 black bears (24 males, 20 females) captured between October 1972 and November 1973 (Table 1). Statistical analysis revealed significant ($P < 0.25$) individual variability for all but 4 parameters, indicating that individual variability is an important factor and should be included in the statistical model (Table 2). Significant ($P < 0.05$) sex, seasonal, and age differences were also observed for several parameters (Table 2).

Sex Differences

Female bears had significantly lower serum calcium, MCH, and MCHC than males (Table 2, Fig. 1). These differences may reflect long-term effects of pregnancy and lactation. The low MCH and MCHC levels indicate that female bears may be suffering from mild anemia that could be due in part to iron deficiency caused by high iron demands during pregnancy and lactation and low dietary replacement. Black bear milk has been reported to contain high levels of iron (Hock and Larson 1966).

Table 1. Base-line blood values obtained from 44 black bears captured in northeastern Pennsylvania.

	Mean	SE of mean (*N*)	Maximum	Minimum
Sodium (mEq/l)	142	<1 (44)	155	131
Potassium (mEq/l)	4.3	0.1 (44)	6.7	3.2
Calcium (mg/100 ml)	9.0	0.1 (44)	10.5	4.4
Inorganic phosphorus (mg/100 ml)	6.3	0.2 (44)	9.0	2.8
Glucose (mg/100 ml)	173	8 (44)	325	95
Urea nitrogen (mg/100 ml)	13	1 (44)	60	2
Uric acid (mg/100 ml)	2.3	0.1 (44)	4.5	1.3
Cholesterol (mg/100 ml)	323	13 (44)	690	170
Total protein (g/100 ml)	7.0	0.1 (44)	8.2	4.0
Albumin (g/100 ml)	2.7	0.1 (42)	3.6	1.4
Globulin (g/100 ml)	4.3	0.1 (42)	5.6	2.4
Albumin/globulin ratio	0.7	<0.1 (42)	0.9	0.3
Total bilirubin (mg/100 ml)	0.2	<0.1 (44)	0.8	0.1
Alkaline phosphatase (IU/l)	69	5 (44)	140	25
Lactic dehydrogenase (IU/l)	787	101 (43)	3,750	330
Serum glutamic oxalacetic transaminase (IU/l)	154	44 (44)	1,650	30
White blood cells $(\mathrm{X}_{10}{}^{3}/_{\mathrm{mm}}{}^{3})$	10.2	0.5 (44)	22.8	6.9
Red blood cells $(\mathrm{X}_{10}{}^{6}/_{\mathrm{mm}}{}^{3})$	8.08	0.1 (44)	9.99	6.51
Hemoglobin (g %)	16.3	0.3 (44)	20.3	13.2
Packed cell volume (%)	48.4	0.8 (44)	61.6	38.6
Mean corpuscular volume (μ^3)	61	<1 (44)	66	56
Mean corpuscular hemoglobin ($\mu\mu$g)	20.2	0.2 (44)	23.3	18.1
Mean corpuscular hemoglobin concentration (%)	33.5	0.2 (44)	37.0	31.0
Nonsegmented neutrophils (%)	1.0	0.3 (44)	10.0	0.0
Segmented neutrophils (%)	77.0	1.4 (44)	94.0	50.0
Lymphocytes (%)	16.0	1.3 (44)	42.5	2.0
Monocytes (%)	3.0	0.2 (44)	7.5	0.5
Eosinophils (%)	2.0	0.4 (44)	1.2	0.0
Basophils (%)	0.0	0.0 (44)	1.0	0.0
Nucleated red blood cells/100 white blood cells	1.0	0.4 (44)	17.5	0.0

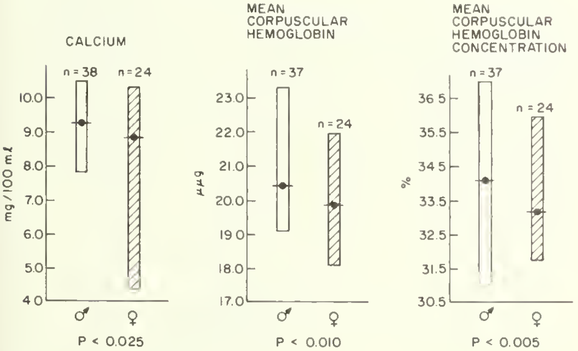

Fig. 1. Means and ranges of blood values that were significantly different between sexes of black bears in northeastern Pennsylvania.

Significantly lower serum calcium levels have also been reported for female black bears in Tennessee (Eubanks et al. 1976) but not for brown bears (*Ursus arctos*) from Yukon Territory, Canada (Halloran and Pearson 1972). Hypocalcemic tendencies in human females during gestation are well recognized (Searcy 1969) and lactating human females may lose 2-3 g of calcium phosphate each day (Guyton 1971). Seasonal variations and lower calcium levels in female white-tailed deer (*Odocoileus virginianus*) have also been attributed to effects of lactation (Sauer 1973). The calcium demand of lactation in bears may be more dramatic because black bear milk contains relatively high levels of calcium (Hock and Larson 1966, Jenness et al. 1972) and the lactation period includes a time of dormancy with no dietary intake of calcium. The probably source of calcium during dormancy is resorption from bone storage areas or reserves. The impact, if any, of this calcium loss on the formation of cemental annuli needs to be evaluated. This evaluation may be particularly necessary in Pennsylvania, where variability in the levels of winter activity has been observed for female bears in differing reproductive conditions (Alt et al. 1979).

If data obtained by Hock and Larson (1966) and Butterworth (1969) hold approximately true for black bears in Pennsylvania, then one can estimate that a dormant female bear nursing 3 cubs (not unusual in Pennsylvania) would lose about 301 g of calcium during the first 12 weeks of cub development. If calcium con-

Table 2. Summary of significance for analysis of variance of blood parameters related to individual variability, sex, season, and age of black bears in northeastern Pennsylvania. Where no values are given, the parameters were not significant ($P < 0.25$ for B, $P < 0.05$ for all other parameters). B = individual variability; S = sex; T = season (predenning 1 July - 31 December and postdenning 1 January - 30 June); R = age (1 for cubs, 2 for yearlings, 3 for adults and unknowns); ST = sex-season interaction; TR = season-age interaction; SR = sex-age interaction; STR = sex-season-age interaction.

Test	Probability less than							
	B	*S*	*T*	*R*	*ST*	*TR*	*SR*	*STR*
Sodium	0.0250							
Potassium	0.2500							
Calcium		0.025						
Inorganic phosphorus	0.0500							
Glucose	0.0250		0.0050				0.025	
Blood urea nitrogen	0.0010							
Uric acid	0.0005							
Cholesterol	0.0050			0.0250				
Total protein	0.0250			0.0010				
Albumin								
Globulin	0.2500			0.0005				
Albumin/globulin ratio								
Total bilirubin	0.0250			0.0500				
Alkaline phosphatase	0.0010							
Lactic dehydrogenase	0.0005							
Serum glutamic oxalacetic transaminase	0.0005							
White blood cells	0.2500							
Red blood cells	0.0500							
Hemoglobin	0.1000							
Packed cell volume	0.0250		0.0250					
Mean corpuscular volume	0.0050		0.0100	0.050				
Mean corpuscular hemoglobin	0.0010	0.010		0.025				
Mean corpuscular hemoglobin concentration		0.005	0.0005			0.025		

centrations presented by Jenness et al. (1972) are used, this value would be 957 g. The human body is reported to contain 22 g of calcium per kg of fat-free body weight; 99 percent of this calcium is stored in bone (Pike and Brown 1975). The average total weight (not fat-free) of female bears 2 years of age or odler in this study was approximately 95 kg (Matula 1976). On the basis of the above estimates and assumptions, it is conceivable that these bears could lose 5-50 percent or more of their total calcium during dormancy. The problem with this estimate is that we have to assume that the calcium storage ability of female black bears approximates that of humans. Nevertheless, the loss may be significant, and therefore the possible calcium and iron deficiencies observed in the present study may have an impact on the dietary requirements and food habits of these animals.

Age Differences

Serum cholesterol increased significantly with age (Table 2, Fig. 2). This increase is similar to responses reported for humans (Searcy 1969) and may be associated with changes in diet. Seal et al. (1975) considered low cholesterol, blood urea nitrogen (BUN), and uric acid in wolf (*Canis lupus*) pups from different years as indicative of diets low in protein and animal flesh.

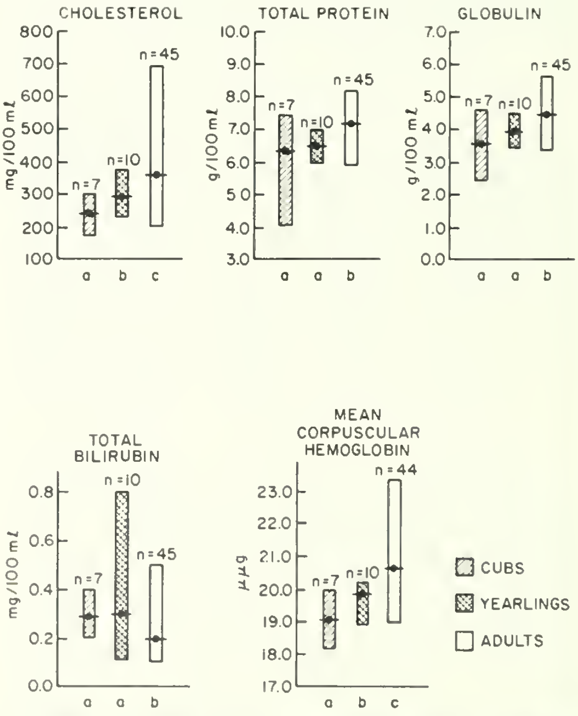

Fig. 2. Means and ranges of blood values that were significantly different among black bears of different ages in northeastern Pennsylvania. Unlike letters indicate significant difference ($P < 0.05$).

Searcy (1969) indicated that an excessive caloric intake without a corresponding increase in energy expenditure or a diet rich in saturated fats would result in increased serum cholesterol levels in humans. It is possible, then, that the increase in black bear cholesterol levels with age might be associated with an increased consumption of high-energy foods and/or animal flesh or may be related to regulatory mechanisms not yet understood.

Total protein and globulin were both significantly higher in adults than in yearlings or cubs (Table 2, Fig. 2). The globulin differences may reflect changes in alpha, beta, gamma, or all fractions due to dietary changes, to development of immunoglobulins, or to a combination of these and other factors (Latner 1975, Henry 1969). However, electrophoretic fractionation of serum proteins was not done, and inferences as to the specific proteins reflecting these differences cannot be made. It should be noted that albumin and globulin values reported here are relative values, due to the dye-binding technique used in the albumin determinations.

Total bilirubin levels in cubs and yearling bears were significantly higher than in adults (Table 2, Fig. 2). Younger animals may be more susceptible to erythrocyte damage or hepatic alterations due to immobilization and handling techniques, or they may demonstrates differences in erythrocyte physiology, rate of red blood cell production and destruction, or hepatic function. The possibility of erythrocyte destruction due to hemolytic, toxic, infective, and/or parasitic factors may also be considered. It is also possible that, although statistical significance is indicated, the differences may be physiologically insignificant.

MCH increased significantly with increasing age of the bears (Table 2, Fig. 2). Similar, although not statistically significant, trends were also noted for MCHC and hemoglobin, which indicates that younger bears may have hypochromic microcytic anemia. Anemia in young bears would be similar to hypochromic anemia observed in human infants and children, which is attributed to iron deficiency due to demands of growth (Wintrobe 1967). The endoparasite and ectoparasite load is also a factor to be considered. Pearson and Halloran (1972) noted that young brown bears had lower red blood cell counts, hematocrits, and hemoglobin concentrations than older animals.

Seasonal Differences

Predenning glucose levels were significantly higher than in postdenning samples (Table 2, Fig. 3). The higher predenning levels may be a function of physiological responses to preparation for denning or to changes in diet and levels of food consumption. Similar spring-to-summer trends have been reported for brown bears (Halloran and Pearson 1972). Erickson and Youatt (1961) noted that some black bears had increasing blood sugar levels during torpor and others had decreasing values.

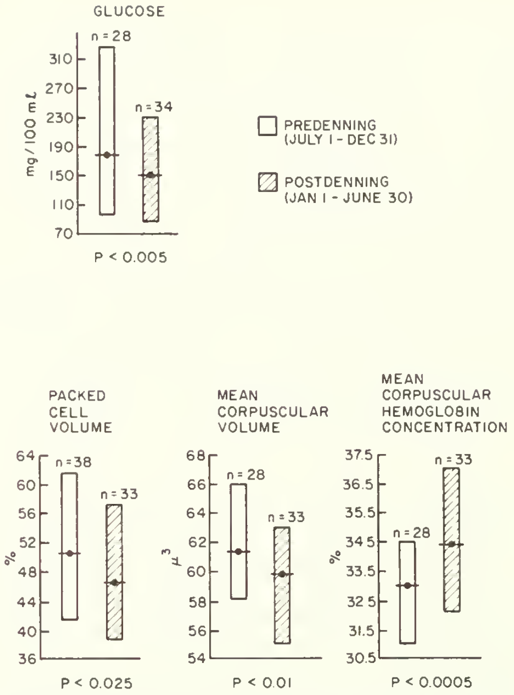

Fig. 3. Means and ranges of blood values that were significantly different between seasons for black bears in northeastern Pennsylvania.

Predenning samples in the present study also demonstrated significantly higher PCVs and MCVs but lower MCHC levels than postdenning samples (Table 2, Fig. 3). Predenning samples also tended to have higher (but not significantly higher) circulating erythrocyte levels. These findings suggest that black bear erythhrocytes increase in size without a corresponding increase in hemoglobin content during the predenning period, which would result in higher PCVs and depressed MCHC levels.

Black bears in general have smaller-sized but greater numbers of circulating red blood cells than do humans (Wintrobe 1967), dogs (*Canis familiaris*) (Schalm et al. 1975), or wolf pups (Seal et al. 1975) (Table 1). This condition appears to be an advantage to a hibernating species because it increases erythrocyte surface area, which in turn provides a more efficient exchange of oxygen and carbon dioxide. However, why would the same species have an increase in MCV before dormancy? The larger erythrocyte size and lower hemoglobin concentration may be a result of increased hematopoietic activity and a release of younger or immature cells into the circulatory system. The release of immature cells into the circulation could be verified by reticulocyte counts. An increase in circulating erythrocytes would not be reflected in the red cell count or PCV if plasma volume proportionally increased. An increase in the total blood volume in black bears between postdenning and predenning would be expected as a result of the large weight gains observed in bears during this period (Matula 1976). Pearson and Halloran (1972) similarly noted an increase in MCV in brown bears between spring and summer, but observed significant decreases in erythrocyte counts and PCVs.

Other Results

Significant interactions were noted for 2 blood parameters: a sex-age interaction for glucose and a season-age interaction for MCHC (Table 2). The sex-age interaction for glucose indicated that male cubs had markedly higher glucose levels than female cubs, but sex differences between yearlings and adults were much less pronounced. The season-age interaction for MCHC demonstrated diverging trends from comparable MCHC values in younger animals to seasonally different MCHC values in adults. Physiological explanations for these 2 trends are difficult to ascertain. We feel that a much larger sample size is needed to verify these results and to help clarify any trends.

Comparisons of blood values from 2 captive bears with those of wild bears indicated that the most important differences were consistently lower levels of glucose, alkaline phosphatase, lactic dehydrogenase (LDH), and serum glutamic oxalacetic transaminase (SGOT) in the captive animals, which probably reflects a lower level of stress and excitability as well as a continuous feeding regimen in captive animals (Matula 1976). The 2 captive bears also had slightly higher MCV and probably normochromic red cells.

Three bears captured with snares each had elevated sodium, total protein, albumin, globulin, red cell count, hemoglobin, and PCV values. An increase in these parameters probably indicates dehydration. They also demonstrated increased levels of glucose, alkaline phosphatase, LDH, SGOT, and a higher white cell count; elevation of these blood parameters is probably associated with increased stress and physical activity. One of the snared bears had previously been captured in a culvert trap, and at that time his blood was judged to be in the normal range (Matula 1976).

Leukocyte differential counts for wild black bears in this study (Table 1) were generally comparable to those reported in other studies (Musacchia et al. 1955, Jacobs 1957, King et al. 1960, Pearson and Halloran 1972). Statistical analyses for sex, season, and age differences were not completed due to the complexity of the analyses, which was compounded by the possibility of large sample-size errors (Davidsohn and Nelson 1969). The data were described, however, according to age, sex, and season to reveal any possible trends. The differentials appeared to be fairly stable for sex and season but cubs may tend to have higher neutrophil and lower lymphocyte levels than older bears (Matula 1976).

Of 48 serum samples submitted for brucellosis and leptospirosis determinations, all were negative for brucellosis; 1 suspicious and 1 positive reaction were observed for leptospirosis. Sera from a 2-year-old female obtained on 2 separate occasions (14 May and 5 June 1973) demonstrated 50 percent or more cell agglutination for dilutions of 1:400 and 1:200, respectively, for *Leptospira pomona* and a possible cross-reaction of 1:200 and 1:100, respectively, for *L. autumnalis*.

Sera from a female cub agglutinated at 1:1,600 dilution for *L. pomona*, 1:400 dilution for *L. icterohaemorrhagiae*, and 1:200 dilution for *L. autumnalis*. Reactions for *L. icterohaemorrhagiae* and *L. autumnalis* are probably results of cross-reaction.

Caution must be employed when interpreting these results because an absolute diagnosis of leptospirosis can be made only if *Leptospira* has been isolated from specimens of the infected host (NADL 205 Form (Revised May 1973), Veternary Services Laboratory, Ames, Iowa). However, blood from the female cub had the lowest MCH and SGOT levels recorded in this study and also had a low MCHC and a slightly increased total bilirubin value. Icterus and anemia are 2 common clinical signs observed in leptospirosis when clinical manifestations are present (Roth 1970). Because the bear was so young, it is tempting to speculate that she was actively infected at the time of sampling.

Examination of approximately 250 blood smears resulted in no observations of blood parasites. Apparently, black bears in northeastern Pennsylvania are relatively free of blood parasites within the limits of our techniques for detecting them. These results are difficult to explain in light of results reported by King et al. (1960) for bears in New York.

Care must be exercised when evaluating blood measurements, for many factors can influence the results. For example, feeding time and quantity and quality of food ingested before blood is sampled can affect blood chemistries in monogastric animals. It is for this reason that human subjects fast for 12 hours before blood profiles are done. Other important factors include capture, handling, and immobilization methods (Franzmann and Thorne 1970, Franzmann 1971, Seal et al. 1972b); the length of time the animal spent in the trap; excitability of the animal (Geraci and Medway 1973); weather conditions; physical condition of the animal; blood collection, handling, storage, and analysis techniques (Wintrobe 1967, Lampasso 1968, Cohen 1969; Davidsohn and Henry 1969, Searcy 1969, Medway and Geraci 1972, Geraci and Medway 1973, Geraci and Engelhardt 1974); and general nutritional status of the animal (Seal et al. 1972a). All of these factors, and others, may influence 1 or several physiological parameters and therefore should be noted and, where possible, standardized.

Another important consideration involves the use of automated blood analyzers for hematology determinations. Some models measure red blood cell counts, hemoglobin, and MCV values and then calculate the PCV, MCH, and MCHC from these values. The analyzer used in this study was the Coulter Counter Model S, Coulter Electronics Inc., Hialeah, Florida. This analyzer had a present red cell size threshold of 30 μ^3, and smaller cells are not counted or averaged into the MCV calculation (personal communication with Coulter consultants). The relatively low mean MCV of 61 μ^3 for bears in this study indicates that an appreciable number ot red cells may have been below the 30-μ^3 threshold. If so, then MCV values reported in this study may be inflated and red cell counts may be underestimated.

Although means and standard error of the means presented in Table 1 may be considered as "normals" for black bears in northeastern Pennsylvania, they are not conclusive. Adequate midwinter and midsummer samples are needed to provide a better understanding of seasonal changes and, in general, larger samples sizes are needed for better representation of all age- and sex-classes. Also, most of the sampling reported here occurred during 1 year, which may not have been a "normal" year, as heavy defoliation of the study area by gypsy moth (*Porthetria dispar*) and mast failure during that year may have affected the food habits and behavior of the bears.

Future studies of blood profiles of black bears should be very critical of the techniques to be used in collecting, handling, and analyzing the samples. In particular, the large number of blood parameters demonstrating individual variability in this study (Table 2) suggests that a concerted effort should be made to obtain repetitive samples from the same animal, including multiple samples taken during a single handling. The resulting variability should then be considered when evaluating the data for sex, age, seasonal, or other effects.

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USE OF THE CATALEPTOID ANESTHETIC CI-744 FOR CHEMICAL RESTRAINT OF BLACK BEARS

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Abstract: Warner-Lambert/Parke-Davis and Company have developed a new drug combination known as CI-744 (to be marketed for veterinary use as Tilazol TM). CI-744 is a 1:1 ratio of the phencyclidine hydrochloride (Sernylan) analogue tiletamine hydrochloride and a non-phenothiazine tranquilizer, zolazepam hydrochloride. Field trials of CI-744 in 39 black bears (*Ursus americanus*) showed its effects to be similar to a 1:1 mixture of Sernylan and promazine hydrochloride. However, CI-744 provides the advantages of shorter restraint time, faster recovery, less salivary and respiratory secretion, and ease of use (no supplemental drugs were needed). Based on 25 immobilizations (22 bears) for which complete and accurate data are available, mean values of 4 important parameters were: induction time, 7 minutes; restraint time, 81 minutes; emergence time, 36 minutes; total down time, 117 minutes. Mean dosage rate was 4.1 mg/kg, but the optimum for routine field work is about 4.0 mg/kg.

Field research on large mammals has been greatly facilitated by the development of chemical restraint techniques. However, species differ in their responses to particular drugs and no single drug works well on all species. In field work, the investigator usually desires a drug that is absorbed rapidly after intramuscular injection, provides adequate restraint with a minimum of troublesome side effects, and has a wide margin of safety. In addition, the drug's effects should be reasonably predictable and permit a quick recovery, and the drug itself should be chemically stable over a wide range of temperatures.

Succinylcholine chloride (Anectine, Burroughs Wellcome; Sucostrin, Squibb) has been used alone or in combination with a barbiturate anesthetic in several studies applying chemical restraint to bears (Erickson 1957, Black 1958, Craighead et al. 1960, Stickley 1961, Troyer et al. 1961, Jonkel and Cowan 1971, Rogers et al. 1976). Succinylcholine is a short-acting neuromuscular blocking agent without anesthetic properties. It is difficult to use because dosage is extremely critical and multiple injections may be fatal (Pearson et al. 1968, Hamilton 1974, Rogers et al. 1976). Aqueous solutions are unstable and must be refrigerated. Barbiturates generally are unsatisfactory for field use because of their critical dosages, profound depression of the central nervous system, and the prolonged recovery required.

Some researchers working with bears (Flygar et al. 1967; Larsen 1967, 1971; McCaffrey et al. 1976; Miller and Will 1976) have successfully employed the potent morphine derivative M99 (Etorphine, American Cyanamid). The great advantage of this drug is that its effects can be reversed in a few minutes by the specific antagonists M50-50 or M285 (Diprenorphine or Cyprenorphine, American Cyanamid). However, the effects of M99 are somewhat unpredictable. Underdosed animals may exhibit a brief period of excitation, or may become drowsy and then revive unexpectedly (Miller and Will 1976; G. Kuehn, Los Angeles Zoo, personal communication). High doses depress heart and breathing rates and deep body temperatures (Larsen 1971). M99 is subject to strict regulations in the United States and currently may be sold only to licensed veterinarians.

Beginning in the late 1960s, phencyclidine hydrochloride (Sernylan, originally Parke-Davis, now Bio-Ceutic) has been the chosen drug in a number of bear studies (Lentfer 1968; Craighead et al. 1971, 1976; Kistchinski and Uspenski 1972; Piekielek and Burton 1975; Amstrup and Beecham 1976; Glenn et al. 1976; Pearson 1976). Sernylan is the prototype of a group of compounds that may be characterized as cataleptoid anesthetics. These compounds produce a state of waxy rigidity without complete muscular relaxation. The degree of anesthesia varies with dosage and may reach the stage of unconsciousness. Even at clinical dosage levels, however, the eyes remain open and certain reflexes (corneal, palpebral, laryngeal, pharyngeal, pedal, and pinnal) are intact (Beck 1972). Although Sernylan meets most of the criteria for a good bear drug, recovery is prolonged, salivation and respiratory secretion may be excessive, tetanic convulsions occasionally occur, and thermoregulation may be impaired (Lentfer 1968, Pearson et al. 1968, Seal and Erickson 1969, Larsen 1971, Beck 1972, Hamilton 1974). These side effects can be minimized or controlled by administering light doses or supplemental drugs, but such efforts often have other undesirable effects and prolong the handling procedure.

In the course of ecological studies on black bears in the San Bernardino and San Gabriel Mountains of southern California, we have been fortunate to work with Warner-Lambert/Parke-Davis and Company in the evaluation of a new drug combination known as CI-744 (to be marketed for veterinary use as Tilazol TM). CI-744 is a 1:1 ratio of the Sernylan analogue tiletamine hydrochloride and a non-phenothiazine derivative tranquilizer, zolazepam hydrochloride (C. Beck, Warner-Lambert/Parke-Davis and Company, personal communication). The development and pharmacology of these drugs have been described by Chen et al. (1959, 1969), Beck (1972), and Conner et al. (1974).

We are deeply indebted to Warner-Lambert/Parke-Davis and Company, and to C. Beck, F. Eads, and J. Moser of the Pharmaceutical Research Division, for providing us with CI-744 and many helpful suggestions. We also sincerely thank the several veterinarians in our local area who enthusiastically donated their time and facilities to aid our study: C. Jenner, G. Esra, W. Blackmore, R. Packard, W. Brindley, W. Comeau, R. Murray, G. Peavy, and G. Gardner. Students who were close to this work and helped in many ways are H. Novick, K. Boyer, V. Kee, S. Merryfield, K. Portolan, and J. DeForge. We appreciate the cooperation of the California Department of Fish and Game, personnel of the San Bernardino and Angeles National Forests, the staff of the Los Angeles Zoo, and the personnel of the Oak Glen Conservation Camp and Camp 18 of the Los Angeles County Sheriff's Department in making this study possible. Funds were provided by the San Bernardino County Fish and Game Commission and the Cal Poly Kellogg Foundation.

METHODS AND MATERIALS

CI-744 was received from Warner-Lambert/Parke-Davis and Company as bulk powder. It was dissolved in distilled water to a concentration of 300 mg/ml. Bears were captured in culvert traps or Aldrich foot snares. The weight of each bear was estimated visually and, after the first few trials, CI-744 dosage was routinely calculated at 4.4 mg/kg. A syringe mounted on the end of a pole was used to inject the drug into the rump, thigh, or shoulder musculature. After a bear was immobilized, it was weighed on a spring scale, measured, tagged, and given a prophylactic dose (5 ml/50 kg) of long-acting antibiotic (Bicillin, Wyeth). Rectal temperature and heart and breathing rates were recorded during most immobilization episodes, usually within 30 minutes of achieving restraint, but no attempt was made to monitor these parameters at regular intervals. The age of each bear was initially estimated on the basis of tooth wear and was later checked in most individuals by counting cementum layers (Stoneberg and Jonkel 1966, Willey 1974) around the root of a third premolar tooth.

CI-744 was evaluated primarily in terms of the following parameters: induction time, from injection to loss of head-lifting response when mechanically stimulated; restraint time, from loss of head-lifting response to beginning of head-lifting response; emergence time, from first head-lifting response to standing position; total down time, from loss of head-lifting response to standing (restraint time plus emergence time); dosage rate, mg/kg needed to produce restraint. Data on these parameters were obtained for each episode of immobilization. However, the tabular data presented here pertain only to those 25 episodes for which complete and accurate records were obtained after single injections. Mean values for immature (1-3 years old) and adult (4+ years old) bears were compared statistically using the Student's t-test.

RESULTS

A total of 39 different bears, all judged to be in good health, were immobilized in the field with CI-744 between August 1974 and November 1976. Ten immature (9 male, 1 female) and 12 adult (all male) bears provided the 25 immobilization episodes for our data on time parameters and dosage rates. The immature female and 2 adult males contributed 2 episodes each. Twenty of the 25 episodes reported occurred in the months May-October, and 5 occurred in November-December.

Estimated weights of the bears tended to be slightly lower than the true weights. As a result, the average dosage rate was 4.1 mg/kg. Mean dosage rates for immature and adult bears were not significantly different ($P > 0.05$). However, mean induction, restraint, and total down times all were significantly ($P < 0.05$) shorter for immature than for adult bears, whereas mean emergence times were nearly identical (Table 1).

Scatter diagrams and regression equations were prepared to obtain estimates of how closely induction, restraint, and emergence times were correlated with dosage rate and body weight. Data points were widely scattered in each case and only the following positive correlations were statistically significant: restraint time/dosage rate ($Y = 34.9X - 63.6, r = +0.44, P < 0.05$); emergence time/dosage rate ($Y = 14.6X - 24.5, r = +0.49, P < 0.05$); restraint time/body weight ($Y = 0.44X + 21.9, r = +0.53, P < 0.01$).

Eight immature (7 male, 1 female) and 22 adult (20 male, 2 female) bears provided 37 episodes in which rectal temperature and heart and breathing rates all were recorded 1 or more times during the restraint period. Means for these parameters in the immature and adult bears were not significantly different ($P > 0.05$). Means, standard errors, and ranges derived from the pooled observations ($N = 49$) were: rectal temperature, 38.1 ± 0.1 C (36.9 − 39.2); heart rate, 113 ± 16

Table 1. Weights, dosages, and time parameters for 25 immobilization episodes using CI-744 in black bears. Data are derived from 10 immature and 12 adult bears. SE = Standard Error.

Age-class	Weight (kg)	Dosage (mg/kg)	Induction (minutes)	Restraint (minutes)	Emergence (minutes)	Total down (minutes)
Immature bears (N = 11)						
$\bar{X}$	85**	4.1	4.6*	60**	37	97*
Range	46-116	3.0-5.3	3-11	31-139	10-70	41-176
SE	±6	±0.2	±0.8	±10	±6	±12
Adult bears (N = 14)						
$\bar{X}$	176**	4.2	8.2*	98**	35	133*
Range	122-244	3.5-4.9	3-17	25-174	13-59	38-207
SE	±8	±0.1	±1.1	±11	±3	±12
All bears (N = 25)						
$\bar{X}$	136	4.1	7.0	81	36	117
Range	46-244	3.0-5.3	3-17	25-174	10-70	38-207
SE	±10	±0.1	±0.8	±8	±3	±9

*$P > 0.05$.
**$P > 0.01$.

beats/minute (87 − 155); breathing rate, 11± 4 breaths/minute (4 − 20).

DISCUSSION

Explanations for the observed differences (or lack of them) between immature and adult bears, with respect to the time parameters studied, are largely speculative. Although variability in our data and in those of other investigators is great, some trends are evident. Young, lightweight polar bears (*Ursus maritimus*) (Larsen 1971) and other mammals (Seal and Erickson 1969) have been observed to require higher dosage rates of Sernylan than adults to achieve restraint and have been noted to recover more quickly. Larsen (1971) attributed the higher dosage rates and quicker recovery to the higher metabolic rate of younger bears. The shorter mean induction and restraint times observed in the younger bears injected with CI-744 also might be due in part to higher metabolic rates. However, a factor of major importance may be the amount of body fat in the individual animal. Fat may account for a greater percentage of body weight in older, heavier bears and may serve as a nonmetabolic reservoir for the drug, thereby increasing both the time required for the drug to reach effective levels in the brain and the time required for its elimination from the body. Unfortunately, we do not have sufficient data to compare bears in specific age-classes at different seasons and to analyze the effects of increasing fat deposits. Since some tiletamine may be excreted without being metabolized (F. Eads, Warner-Lambert/Parke-Davis and Company, personal communication), another consideration is that any impairment of kidney function that might occur in older bears would also increase excretion and restraint times.

The lack of a statistically significant difference between the mean emergence times of immature and adult bears may be an artifact of our small sample size and the relatively imprecise end point of emergence. We therefore refrain from speculating on any pharmacodynamic implications. However, the observation that restraint and emergence times increased with dosage rate seems explicable on the basis that the drug was metabolized and/or excreted at a constant rate by the animal. If so, larger doses required a longer time to be eliminated from the body, and restraint and emergence times were prolonged.

The observable sequence of effects of CI-744 was similar to that described for Sernylan by Pearson et al. (1968). Bears in culvert traps often assumed a sitting position soon after injection, though this action did not seem to be a response to the drug *per se*. Drooping of the head and a slow swaying motion, together with slight salivation and/or nystagmus, usually indicated the first stages of induction. Coordination was lost in posterior to anterior sequence and was regained in reverse order. Compared with the reports of other investigators (Lentfer 1968, Pearson et al. 1968, Seal and Erickson 1969, Larsen 1971) and our own experience with Sernylan, salivary and respiratory secretions were slight to moderate and posed no problem for the bears. Induction time was similar to that of Sernylan, but emergence was much more rapid and restraint was of shorter duration.

Piekielck and Burton (1975) achieved comparably short restraint times with Sernylan by administering very light doses (0.55 − 0.73 mg/kg). However, their induction times were quite long ($\bar{X}$ = 30 minutes), and the results of drugging were probably less predictable. Seal and Erickson (1969) recommended the use of promazine hydrochloride (Sparine, Wyeth) in a 1:1 ratio with Sernylan to promote muscle relaxation, prevent convulsions, and control hyperthermia. While this combination is effective, it is our impression that promazine potentiates the action of Sernylan and lengthens total down time. The combination of zolazepam with tiletamine to make CI-744 has the same synergistic effect, but tiletamine has only about one-half the potency of Sernylan and is not so long-acting (Beck 1972).

No convulsions occurred in bears immobilized with CI-744. Heat stress was minimized by working in the shade during daylight hours, and ambient temperatures for our series of immobilization episodes ranged from 4 to 28 C. There was considerable variation in rectal temperatures and in heart and breathing rates. Although some of this variation might have been due to different dosage rates or to the circumstances of immobilization and handling, the available data are not sufficient to demonstrate consistent relationships. The rectal temperatures of bears immobilized with CI-744 were virtually the same as those Hock (1957, 1960) reported for nonhibernating, unanesthetized bears. Heart rates were notably higher than those reported for sleeping bears in summer (Folk 1967, Folk et al. 1972) and were comparable to those of bears in "a very active state" (Folk 1967:76). This tachycardia may have been due to the influence of tiletamine on cardiovascular regulatory centers in the brain (Chen et al. 1969). We are not aware of any published data on breathing rates in resting bears, but Chen et al. (1969) found that tiletamine did not cause respiratory depression in monkeys at anesthetic dosages, which is probably true for bears also. In our experience, the effects of CI-744 on rectal temperature and on heart and breathing rates are similar to the effects of Sernylan and Promazine in combination.

The optimum dosage rate of CI-744 for routine field work with adult black bears appears to be about 4.0 mg/kg. Younger bears may require 4.4 mg/kg to provide adequate restraint. As a matter of procedure, this latter dosage rate is probably the best for routine use because some degree of control will be achieved with a good injection even if the weight of the bear is slightly underestimated. CI-744 has at least a 3-fold safety margin, as does Sernylan (Pearson et al. 1968), and overestimation of weight usually will result only in somewhat longer restraint and emergence times. The maximum dosage rate applied to a bear in our study was estimated to be approximately 9.5 mg/kg. In this instance, an 83-kg female with 3 8-month-old cubs was restrained for 91 minutes (emergence time not recorded). Warner-Lambert/Parke-Davis and Company have a limited amount of data on the use of CI-744 in other Ursidae. The indications are that a dosage rate of about 4.4 mg/kg is generally satisfactory for the restraint of all species (C. Beck, Warner-Lambert/Parke-Davis and Company, personal communication).

Although we did not attempt definitive tests, most of the bears we worked on appeared to be in a state of surgical anesthesia (Conner et al. 1974) for much of the restraint period. Minor surgery was performed on 1 5¼-year-old female (weight, 98 kg) to implant a temperature-sensitive transmitter subcutaneously. This bear was adequately anesthetized for the procedure with an initial dose of 5.8 mg/kg and a supplemental dose of 1.4 mg/kg administered 48 minutes later. Restraint lasted 144 minutes.

The development of tolerance for CI-744 was observed in 2 young males (siblings) over a period of 10 months while they were maintained in an outdoor enclosure. One (age, 2¼ years) required 2.4 times as much CI-744 for restraint on its fourth exposure (16 May 1976) as on its first exposure (20 July 1975). The second bear exhibited a 2.8-fold increase in dosage requirement over the same period after receiving 5 previous exposures. Both bears subsequently required about twice the dosage rate of Sernylan and promazine that we have found to be effective (2 mg/kg instead of 1 mg/kg). Seal and Erickson (1969) also noted increased tolerance for Sernylan as evidenced by increasing dosage requirements for restraint.

In Summary, we find that the advantages of CI-744 compared with the Sernylan-promazine combination are (1) shorter emergence and restraint times; (2) less salivary and respiratory secretion; and (3) greater ease of use, because two drugs do not have to be mixed and supplemental drugs (such as atropine) are not needed.

Aqueous solutions of CI-744, freshly prepared at a concentration of 300 mg/ml, are pale yellowish brown. We have noted some darkening with age, though potency does not seem to have been affected. Refrigeration probably should be used to maintain long-term potency.

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POPULATION CHARACTERISTICS OF THE JAPANESE BLACK BEAR IN HAKUSAN NATIONAL PARK, JAPAN

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Abstract: A population study of the Japanese black bears (*Selenarctos thibetanus japonicus*) harvested by the traditional hunting method was initiated in 1970 in Hakusan National Park and vicinity, central Japan. The hunting season lasts about 40 days from early April until early May during a time of heavy snow cover. A total of 265 bears were killed from 1970 to 1976 and 88 skulls were available for age determination. Their average age was 6.64 years (SD = 5.38 years), and younger bears (1-6 years old) made up approximately 65 percent of the sample. The sex ratio did not significantly differ from 50:50. Age structure and sex ratio are likely to be biased because of the lesser vulnerability of females with cubs to hunting.

The Japanese black bear is the largest game species on Honshu, the central and largest island of Japan. Hakusan National Park is known for its high density of bears, and the natural environment is well preserved in the park. Bear hunting has long been practiced in the park and its vicinity.

The purpose of this study was to accumulate fundamental data on population characteristics such as natality, mortality, sex ratio, and age structure that are necessary for effective management of the bear population. Bear populations cannot be easily studied because direct observation is difficult. However, bear population trends can be analyzed through bear harvest data.

The study was initiated in 1970 and was carried out during every hunting season through 1976. This report deals with the data collected on population characteristics of the Japanese black bear, principally its age structure and sex ratio. As the skulls of hunter-killed bears were obtained, their ages were determined by counts of tooth cementum layers. Longitudinal sections were cut from the root of the upper right canine. After decalcifying, these sections were stained with Mayer's hemalum (Sakurai et al. 1973).

STUDY AREA

The study was conducted in Hakusan National Park and vicinity (Fig. 1). There are numerous valleys in this area and abrupt changes in elevation from 400 m to 1,840 m at the highest point. The area receives the greatest snowfall in Japan. From November through April, heavy snow covers the area, with the maximum depth reaching 4-5 m every year.

Most of the study area lies in the mountain zone, characterized by deciduous broad-leaved forests in which beech (*Fagus crenata*) is the dominant species. On the steep slopes where snowslides create treeless areas, the tall herb community develops. Such areas are especially important as substantial food reserves for bears immediately after hibernation. The beech forest is replaced at low elevations by secondary forests dominated by oak (*Quercus mongolica*) and by plantations.

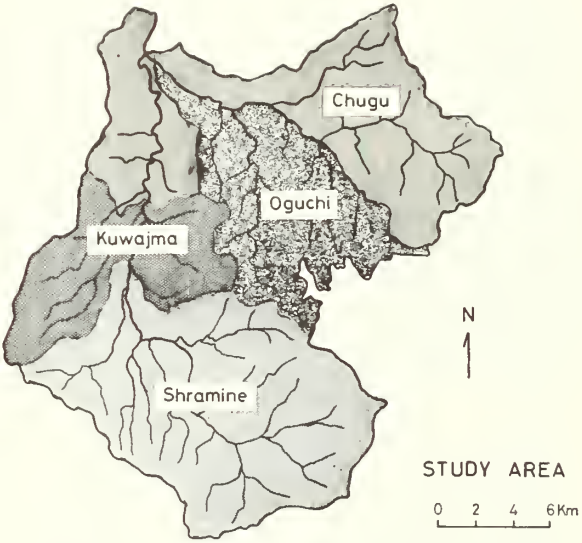

Fig. 1. Locations of the four hunting areas within Hakusan National Park, Japan.

DESCRIPTION OF HUNTING

Bears have been hunted in the study area for at least 150 years and the traditional way of hunting is still employed. It is a sort of grand hunt. Five to 10 skilled hunters and beaters compose 1 group that surrounds the resting sites of bears. As the beaters drive the bears from cover, the hunters shoot.

The study area is divided into 4 hunting areas, and each area is covered by 1 group. The hunting season generally begins in early April and usually lasts about a month. It may start earlier or later, depending on snow conditions. The bears emerge from their dens about this time to feed on herbs, beech buds, or other plants and are then harvested. Hunting effort during the season varies among the 4 groups.

HARVESTED BEARS

The total number of bears killed by the 4 groups from 1970 through 1976 was 265 (Table 1). The number of bears killed by each group differs every year. Annual fluctuations in the total number of bears killed reflect the numbers harvested by the groups having the larger hunting areas. Fluctuations cannot be avoided, for hunting effort of the groups is not the same every season. However, since the total number of bears killed varies with the snow depth in a given hunting season, hunting effort is not the only factor causing annual fluctuations (Fig. 2).

Table 1. Number of bears harvested by each hunting group, sex ratio, and number of skulls collected for age determination, Hakusan National Park, Japan, 1970-76.

	Area (km²)	1970	1971	1972	1973	1974	1975	1976
Hunting group								
Shiramine	155.3	26	6	5	16	24	6	9
Chugu	124.6	13	16	5	21	25	19	11
Kuwajima	61.7	8	5	7	7	10	8	0
Oguchi	82.6	4	2	0	0	8	3	1
Total	424.2	51	29	17	44	67	36	21
Sex ratio (male/female)		27/27	5/7	9/7	19/23	33/26	14/15	8/21
No. of collected skulls		20	6	4	12	26	13	7

Fig. 2. Comparison of the annual harvest of bears to snow depth as measured on April 1, Hakusan National Park.

Age Structure

Ages of 20, 6, 4, 12, 26, 13, and 7 skulls were determined each year from 1970 to 1976, respectively (Table 1). They represented 20-40 percent of all harvested bears in each hunting season. On the average, only 33 percent of the skulls of all killed bears could be collected each year. The remainder were sold as trophies or the skeletons were simply abandoned at the kill sites.

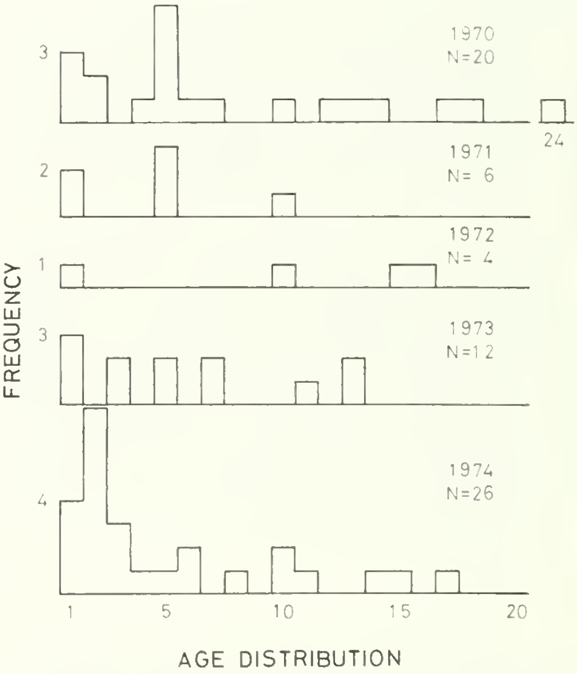

Fig. 3. Age distribution, determined from skulls, of bears killed in Hakusan National Park and vicinity, 1970-74.

Fig. 3 shows the age distribution determined from the skulls collected during 5 hunting seasons, 1970-75. The oldest bear was a 24-year-old male killed in 1970. Fig. 3 shows the larger ratio of younger animals (yearlings and subadults) to adults. If the bear population in the study area is assumed to be stable, age frequencies for 5 hunting seasons can be estimated. The age structure presented in Fig. 4 was obtained by

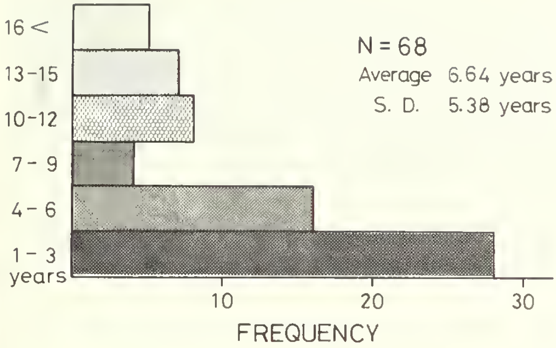

Fig. 4. Age structure of bears killed in Hakusan National Park and vicinity, 1970-74.

grouping the bears into 3-year age categories. The youngest group (1-3 years old) constituted 42 percent of the total sample. If the next group (4-6 years old) is added, these younger bears make up approximately 65 percent of the harvested bears. Ages were determined for 68 of the bears harvested in 1970-74. The average age was 6.64 years (SD = 5.38 years). Females with cubs, however, are less vulnerable to hunting than other segments of the bear population, because they seldom emerge from their dens during the hunting season. Therefore, it is suggested that the average age of bears in this population is actually slightly greater than presented here.

Sex Ratio

Table 2 shows the sex ratio of the harvested bears in each hunting season. The difference in number between males and females is rather slight, although more males may be harvested in one season and more females in the next. The chi-square test indicated that the sex ratio of killed bears did not significantly differ from 50:50 except in 1971, 1972, and 1976 when harvests were smaller. If the sex ratio of the natural bear population in the study area is assumed to be 50:50, males and females can be considered equally vulnerable to the gun.

Table 2. Sex ratio of harvested bears in each age-class, Hakusan National Park, Japan.

Age-class	Male	Female	Total	Years
Cub	7	8	15	1970-76
Yearling	25	24	49	1970-76
Subadult (2-5)	14	14	28	1970-74
Adult (>6)	26	33	59	1970-74
Total	72	79	151	

The sex ratio of cubs and yearlings harvested during the study period was approximately 50:50 (Table 2). Likewise, that of subadults (2-5 years old) and adults (greater than 6 years old) was also about 50:50. These results indicate that the sex ratio of the natural bear population in the area was 50:50. However, adult females constitute a higher proportion of the population because, as mentioned before, females with cubs emerge from their dens later than other bears.

DISCUSSION

McIlroy (1972) pointed out in his study of the black bear (*Ursus americanus*) in southern Alaska that older bears were harvested in the area where hunting had recently begun. He also stated that the average age of harvested bear populations tends to become younger the longer they are hunted. The age structure of the harvested bear population in the present study shows that younger bears outnumber older bears. Therefore, it can be assumed that hunting pressure in this area is quite heavy. The senior hunters of the area say that fewer bears were harvested before rifles came into use but that those bears were larger. This statement implies that hunting pressure has become heavier in recent years.

Annual fluctuations in numbers of bears harvested can be attributed to changes in hunting effort and depth of snow cover rather than to changes in the natural population. The fact that the number of younger bears in the harvest exceeds the number of older bears in every hunting season suggests that younger bears are dispersing from nearby unhunted areas to the hunting area. Jonkel and Cowan (1971) reported that dispersal is more common in younger bears. Some areas near the current study area and the remote parts of the hunting area are not covered by the hunters.

Sex ratios of the Japanese black bear in other areas are reported by Torii (1974) and Watanabe (1974). According to them, more males than females are harvested by trapping, with sex ratios of 2.04:1 and 1.25:1, respectively, whereas the sex ratio in the present study was 1:1. The difference seems to have arisen from different methods of hunting. In general, more males than females are trapped because of the greater mobility of males. The discrepancy in sex ratios between the natural and the harvested population is thought to be smaller in shooting than in trapping, since all members of the natural population tend to be under equal hunting pressure in the case of shooting.

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DAMAGE TO CONIFERS BY THE JAPANESE BLACK BEAR

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Abstract: The Japanese black bear (*Selenarctos thibetanus japonicus Schlegal*) removes bark from both broad-leaved and coniferous trees in Japan. These injuries are predominantly inflicted on coniferous species over an extensive geographical area on Honshu and Shikoku islands. Seventeen conifer species are known to be attacked. The bark is typically removed at the base of the tree and the exposed sapwood is gnawed and presumably eaten by bears. Tree feeding occurs mainly between mid-June and mid-July. Japanese cedar (*Cryptomeria japonica*) and Japanese cypress (*Chamaecyparis obtusa*), the most useful timber species in Japan, sustain the most severe damage. Most Japanese cedar trees sustain bole circumference girdling of 10-40 percent without showing symptoms of distress, but trees with 50 percent or more girdling usually display evidence of serious weakening. Trees completely girdled eventually die. Tree wounds are subject to infections that can deteriorate wood quality. Prevention of bear damage is an imposing challenge to Japanese forestry.

The Japanese black bear is the mammal most injurious to conifers in Japan, especially to artificial regeneration of mature trees. Bears strip bark from trees, either completely or part way around the bole, on an extensive scale, and these injuries cause a substantial loss in wood volume. Prevention of bear damage is presently one of the most significant challenges in Japanese forestry. Bears are being vigorously controlled in an attempt to reduce damage, although the bear population is obviously declining as a result of habitat deterioration caused by developmental activities in remote areas and by expansion of forest regeneration.

This situation has created constant antagonism between proponents of bear conservation and proponents of bear damage prevention in forests. To help resolve this controversy, comprehensive information is being collected on the bear damage problem and on the biology and ecology of the Japanese black bear.

This paper presents information concerning the characteristics, distribution, and impact of bear damage in Japan. This damage is very similar to tree damage by black bears (*Ursus americanus* Pallas) in North America (Lutz 1951, Levin 1954, Glover 1955, Zeedyk 1957, Molnar and McMinn 1960, Poelker and Hartwell 1973), although there are also significant differences.

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TREE SPECIES DAMAGED

Seventeen conifer tree species have been reported damaged by the Japanese black bear in Japan (Table 1). All of these conifers are native, except the Norway spruce (*Picea abies*), which was introduced from Europe. The most frequently and severely damaged species are the Japanese cedar and Japanese cypress, which are common in natural mixed-species stands, are planted extensively, and are the most useful tree species in Japan. During the last 5 years, the area of bear damage had ranged between 400 and 1,200 ha annually.

Table 1. Conifer tree species damaged by the Japanese black bear.

Common name	Scientific name
Japanese cedar, cryptomeria	*Crytpomeria japonica*
Japanese cypress	*Chamaecyparis obtusa*
Sawara cypress	*Chamaecyparis pisifera*
Fir	*Abies firma*
Veitch fir	*Abies veitchii*
Maries fir	*Abies mariesi*
Nikko fir	*Abies homolepis*
Japanese hemlock	*Tsuga sieboldii*
Hiba arborvitae	*Thujopsis dolabrata*
Japanese white pine	*Pinus pentaphylla* var. *himekomatsu*
	Pinus pentaphylla var. *pentaphylla*
Japanese red pine	*Pinus densiflora*
Japanese larch	*Larix leptolepis*
Tigertail spruce	*Picea polita*
Hondo spruce	*Picea jezoensis* var. *hondoensis*
Umbrella pine	*Sciadopitys verticillata*
Norway spruce	*Picea abies*

Although the Japanese black bear apparently has a definite preference for conifers, damage to broad-leaved trees such as chestnut (*Castanea crenata*), spicebush (*Lindera erythrocarpa*), cucumber tree (*Magnolia obovata*), wingnut (*Pterocarya rhoifolia*), oak (*Quercus mongolica* var. *grosseserrata*), and linden (*Tilia japonica*) also occurs in Japan but is rarely reported (Watanabe et al. 1970).

CHARACTERISTICS OF DAMAGE

Infliction of Damage

The Japanese black bear typically loosens the bark at the base of the tree and peels it upward, apparently with the teeth and claws. The bark is usually removed in strips 3-5 cm in width and the injury may extend up the trunk to a height of 2-4 m. Peeled bark of the Japanese cedar remains attached to the tree, dangling in long strips. The bark of other conifer species, such as fir (*Abies firma*), Japanese larch (*Larix leptolepis*), and Japanese hemlock (*Tsuga sieboldii*), does not remain attached to the trunk (Fig. 1).

Fig. 1. Injuries inflicted on coniferous trees by Japanese black bears. A. Japanese cedar. B. Nikko fir. C. Hondo spruce. D. Japanese larch.

After removal of the bark, the exposed sapwood is apparently eaten, since shallow grooves 2-3 mm deep are distinctly imprinted on the sapwood. These grooves are typically vertical on wounds above the root collar and horizontal or diagonal on wounds near the root collar (Fig. 2). The bark is not eaten or removed from the site of injury.

Damage is typically basal, and gnawing on sapwood may extend to a height of 1.0-1.5 m on the trunk, or approximately as high as the bear can reach when standing on its hind legs. Unlike the American black bear (Poelker and Hartwell 1973), there is no evidence that the Japanese black bear will climb trees to feed on sapwood in their upper portions.

The characteristics of damage vary considerably. Observations indicate that the upper sides of the trunks of trees growing on slopes are sometimes damaged first and the lower sides at a later time. Far more trees are partially girdled than are completely girdled, and trees growing on level sites seem to be more prone to complete girdling.

Fig. 2. Grooves on tree wounds caused by Japanese black bears. A. Vertical grooving on exposed sapwood. B. Horizontal grooving on the root collar.

Observations also indicate that an individual bear typically damages several trees (up to about 10) during 1 tree-feeding period. These trees are usually adjacent to each other and the feeding period appears to be of short duration.

The total area of bark removed from conifers varies from 0.9 to 2.1m^2, and approximately 60-90 percent of the exposed sapwood area is gnawed. The area of bark removal is much smaller among broad-leaved trees, apparently because their bark is more difficult to remove than that of conifers (Watanabe et al. 1970).

Diameter of Damaged Trees

The diameter at breast height (dbh) of recently damaged trees ranges from 12 to 93 cm, and trees from 20 to 50 cm in diameter are most frequently damaged in natural stands. In planted stands of Japanese cedar and Japanese larch, the frequency of damage tends to be greatest among trees over 10 cm dbh, and trees from 15 to 30 years old, particularly those over 20 cm dbh, are often selected by bears (Fig. 3)(Watanabe et al. 1973).

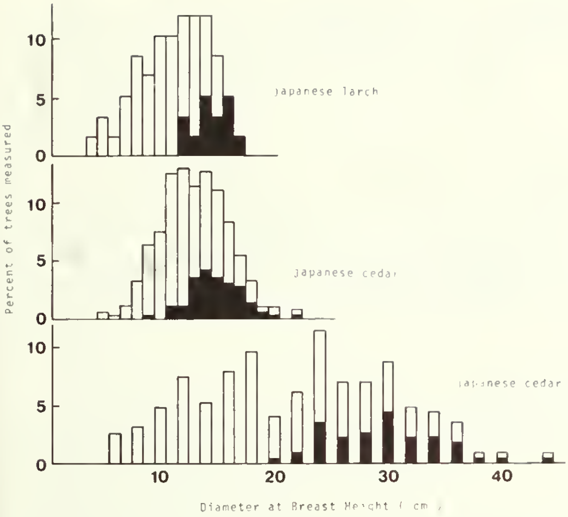

Fig. 3. Relationship of bear damage to tree diameter. Shaded areas indicate damaged trees.

Slight differences in size or age of damaged trees can be detected in separate stands, possibly due to differences in age structure of the stands. Frequency of damage is generally considered to vary significantly with density and age structure in Japanese timber stands, and the same assumption has been made regarding bear damage in North America (Poelker and Hartwell 1973).

Necessary precautions against bear damage are taken in Japan when trees reach a diameter of about 10 cm.

DISTRIBUTION AND SEASON OF DAMAGE

The approximate distribution of the Japanese black bear and the regions where damage has occurred are shown in Fig. 4. Significant bear damage has been reported throughout a large portion of the Pacific coastal region in the Shizuoka, Gifu, Shiga, Kyoto, Mie, Nara, Wakayama, Tokushima, and Kochi prefectures on the islands of Honshu and Shikoku.

In contrast, in the Hokuriku and Tohoku districts on Honshu, where bears are abundant, damage is absent or negligible. It is very peculiar and consequently of considerable interest that bear damage has not been observed in Tohoku and Hokuriku, where many native conifers occur and where Japanese cypress, Japanese cedar, and Japanese larch are planted extensively. The presence of American black bears with no evidence of bear damage to trees is also a well-known phenomenon in many areas of North America (Poelker and Hartwell 1973).

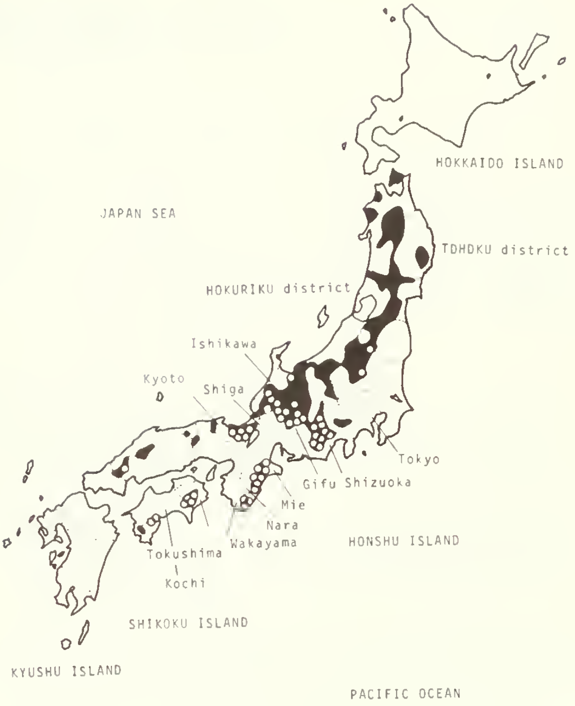

Fig. 4. Distribution of the Japanese black bear and regions where bear damage has occurred in Japan. Circles indicate occurrence of damage.

Bear damage to trees occurs mainly between mid-June and mid-July in the rainy season, when the bark can be readily stripped.

TREE DETERIORATION AND MORTALITY CAUSED BY DAMAGE

The relationship between the percentage of bole circumference girdled and subsequent unthriftiness or mortality of damaged trees is shown in Fig. 5. Complete girdling results in eventual death of the tree. The majority of Japanese cedar trees sustain bole circumference girdling of 10-40 percent without showing evidence of physical distress, trees with approximately 50 percent girdling usually exhibit distress symptoms such as defoliation and cone production, and trees with partial girdling of more than 60 percent typically exhibit a distinct lack of vigor. Partial girdling can also cause reduction in the rate of tree growth. All types of bear-caused wounds permit infection by stain and decay organisms, and such infections can result in deterioration of wood quality (Watanabe and Komiyama 1976).

Since bear damage usually occurs sporadically over large areas, it is generally impractical to remove damaged trees before actual stand harvest. In most cases, the damaged trees are left standing. At present, the control of Japanese black bear populations appears to be the only practical way of alleviating this waste of Japan's vital timber resource.

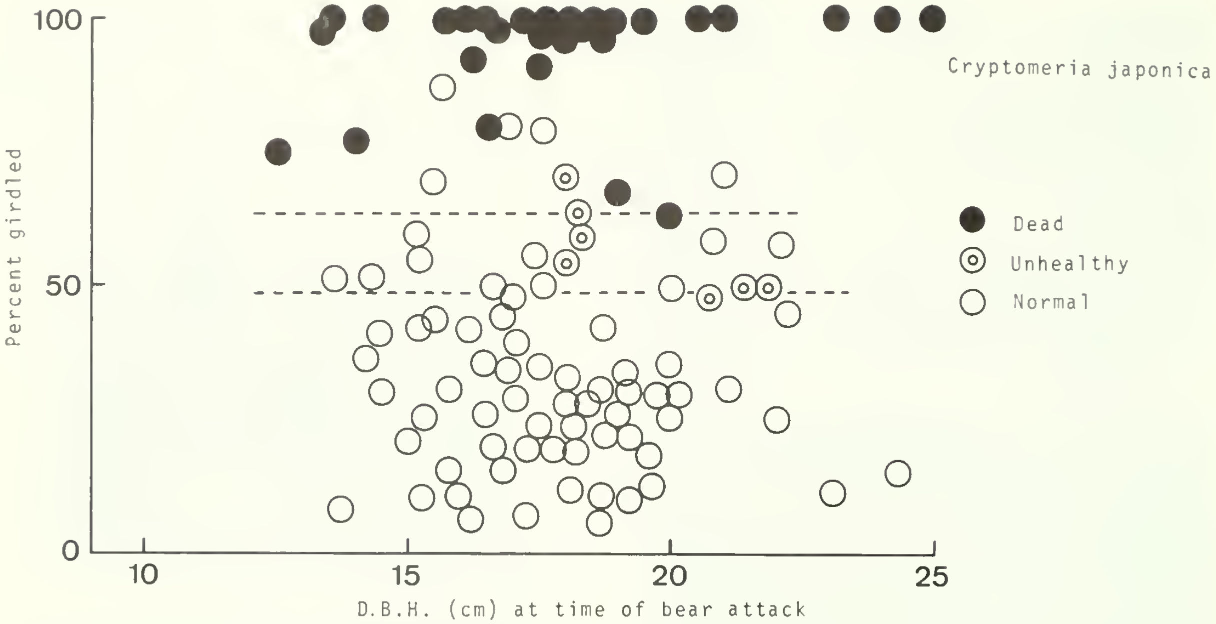

Fig. 5. Relation between percentage of bole circumference girdled and subsequent physical effect on girdled trees.

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IMPACT OF HUMAN ACTIVITIES ON SURVIVAL OF THE JAPANESE BLACK BEAR

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Abstract: The range of the Japanese subspecies of the Himalayan black bear (*Selenarctos thibetanus japonicus*) has declined in western Honshu. In Kyushu and Shikoku, local populations are approaching extinction. Meanwhile, the annual harvest of bears has increased from less than 1,000 to over 2,000 between 1950 and 1972, largely resulting from the increasing number of control kills. The distribution dynamics and the ecological consequences of the impact of human activities on 4 subpopulations were studied. Reductions in bear range and outbreaks of tree damage by bears were found closely associated with the rapid disappearance of natural forest. Present control practices and the various types of habitat destruction made these subpopulations increasingly vulnerable, and in 2 cases, partial or complete elimination of a subpopulation was confirmed.

Japanese forms of the Himalayan black bear are found on the islands of Kyushu, Shikoku, and Honshu. A form of the Asiatic brown bear (*Ursus arctos yesoensis*) occurs on Hokkaido.

The original habitat of the black bear in central Japan is believed to have extended from subalpine coniferous forests at elevations of 1,500-2,300 m to warm-temperate evergreen broad-leaved forests that ranged from the coast to low-altitude slopes up to 500 m elevation. Forests in the warm-temperate zone have long been exploited and are now largely destroyed. The range of the Himalayan black bear was progressively reduced and became confined to mountainous areas in the cool-temperate (500-1,500 m) and subalpine zones at medium to high elevations. This situation remained fairly stable until the early 1950s.

Large-scale exploitation and destruction of natural forests in the cool-temperate and subalpine zones began in the late 1950s. Bear damage to conifer regeneration has apparently increased since 1970 (Watanabe 1974). As a counter measure, bears were classified as a verminous species and trapping and killing have been encouraged by the government. The status of this species, the largest land carnivore in Japan, must be kept under rigorous scrutiny in view of the critical circumstances stated above.

Records of the total number of bears killed annually in each prefecture and of timber and agricultural damage by bears are available from the Environmental Agency and the Forestry Agency, respectively. However, the records are too meager for critical evaluation of the changing population status and of the consequences of recent human actions. Studies of the combined effect of habitat changes and hunting pressures are exceedingly scarce, and thus the present status of black bears is not well understood.

Takahashi (1974), Watanabe and Komiyama (1976), and others have expressed grave concern over the risk involved in present land-use and forestry practices, which threaten the survival of black bears. The aim of this paper is to present interim results of studies of 2 subpopulations in central Japan and a literature review of the status of 2 subpopulations in western Japan, which may be informative and may help us to evaluate the impact of present policies on the bear population.

Sincere appreciation is due K. Imanishi, former president of Gifu University, who encouraged the initiation of, and made arrangements for, the start of the research project. The field studies (1973-75) in Gifu were financed by the Department of Environment, Gifu prefecture. Throughout all phases of the work, we received active cooperation from the members of the Crescent Bear Research Group: T. Itoh and K. Maeda of Gifu College of Dentistry, E. Nozaki of Tokyo University of Agriculture and Technology, T. Aoi of Hokkaido University, and others. Field assistance by the students of the Brown Bear Research Group was most helpful. Without their participation, the field studies would not have been possible. M. Asahi of Hyogo Medical College and K. Hayashi of the Japan Monkey Center supplied valuable information and advice and, with K. Eguchi of Kyushu University, kindly allowed citations from their unpublished data. Last, but not least, heartfelt thanks are due the residents of our study areas, who generoulsy shared with us their knowledge of bears and rendered assistance in many ways. This paper is in fact the joint product of all those who contributed to the study.

TRENDS IN HUNTING STATISTICS

The following is an analysis of hunting statistics from 1950 to 1972 taken from Asahi (1977). During the past 22 years, the number of black bears killed has increased from less than 1,000 to over 2,000 animals per year. a linear regression on harvest (H) and year (X), $H=801.78+62.18X$, was obtained and found to be highly significant ($P<0.01$)(Fig. 1). The rate of in-

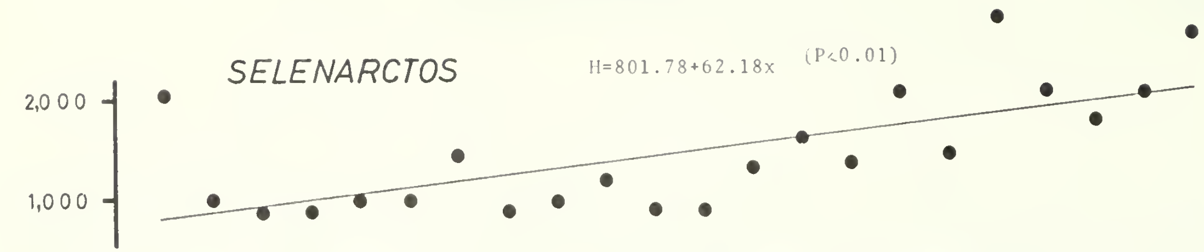

Fig. 1. Trend in the total number of black bears killed annually in Honshu, Shikoku and Kyushu. Data taken from hunting statistics of the Environmental Agency, 1950-72. (Redrawn from Ashai 1978.)

crease is 7.75 percent per year. The number of bears killed by control measures has increased from 410 in 1961-62 to 1,340 in 1970-71 (sliding mean for 2 years) and is the principal source of the rapid increase in the harvest.

The harvest per square kilometer of natural forest (harvest density) exhibits a conspicuous geographical distribution (Fig. 2). Harvest density is low on the islands of Kyushu and Shikoku and in the Chugoku district (western Honshu), moderate in Tohoku district (northeastern Honshu), and high in several prefectures in the central part of Honshu (Shiga, Fukui, Gifu, Toyama, Nagano, Gumma, and Yamnashi). The range of yearly fluctuation, as indicated by the coefficient of variation (CV) of annual kill, shows an interesting geographical pattern (Fig. 3). CV is high along the periphery of the areas of high harvest density, that is, along the pacific coast and western Japan; although within the areas of high harvest density, CV is generally below 5 and harvests are rather stable.

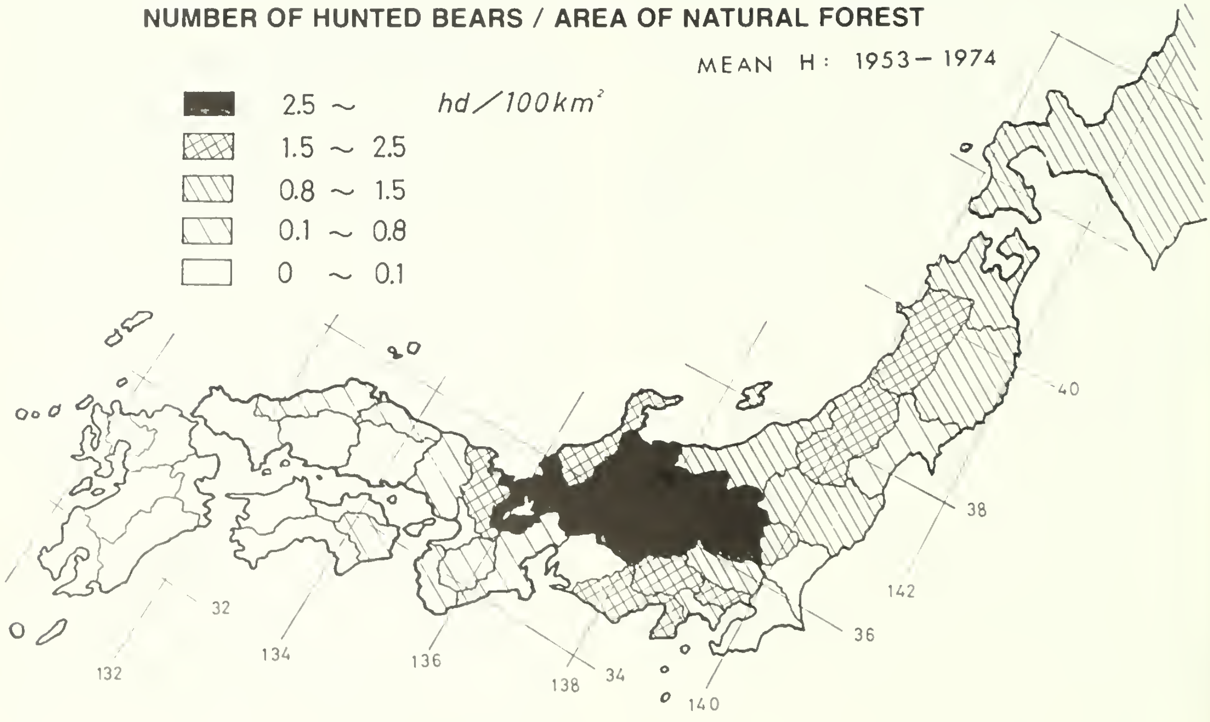

Fig. 2. Harvest density (number of bears killed per area of natural forest) of black bears in Japan. Number of kills is the mean for 1953-1974(Redrawn from Asahi 1978).

However, stable harvests in these areas do not necessarily indicate the stability of either the populations or habitat quality. The following case histories of 4 regions are presented in order to delineate the current situation in Japan.

REGIONAL CASE HISTORIES

Kyushu Sanchi (Mountain Range, Central Kyushu)

Historical documents from the 8th century record the harvest of bears in secluded mountain villages of Shiiba and Gokanosho for medical use, which indicates that bears once occurred over a wide range along the central mountains of Kyushu. The last remaining stronghold of Kyushu bears is the Sobo-Katamuki Range (1,768 m in elevation), the highest mountain mass of Kyushu Island.

Since 1860, 45 known kills have been recorded, and sites of these kills show that a considerable reduction of range has occurred (Fig. 4). The population was estimated at 20-30 animals in 1960 (Kato 1959). Since then, however, heavy clearcutting has advanced to the 1,600-m level, leaving only a small portion of the original forests of fir (*Abies firma*), beech (*Fagus crenata*), and hemlock (*Tsuga sieboldii*) in the cool-temperate zone. The present range is a narrow high-elevation belt of about 16 km x 2km, in which 4 sightings of bears or bear tracks were reported during the past 30 years (Eguchi 1976).

Chugoku Sanchi (Chugoku Range)

Characteristics of habitat degradation are somewhat different in the Chugoku Sanchi, which extends over 6 prefectures in western Honshu. All along the watershed of the district of Chugoku, sizable expanses of deciduous hardwood forest remain in only 4 small, isolated blocks, each sustaining only a few bears. These are Hyonosen-Funabuse mountains, Mount Ohmangi, Mount Daisen, and Hikimi-Ochi counties of Shimane prefecture (K. Hayashi, personal communication; Yukawa 1975).

The average annual kill for the entire region is 25, but the number of kills for each subpopulation fluctuates irregularly and is not synchronized with the others. For instance, kills in the Hyonosen subpopulation, although numbering 1-3 in normal years, rose to over 20 in 1970 and in 1974. Here, the population of bears was roughly estimated at 20^+ in 1974 (Kuwamura et al. 1974), and the remaining suitable habitat is only 10 kmx12 km. In some years, bears wander as far as 20 km from their usual ranges in summer and fall, damage orchards, crops, and coniferous plantations, and are often trapped and killed. We suggest that the reduced area of the habitat and the encroachment of human

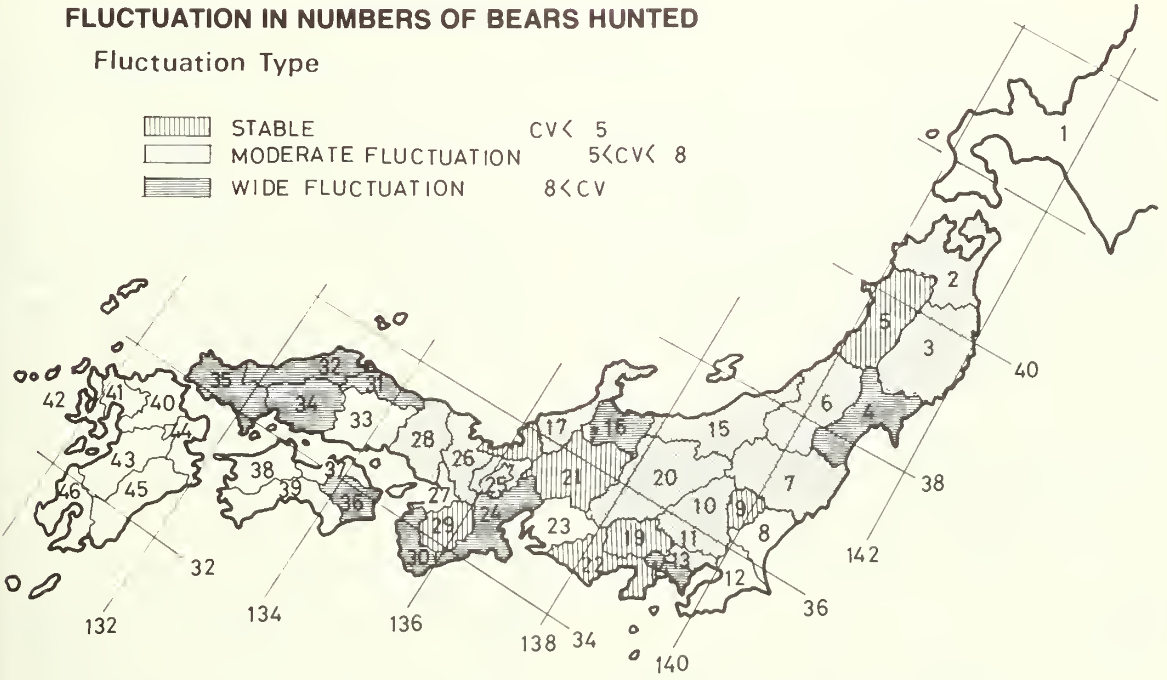

Fig. 3. Relative fluctuations in the harvest of black bears in Japan. Stable: coefficient of variance (CV) less than 5. Moderate fluctuation: CV between 5 and 8. Wide fluctuation: CV greater than 8 (Asahi 1978).

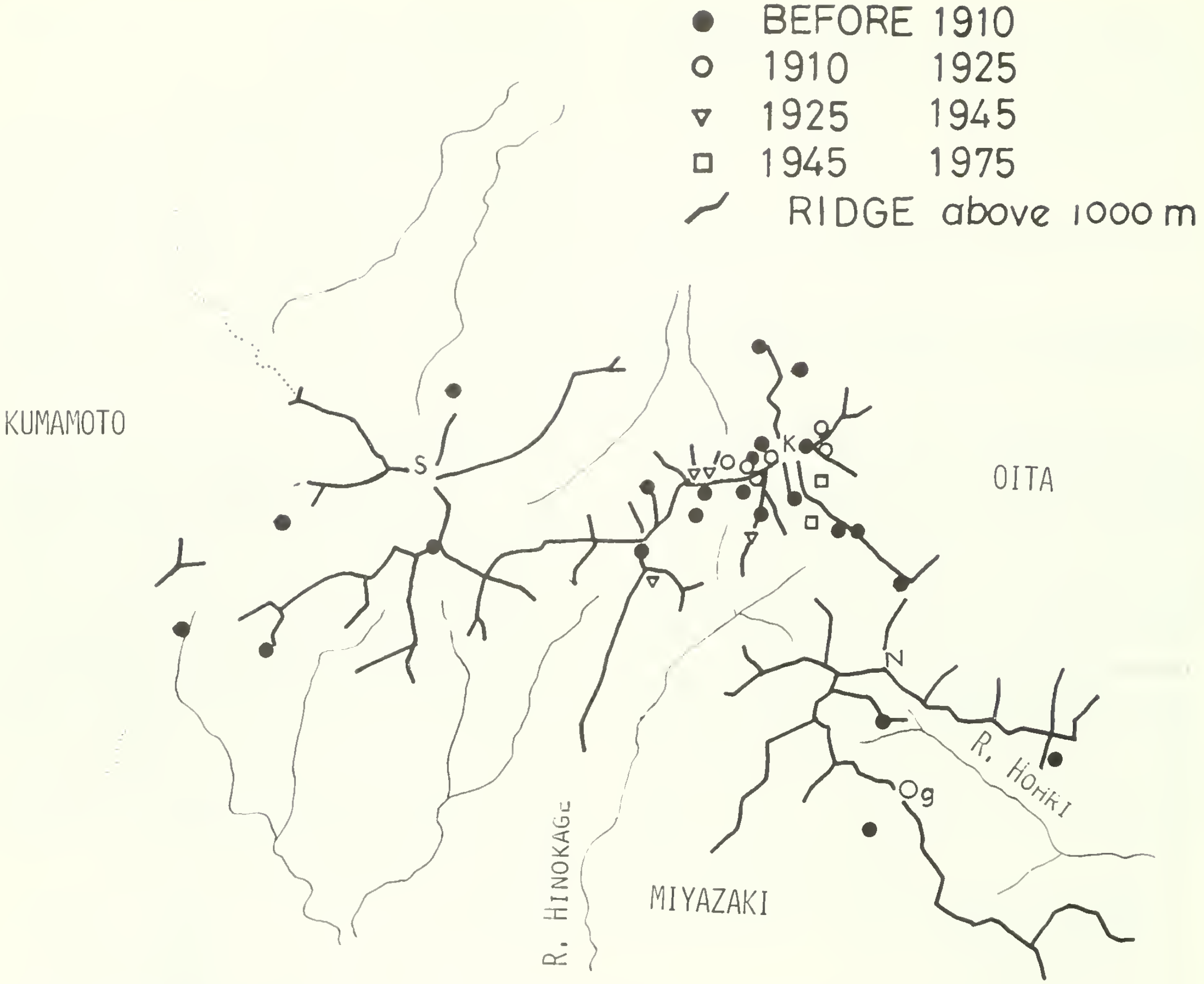

Fig. 4. Sites of black bears kills in Sobo-Katamuki Range, Kyushu, 1860-1975. (Drawn from Kato 1959 and Eguchi 1976.)

disturbances into the area, such as timber-felling and construction of roads and power dams, in addition to poor mast crops, are responsible for the dispersal of bears (Leopold 1933, Schorger 1946). Furthermore, nuisance control in these cases may be effective in eliminating a substantial part of the subpopulation.

Western Part of Gifu Prefecture

Gifu prefecture shows the highest statistics for annual bear kills in Japan, with the numbers ranging between 300 and 400 for the past 5 years. The upper basin of the Neo and Ibi rivers in the western part of Gifu prefecture has been our study area since 1972 (Azuma et al. 1976).

The area is mountainous, with elevations from 400 m to 1,600 m. Four hundred square kilometers of steep terrain are dominated by a hardwood forest of beech on the upper slopes and a *Quercus serrata-Castanea crenata* secondary forest on the lower slopes. Both of these forest types are interspersed with stands of Japanese cypress (*Chamaecyparis obtusa*) and fir, which usually occurs on steep, rocky ridges. Artificial plantations of cryptomeria (*Cryptomeria japonica*) and Japanese cypress are largely restricted to lower elevations, along valleys and near villages. Percentages of afforestation are low (13-29 percent).

A map of bear range in this region was drawn from interviews with hunters, forestry workers, and local residents (Fig. 5). The area where bear sign was found during spring and summer in most years may be considered the normal range. Den-hunting occurs in this part of the country and pursuit hunting takes place in fall and spring. The known sites of the dens where bears were taken fall within or on the margin of their normal

Fig. 5. Distribution of black bear range, known winter dens, hunting areas, and sites of tree damage by bears, western Gifu prefecture.

range. Bears are known to have appeared in some locations outside their usual habitat in a few of the past 10 years.

Distribution and trends of bear damage. — Bear damage to trees is localized and occurs only in the blocks of forest land in the eastern part of the region. In the western part of Neo Dani Valley, where hardwood forests cover over 75 percent of the terrain, mature conifer plantations are rarely damaged by bears. We found only 8 instances of damage in 450 ha, sporadically and thinly distributed. Some bear damage is found occasionally in the marginal areas of normal range; it occurs for 1 or 2 years and then subsides for several years.

The area of heaviest bear damage in the eastern blocks overlaps the area of nearly continuous mature man-made forest, where forest cover exceeds 70 percent. Although the history of planting conifers dates back to the 1880s, bear damage was not a problem until 1960.

Population density. — Estimates of the size and composition of the bear population occurring on a 2,700-ha survey plot at the headwaters of the Neo Nishitani River were obtained from 1973 to 1975. Estimates were made by distinguishing sighted individual bears through physical characteristics, size, and accompanying young. Size and location of tracks of non-sighted bears were used as supplementary information.

The figures remained fairly stable for the 3 years. Apparent density for the area was 0.19-0.29 bear per km^2 (Table 1).

In the spring of 1976, extensive tree damage was found in the neighboring valley of the Neo Higashitani River, where control operations were undertaken. Five traps were set over an area of 2,200 ha from June through August. Elimination of bears from the sector was confirmed by 15 August (Table 2). The apparent density was 0.32 bear per km^2 before the control operation. This example shows the efficacy of the trap-and-kill method of control that is commonly followed in Japan.

Table 1. Estimates of the size and composition of the bear population in the 2,700-ha survey plot at the headwaters of the Neo Nishitani River, Gifu prefecture.

Season and year	Bears sighted	Number of Units
Spring (April-May) 1973	Adult, large	2
	Adult female and cub (0 yr)	1
	Adult female and yearling (1 yr)	1
	Immature (2-3 yr)	1
	Unknown	1
	Total	8
Spring (April-May) 1974	Adult, unknown sex	1
	Adult, female and cub (0 yr)	1
	Adult female and yearling (1 yr)	1
	Unknown	2
	Total	7
Fall 1975	Adult, unknown sex	1
	Adult female and yearling (1 yr)	1
	Young adult male	1
	Immature male (2 yr)	1
	Unknown	1
	Total	6

Table 2. Estimates of the size and composition of the bear population in a 2,200-ha area of tree damage in the valley of the Neo Higashitani River, Gifu prefecture. Determined by complete elimination of bears through control procedures, June-August 1976.

Bears eliminated (N = 7)				
Age	Sex	Weight (kg)	Date of capture	Trap site
Immature	M	18.0	2 Aug 76	4
Immature	Unknown	20.6	16 June 76	1
Adult (old)	F	42.2	28 June 76	1
Adult	F	43.1	22 June 76	2
Adult	M	50.6	18 July 76	3
Adult	Unknown	Unknown	30 July 76(?)	5
Unknown	Unknown	Unknown	2 Aug 76(?)	Unknown

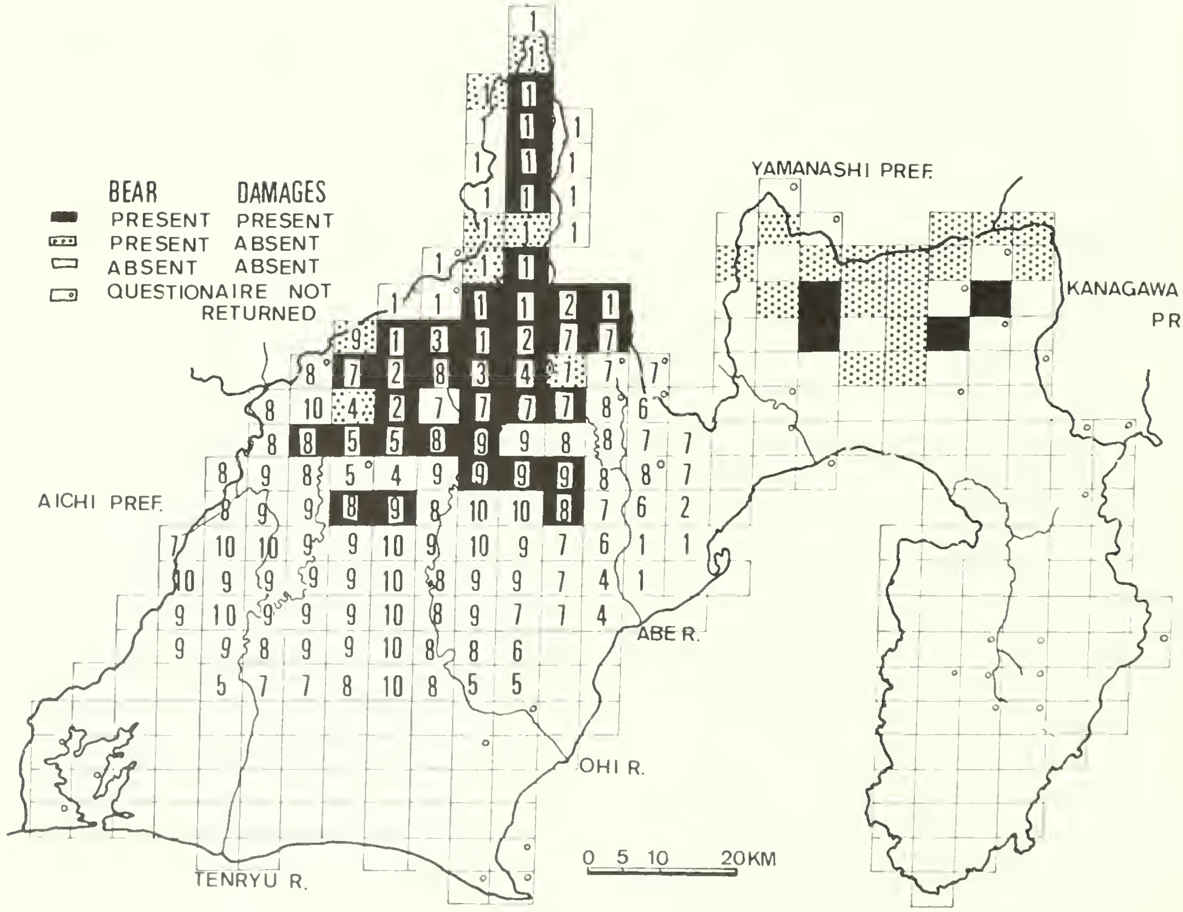

Fig. 6. Distribution of bear damage and percentages of forest cover in Shizuoka prefecture. Figures in the blocks denote percentage of forest cover taken fro vegetation map prepared by F. Konda. Data on distribution are based on questionnaires.

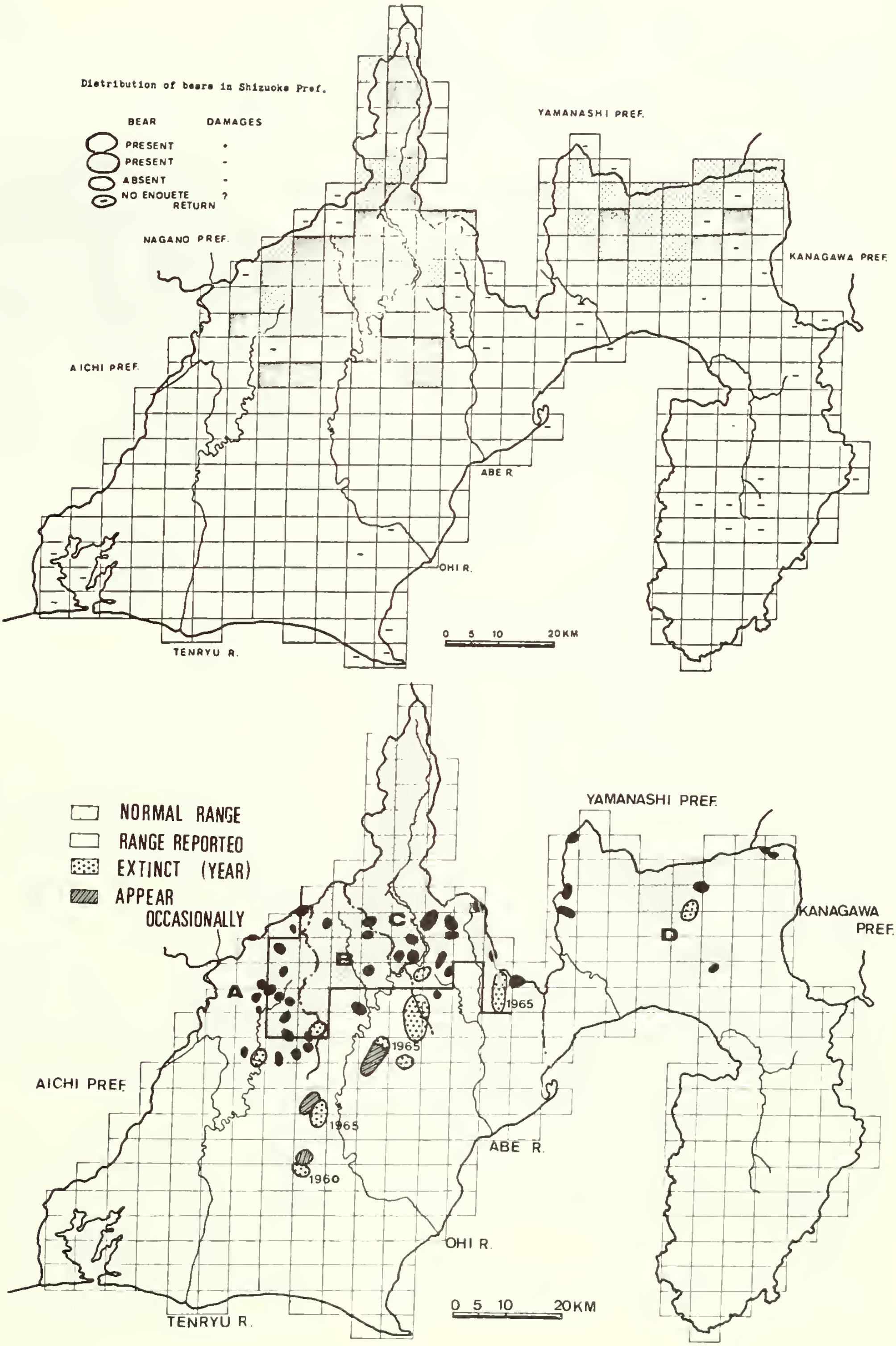

Fig. 7. A. Bear range in Shizuoka prefecture. Normal range has decreased during 1960-76. B. *Normal range* is based on survey data. *Reported Range* is based on hunters' reports of areas where bears survive. *Appear occasionally* also includes declining small populations (see text). Heavily lines along the grid (A, B) outlines areas where forest cover is less than 70 percent.

Western Part of Shizuoka Prefecture

Torii has been gathering hunting data here since 1968 (Torii 1977). The middle and upper reaches of the Tenryu, Ohi, and Abe rivers embrace a largely forested area of about 2,500 km$_2$. Elevations vary from 200 m to 3,000 m.

The lower portion of the black bear range is covered by *Quercus-Castanea* coppice-regeneration forests. On higher slopes in the cool-temperate zone, oak (*Q. mongolica*) — maple (*Acer mono*) forests and *Abies-Tsuga* coniferous forests occur. Above 1,800 m, subalpine conifers cover steep slopes and ridges. Along the middle streams, *Cryptomeria* and *Chamaecyparis* forest cover is widespread and is advancing upstream (Fig. 6).

The range map of black bears in Shizuoka (Fig. 7A, B) was based on information obtained from questionnaire returns from game guards, forest-owners' associations, and hunters. Areas of reported local extinction often occur close to areas of "occasional appearance." We could not discern whether a particular area represented a recent decrease in the size of a detached segment of a breeding population that was locally near extinction or was simply a place where stray bears were seen infrequently. These questionable sites were located at a distance of about 10 km from the normal range. The normal range of bears is, however, broadly determined by the amount of forest cover. The range is outlined by the blocks where forest covers over 70 percent of the area, which shows that the survival of bears is negatively influenced by extensive man-made forest cover.

Bear damage is seen along the periphery of natural forest areas, where susceptible forest stands (Poelker and hartwell 1973) are increasing at the same time.

Harvest trends show a drastic decrease in numbers of bears killed in Misakubo and Senzu (Fig. 8). The population of bears resident in these areas is believed to have been almost eradicated. This conclusion is also supported by the lack of bear damage in these areas.

SUMMARY OF THE ECOLOGICAL CONSEQUENCES OF HUMAN INTRUSION INTO BLACK BEAR RANGE

Through examination of these 4 regional cases of bear-habitat-human interaction, the following dynamics are indicated:

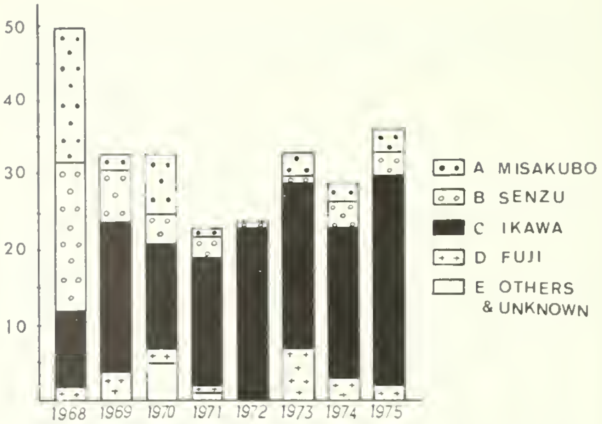

Fig. 8. The number of bears killed each year in different regions of Shizuoka prefecture. A-D refer to locations on Fig. 7B. Harvests in Misakubo and Senzu have rapidly decreased as bears become locally extinct. (Bears caught in the last few years had probably entered these areas from other regions only recently.)

1. A rapid increase in the percentage of forest cover in a regime usually not only reduces the favorable habitat of bears but also induces increased outbreaks of tree damage by bears in mature regenerated stands in neighboring areas.

2. In areas where tree damage by bears is severe, mature stands generally sustain the most extensive damage.

3. As the only means of forest protection, trap-and-kill practices using cage traps with beehive baits are encouraged by the government. These measures are so effective that the natural population of bears over a wide area is eliminated within a few years.

4. Reduction of natural forest, large-scale lumbering, and road and dam construction in an area tend to increase the possibility and the extent of bear intrusion into adjacent agricultural and forest lands. Combined with the vermin-control practices, this displacement increases the vulnerability of the remaining subpopulations of bears.

5. Where sufficient natural habitat is left intact, tree damage is sporadic, inconspicuous, and limited to conifers of natural forests, and the influx of bears into other areas is restricted to comparatively short distances, even in years of poor *Fagus* and *Quercus* crops.

6. Some areas continue to show stable harvest statistics when bear range is reduced, even when the subpopulation has been eliminated.

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RELATIONSHIPS BETWEEN OCCURRENCE OF BEAR DAMAGE AND CLEARCUTTING IN CENTRAL HONSHU, JAPAN

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Abstract: Damage to coniferous trees by black bears (*Selenarctos thibetanus japonicus* Schlegel) was studied in 1 man-made stand recently clearcut and in another stand 20 years old, in west-central Honshu. Diameters of stumps of bear-damaged trees in the man-made stand ranged from 9.8 cm to 29.8 cm, and, in the 20-year-old stand, trees with a dbh greater than 10.4 cm became susceptible to damage. Information on geographical distribution and history of bear damage and on species and ages of bear-damaged trees was obtained by questionnaire. Relating changes in the pattern of bear damage to the practice of clearcutting and to great declines in natural forests more than 51 years old shows that when clearcutting and man-made forests are extensive, bear damage to man-made forests increases.

Tree damage by the Japanese black bear usually occurs on coniferous species such as Japanese cypress (*Chamaecyparis obtusa*), Japanese larch (*Larix leptolepis*), cryptomeria (*Cryptomeria japonica*), fir (*Abies firma*), and Japanese white pine (*Pinus parviflora*). The damage occurs when the bears peel the bark from the basal portions of the trees and eat the exposed sapwood, leaving a pattern of vertical grooves made with their teeth.

The objective of this study was to find out why bears feed on sapwood or the inner portion of the bark of coniferous trees. As a first step in our study, the following subjects were investigated: (1) characteristics of bear damage, (2) geographical distribution and past history of bear damage, and (3) changes in clearcut areas of natural forests, and in man-made forests apparently susceptible to bear damage.

The term *natural forest* refers to forest stands older than 51 years, because in these stands, the natural Japanese cypress, Japanese white pine, and fir are scattered and might be the objects of bear damage. Also, a more abundant supply of food might be available in the older stands than in man-made forests and young natural forests.

STUDY AREAS AND METHODS

To determine the characteristics of bear damage, diameter measurements were made in August 1975 and July 1976 at 2 damaged Japanese cypress stands in the vicinity of the yamanokuchi River, Mashita district, Gifu prefecture (Fig. 1). One stand was cut in 1974 and the other was a 20-year-old stand. Most trees in man-made forests in this district are Japanese cypress. In the area that had been cut, diameters at heights ranging from 20 cm to 50 cm from the ground were measured both for bear-damaged trees and nondamaged trees. In the 20-year-old forest stand, which was damaged in 1976, diameters at breast height (dbh) were also measured. In addition, in the cutover area, the year and diameter of damage occurrence were determined from an examination of scars that remained on stumps. The area covered by this investigation was about 4 ha, at an elevation of about 1,000 m.

A questionnaire was found to be the only practical way of obtaining information on the geographical distribution and history of bear damage. The questionnaire was sent to personnel directly involved in the management of forests in the villages of Maze and Kiyomi and the town of Hagiwara. Of 890 questionnaires sent, 369 were returned.

The questionnaire asked for the following basic information (1) geographical distribution of bear damage, (2) past history of bear damage, and (3) species and ages of bear-damaged trees.

To study changes in forest areas susceptible to bear damage, the vegetation was divided into 4 forest types — man-made Japanese larch forest; man-made cryptomeria forest; man-made Japanese cypress forest; and natural forest, including virgin and second-growth forest. Age-class areas in each forest type were calculated from their forest description tables.

RESULTS

The investigation showed that bear damage in the cutover area in the man-made Japanese cypress forest was first seen in 1947 and had been seen, since then, over a period of 24 years. It was also determined that concentrated bear damage was observed during 1961-63, affecting about 81 percent of all bear-damaged trees counted. The ratios of the diameters (at

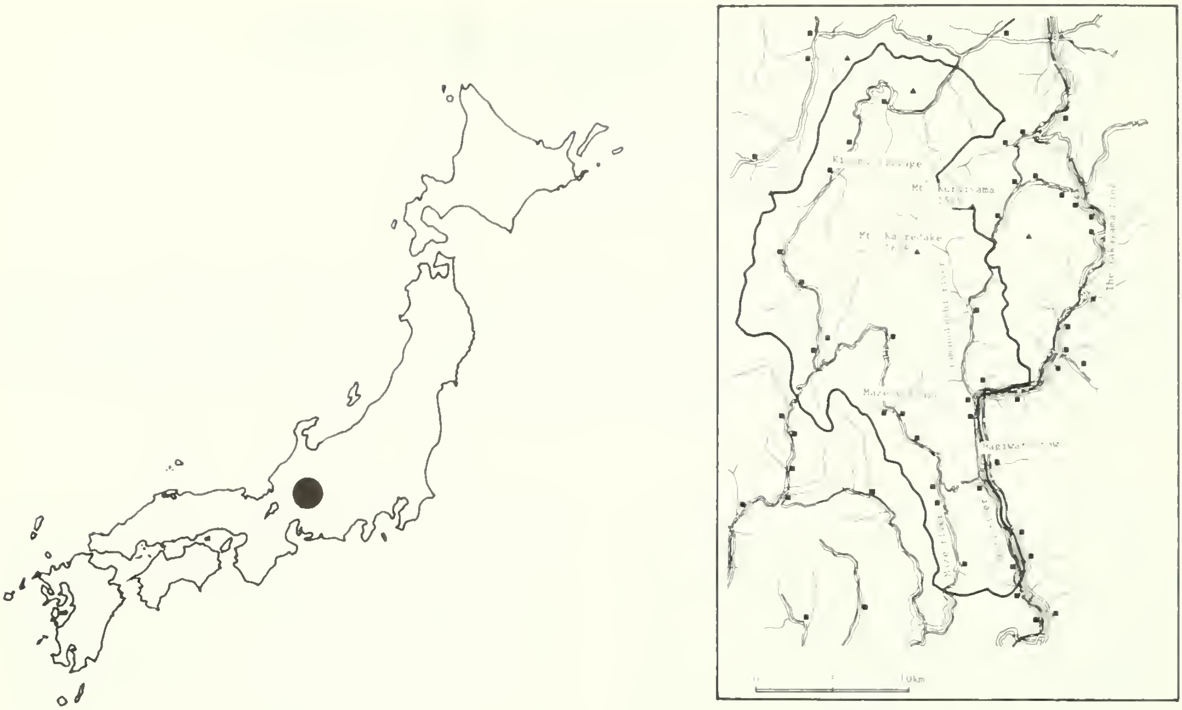

Fig. 1. Study area, Gifu prefecture, Honshu. Study area is enclosed in bold line. ■ rural settlement

stump) of nondamaged trees in this forest stand to those of bear-damaged trees at that time are shown in Fig. 2.

The bear damage occurred to the larger trees. Diameters of stumps of bear-damaged trees ranged from 9.8 cm to 29.8 cm. The average stump diameter of all trees was 15.8 cm.

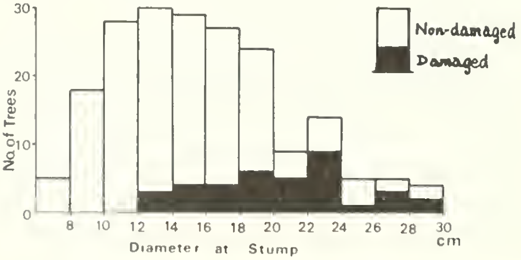

Fig. 2. Number of damaged trees by diameter class as determined from examination of 199 trees in cutover areas of Japanese cypress stands.

Fig. 3 shows dbh of trees and percentage occurrence of bear damage in the man-made Japanese cypress forest that is 20 years old. When the average dbh exceeded 10.4 cm, bear damage was seen. The relation between dbh and bear damage, according to the data currently available, is shown in Table 1. It is known that bear damage appears when the average dbh in man-made Japanese larch forests and man-made cryptomeria forests exceeds 10-12 cm. As a result, a forest stand where average dbh is greater than 10 cm is hereinafter called an *apparently susceptible man-made forest*.

According to the standard growth curve obtained for man-made forest stands in this region, Japanese cypress, cryptomeria, and Japanese larch attain an average dbh of 10 cm in 20-30 years, 20 years, and 16-20 years,

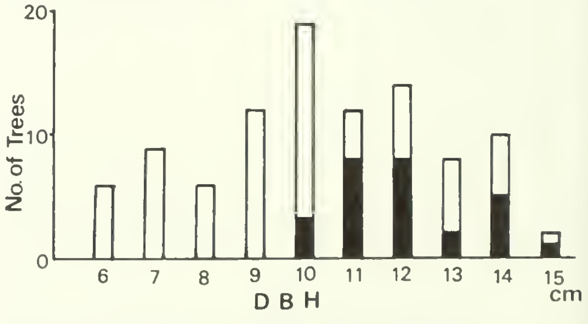

Fig. 3. Number of damaged trees by diameter class as determined from examination of 105 trees in stand of 20-year-old Japanese cypress.

Table 1. Average size of timber in damaged forest stands in 4 prefectures, Honshu.

Tree species	Age (years)	Average dbh (cm)	Sampled area (ha)	Study area	Source
Japanese cypress	30	18.0	1.03	Shizuoka	Teramoto and Omori 1952
Japanese cypress	29	14.9	1.27	Shizuoka	Kobayashi and Morisawa 1952
Cryptomeria	37	25.6	0.20	Yamagata	Imano et al. 1969
Cryptomeria	About 30	22.6	0.07	Kyoto	Watanabe et al. 1970
Cryptomeria	About 30	22.0	0.15	Kyoto	Watanabe et al. 1970
Cryptomeria	17-20	14.7-16.1	0.25	Kyoto	Watanabe and Komiyama 1976
Cryptomeria	16-18	12.3-14.1	0.25	Kyoto	Watanabe and Komiyama 1976
Japanese larch	22	19.2	0.25	Nagano	Furubayashi et al. 1975
Japanese larch	20	10.6	0.08	Nagano	Furubayashi et al. 1975
Japanese larch	20	20.2	0.10	Nagano	Furubayashi et al. 1975
Japanese larch	18	12.2	0.10	Nagano	Furubayashi et al. 1975
Japanese larch	13	15.1	0.09	Nagano	Furubayashi et al. 1975
Japanese larch	12	11.8	0.06	Nagano	Furubayashi et al. 1975
Japanese larch	11	10.9	0.10	Nagano	Furubayashi et al. 1975

respectively. Apparently susceptible man-made forest stands in the study areas would be those that are older than the ages mentioned above.

The distribution and historical changes in locations of bear damage in the natural forests and in the apparently susceptible man-made forests were studied to determine the effects of clearcutting natural forests areas. The results are shown in Figs. 4 and 5.

DISCUSSION

Natural forest older than 51 years has dramatically decreased over time. Only remnants of natural forest remain; the apparently susceptible man-made forest has increased rapidly since 1970. Paralleling this trend, areas of bear damage are expanding (Fig. 6). These trends are particularly marked in the central part of the

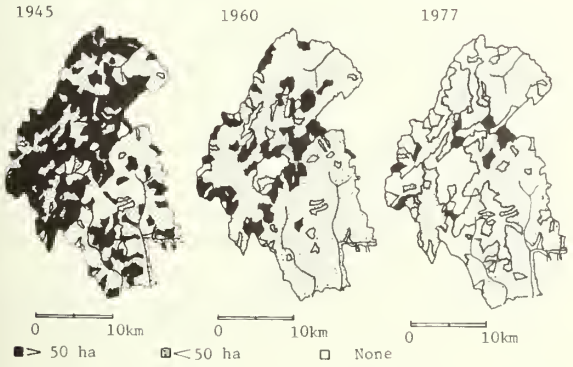

Fig. 4. Distribution of natural forest land in 1945, 1960, and 1977 as determined from forest description table.

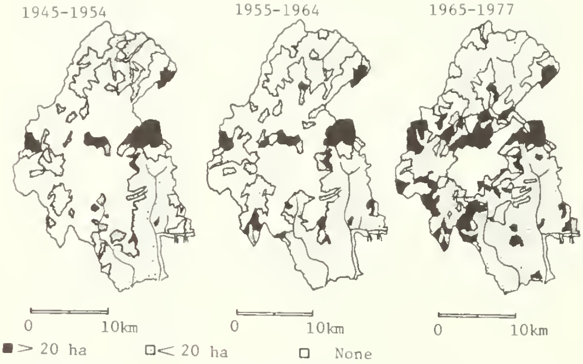

Fig. 5. Distribution of man-made forests apparently susceptible to bear damage as determined from forest description table.

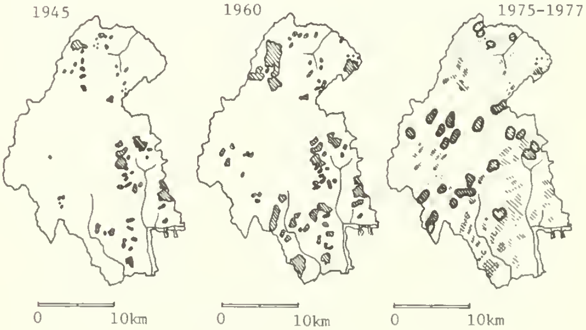

Fig. 6. Distribution of bear damage as determined from questionnaire data. Dotted areas indicate bear damage in natural forests. Shaded areas indicate bear damage in man-made forests. Areas in bold outline indicate locations of bear damage since 1972.

study area. In this central area, about 3,000 ha were clearcut after 1955. The clearcutting must have caused a very sharp decrease in the number of coniferous trees likely to receive bear damage. Possibly because of this decrease, bear damage is occurring more frequently and more widely in the man-made forests surrounding the clearcut natural forests. Even in the area where bear damage was seen before 1955, and where man-made forest stands are now susceptible to bear damage, damage spreads from 1 forest stand to another.

In the man-made forests of Japanese cypress, cryptomeria, and Japanese larch, all of which were planted in the cutover areas, bear damage first occurred about 1975, the time when the trees became big enough to be subject to bear damage. In other words, where clearcuts and man-made forest plantations are extensive, bear damage is generally seen more frequently in man-made forests. The increase in man-made forest stands serves to impair the quality of bear habitat by reducing the supply of the bear's natural foods. Even without hunting pressure, it will become harder for the bear to survive in these large man-made forest areas.

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NATURAL AND SYNTHESIZED AGGRESSIVE SOUNDS AS POLAR BEAR REPELLENTS

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Abstract: Aggressive sounds were recorded during a confrontation between 2 male polar bears (*Ursus maritimus* Phipps). These sounds were analyzed for frequency content, envelope, rhythmic patterns, and duration. Nine synthetic versions were generated to simplify, duplicate, or exaggerate components of the original sounds. The behavior of 5 captive polar bears, 2 captive brown bears (*U. arctos* L.), 13 wild black bears (*U. americanus* Pallas), and 18 wild polar bears was observed in response to these sounds. One or more of the variants produced a significant repellent effect in each bear tested. We defined a repellent effect as an immediate and rapid movement away from the speaker, with a continued retreat as long as the sound was produced. The effects of these sounds on the heart rate of captive polar bears were measured with an implanted heart-rate transmitter. The 4 sounds with the greatest apparent effect in the field also produced the greatest increases in heart rate in the captive implanted polar bear.

Many confrontations between man and bears have resulted in death or damage to man or his property. Increased utilization of Canada's arctic regions has increased the numbers of human encounters with polar bears. In January 1975, an employee for Imperial Oil, stationed on an offshore drilling island located in the Beaufort Sea, was attacked and killed by a polar bear. This rig and others are now under the protection of armed Inuit hunters. Since that time, 3 intruding bears have been shot after unsuccessful attempts to drive them away. Pederson (1956) cited 2 cases of attacks on men by polar bears, and Manning (1973), Parker (1974), and Stirling (1975a) report apparently unprovoked attacks on men. Jonkel (1975) reports an attack at Norwegian Bay on a sleeping man and suggests that the bear may have mistaken the man for a loafing seal. He also reports an attack in which an employee of the Department of Energy, Mines and Resources was bitten and hit before the bear was shot by another worker. In August 1975, a reported attack proved to be a probable suicide upon which the bear fed (Jonkel 1975). National Personnel of the Canadian Department of National Defense have had some encounters with curious polar bears in the course of their summer field research camps on Devon Island. Safety in their camps is improved with a trip-wire detection system.

Churchill, Manitoba, experiences a large influx of polar bears each fall for approximately 2 months, but few attacks have been recorded. The area is protected by a 24-hour patrol, manned by personnel from the Department of Renewable Resources. Jonkel (1970a, b) concludes, on the basis of the behavior of captive North American bears, that the polar bear is probably less aggressive than the grizzly bear. One reason for the apparent seasonal change in numbers of man-bear encounters in the Arctic must be the nutritional stress that the polar bears undergo in late fall and winter. Mature males add territorial challenges to the problems facing subadult males, which have proved to be the most common problem animals. These 2 factors combine to produce an animal that is likely to investigate any potential food source.

The use of sound to repel vertebrate pests has been investigated by Frings et al. (1955), Frings and Frings (1957, 1963), Maclean (1974), Stewart (1974), Dracy and Sander (1975), and Belton et al. (1975). Frings et al. (1955:340) and Frings and Frings (1957:91) observed that "biologically significant" sounds were more distressing to birds than simple ultrasonic or sonic sounds. Frings et al. (1955) noted the ability of such sounds to evoke flight in the starling (*Sturnus vulgaris*). Frings also noted an interspecific response to recorded alarm calls of the herring gull (*Larus argentatus*) by both the great black-backed gull (*L. marinus*) and the laughing gull (*L. atricilla*). Maclean (1974) produced repellent sounds to which both laboratory and field-tested rats responded. He employed intense ultrasonic fields (20 kHz at 130 dB) although the repellent effects were permanent only if food and water were alternately accessible. Dracy and Sander (1975) were able to induce anxiety in coyotes (*Canis latrans*) by exposing the test animals to an 18-kHz sound; no intensity was specified. Belton et al. (1975) investigated the use of ultrasonic and sonic sounds as repellents in polar bear control. Some evidence of discomfort was observed in the bears when they were exposed to 7 kHz at 100 dB. Stewart (1974) suggests that his Av-Alarm system operates as an auditory jamming sound, leading to increased levels of psychological stress.

The objectives of this study were to determine the response of captive and free-ranging black, brown, and polar bears to natural and synthetic aggressive sounds.

The intent of these experiments is the development of an acoustic repellent system that might reduce or prevent dangerous bear-man encounters.

This research, conducted from 1975 to 1977, was supported in part by grants from Imperial Oil and the National Research Council of Canada. B. Hodges of the Olympic Game Farm; N. Oritsland and C. Jonkel of Churchill, Manitoba; B. Haagensen and T. Melnyck of Imperial Oil; J. Lay of the British Columbia Department of Fish and Wildlife; and C. Mueller of Simon Fraser University are gratefully acknowledged.

METHODS AND MATERIALS

Recording Natural Aggressive Vocalizations

Natural aggressive vocalizations of 2 male polar bears were recorded at the Olympic Game Farm, near Sequim, Washington. Both bears were positioned in 1 cage and were offered a single piece of raw beef, vocalizations included hisses and throaty growls. Loud directed roars were recorded with a Uher 4000-L Reprt recorder and a Grampion parabolic reflector. The bears were approximately 5 m from the microphone during recording.

Analysis of the Natural Aggressive Vocalizations

Sounds were analyzed for frequency content on a Kay Elemetrics Co. Type 8/65 Sonagram that gives a plot of frequency versus time on a calibrated drum. The sounds were also analyzed on a Bruel & Kjaer Third-Octave Band-Pass Filter Analyser that verified the Sonagram analysis and gave a more accurate indication of the relative amplitudes of each of the frequencies within the vocalizations (i.e., the amplitude envelope).

Synthesis of Aggressive Sounds

The analysis of the natural vocalizations yielded information on frequency, rhythmic patterns, and duration, which allowed us to synthesize analogs of the natural sounds. The synthesis was achieved through modulation and modification of 3 basic sounds: a foghorn and 2 types of automobile engines. These basic sounds were chosen because of the ease with which we could alter their characteristics.

Modulation of each base sound was carried out by passing the sound content through a series of electronic devices that shaped and clarified the content into that which we desired. The basic sounds were passed through a filter bank that smoothed the sounds. This low-level input was then amplified and passed through a ring modulator, an additive unit that produced a preprogrammed modification of the sine wave components of the base sound. F_1 sine wave frequencies of the base sound were added to by specific chosen F_2 frequencies, according to our program formula:

$$(F_1 \pm F_2) + (3F_1 \pm F_2) + (5F_1 \pm F_2).$$

It is apparent from this program that larger values of F_2 (which were specified) resulted in a wider but emptier sound, whereas smaller values of F_2 generated a denser sound. it was therefore possible to create sounds loaded around the base sound frequencies or to create lightly loaded sounds with a greater overall spectrum.

Finally, the resultant complex sound was passed through a Krohn-Hite 3100R Band-Pass Filter, adjusted so as to limit the harmonics and the upper and lower limits of the sound and to produce the sharp attack or initiation of the sound, which we had noted in natural vocalizations. The resultant sounds were analyzed on the Bruel & Kjaer equipment to verify their fit with respect to our original intentions.

The F_2 modulation frequencies supplied to the ring modulator program were (1) foghorn: 220, 20, 150 Hz; (2) auto source 1: 160, 25 Hz; and (3) auto source 2: 150 Hz.

Captive Polar and Brown Bears

Captive polar and brown bears at the Olympic Game Farm were subjected to our test sounds and to the original natural vocalizations. An interval of approximately 15 minutes was allowed between each test. We defined a positive response as an immediate and rapid reaction resulting in the swift retreat of the target animal. The bear had to continue to respond in this way for the duration of the test. Free-ranging animals tested later were required to continue their retreat for a distance of 100 m. Any response less than our defined response was discarded as not being of value in an actual situation. Captive subjects, because they were unable to run away, required careful evaluation. Obvious behavioral changes were noted in these instances.

Wild Black Bears

The responses of free-ranging black bears to our test sounds were evaluated at a dump in the lower mainland area of British Columbia and at 3 dump sites and a fire suppression camp in the eastern interior of the province. Seven- to 10-minute intervals were maintained between acoustic tests. Bears that could be visually identified and that were frightened by a specific sound were tested with different sounds the next day. Because more than 1 sound proved effective with particular animals, some bears did not return after 2 or 3 tests, and it was therefore impossible to try all sounds on each animal. A 20-W amplifier, cassette, and 0.5 m reflex horn were used to produce test sounds.

Wild Polar Bears

The dump area and the incinerator site at Churchill, Manitoba, were the sites of our field tests on free-ranging polar bears. Attractant stations were maintained at suitable locations. Gainsburger dogfood patties soaked in sardine oil were used to bring the bears close to our test apparatus. A 20-W public address system, a 0.5 m double reflex horn, and a cassette deck were used to generate sounds. The open country allowed us to test bears over long ranges, and sounds were played to animals up to 250 m away.

Captive Polar Bears: Telemetry

A recently captured polar bear from the Churchill area was fitted with an implanted heart-rate transmitter. The device was a silicon-wax embedded FM transmitter, and was placed under the skin in the ventral thorax region. Two stainless steel electrodes ran laterally from this unit and picked up cardiac electrical impulses. The FM signal, picked up on an FM receiver, was then placed on a Gould-Brush Accuchart recorder for permanent record. Three tests of each sound were run, and average heart-rate increases were subjected to a 1-tailed *t*-test for significance at the 0.95 level. A level of 60 dB (measured on a sound meter 1 m from the speaker) was used in all tests.

On-site Installation: Beaufort Sea Drilling Rig

In December 1975, Wooldridge installed an acoustic repellent system on one of Imperial Oil's offshore drilling rigs. The system consisted of 4 speakers, a cassette player, and a 70-W amplifier. The speakers were positioned so as to broadcast the sounds outward from the rig. The sound level was adjusted to approximately 120 dB measured 1 m from the speaker.

RESULTS

Analysis and Synthesis of Sounds

Sonogram analysis (Fig. 1) gave us the frequency spectrum of an aggressive polar bear roar. We analyzed several of these plots in order to establish all of the required frequencies inherent in the vocalization. Apparent frequencies were in the ranges of 80, 100, 150, 200, 220, 300, 400, and 600 Hz, with some hiss sounds in the background. Frequency amplitude envelopes for the natural and synthesized sounds are given in Fig. 2; T refers to *sound type* in this figure. Some roars consisted of 2 or 4 roars; the majority of vocalizations consisted of 3 bursts. The lung capacity of a polar bear may be the upper limiting factor in the number of roars produced. This possibility suggested the synthesis of longer and more frequent roars, thereby producing a suprastimulus. T_2, T_4, and T_6 are all of longer duration than T_1, the natural sound. The rapid attack seen in the amplitude envelopes of T_2, T_4, and T_5 exaggerate this characteristic. T_5, T_6, and T_7 show a level of background "white" noise similar to that in natural sounds. T_7 attempted to duplicate the general rhythmic and amplitude patterns of the T_1 sound.

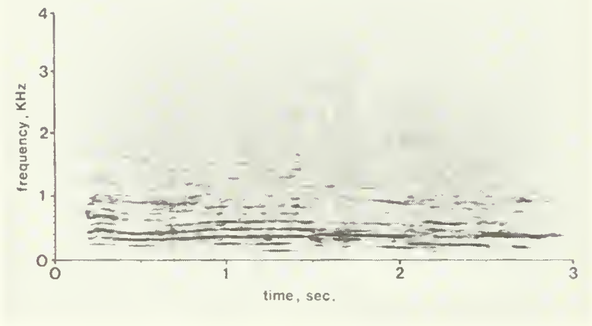

Fig. 1. Sonogram of a typical polar bear aggressive vocalization.

Frequency envelopes show good correlation with natural vocalizations and indicate that the synthesized sounds closely approximated natural sounds.

Captive Polar and Brown Bears

A total of 5 polar and 2 brown bears were subjected to our test sounds. The 2 polar bears that were the original source bears for our recordings of natural vocalizations responded the least of all captive animals. One polar bear did not react to any of the sounds and exhibited typical signs of "zoo neurosis." The 3 other polar bears were either younger, female, or both, and were apparently intensely frightened by our tests. They attempted to escape through the wire at the rear of their cages by running at it. Unable to escape, they cowered in the far corners of their cages. The brown bears gave the most dramatic responses; both of them tried to run through the wire backs of their cages and then attempted to climb up and out through the bars. Towards the end of our tests, our mere approach caused these bears to retreat. They had rapidly become conditioned to the fact that we produced the repellent sounds.

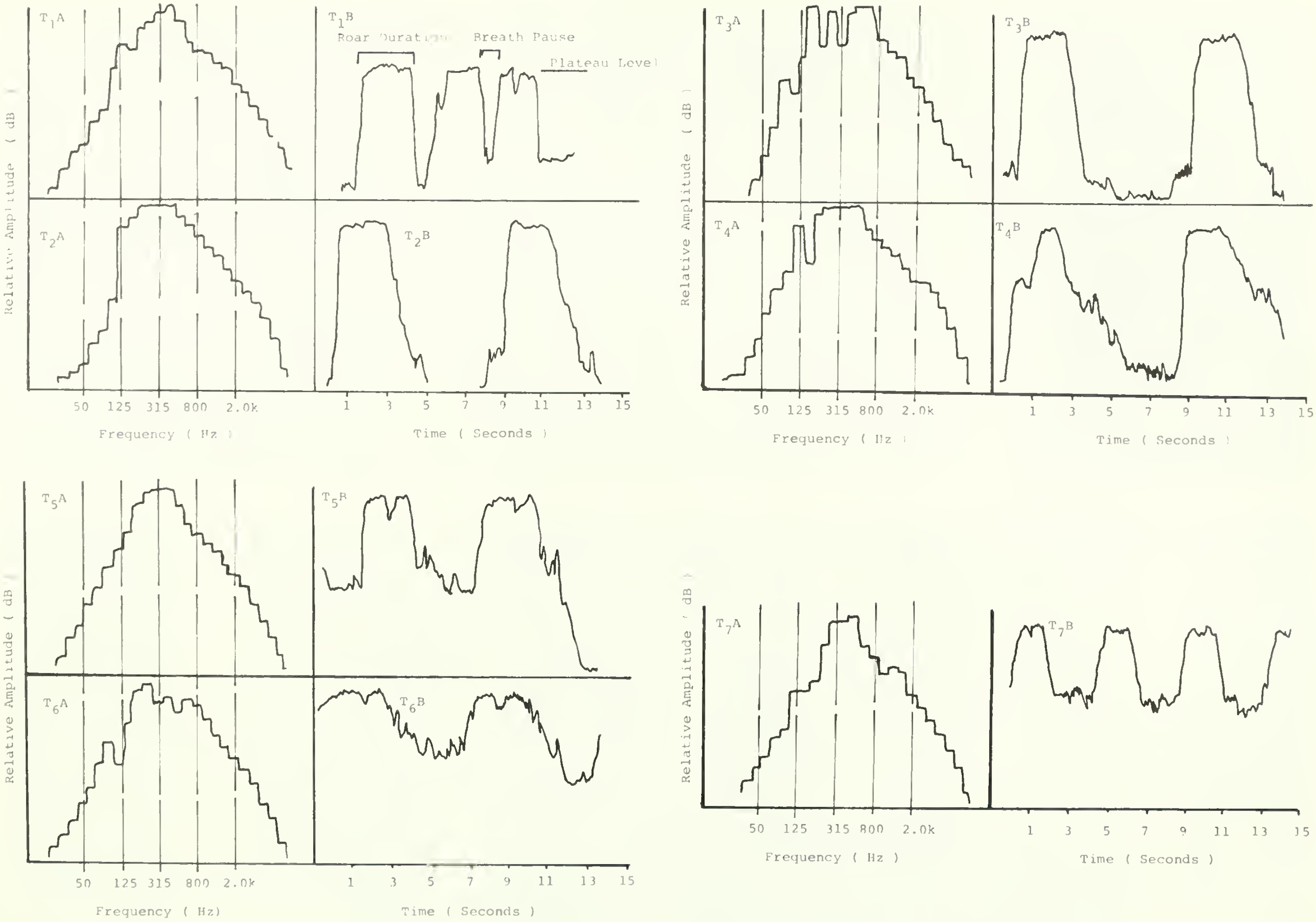

Fig. 2. Amplitude vs. frequency and amplitude vs. time. T$_1$ = natural sounds: T$_{2\text{-}7}$ = synthetic sounds. Relative amplitudes for frequencies are given for natural (T$_1$) and synthesized (T$_{2\text{-}7}$) sounds in "A" on these plots. Relative amplitudes vs. time are given in "B" on these plots.

Wild Black Bears

A total of 13 free-ranging black bears were exposed to our test sounds. All responded significantly to at least 1 of the sounds, and most responded to 3 or more (Fig. 3). We were able to carry out multiple tests at dumps, because the bears at those sites seemed to be permanent residents. Insignificant responses were characterized by hesitation and apparent indecision to leave the area. Often, ineffective sounds resulted in the immediate return of the bears. We were then able to try other sounds. Effective responses were characterized by the rapid retreat of bears, followed by their absence from the area for at least 2 hours. In most instances the bears did not return while we were at the test site. We observed no aggressive reactions to the sounds.

Wild Polar Bears

A total of 19 wild polar bears were subjected to our test sounds. One female, with 2 cubs, reacted aggressively towards sound type T_2. This same bear was exposed to T_1 3 days later, and she retreated rapidly after initial hesitation. All other polar bears tested retreated upon exposure to an effective sound. One bear, sleeping at an estimated distance of 250 m, was awakened by T_6; he retreated rapidly until he was out of our sight and range. Four polar bears were subjected to repeat tests carried out on subsequent days.

Telemetry Studies

Table 1 summarizes our heart-rate data. Percent increases were greatest for sound types 1, 3, 5, and 6 with corresponding values of 54, 75, 138, and 180 percent increases. Types 4 and 10 gave values of 30 and 31 percent. Rates before and after initiation of each test were averaged for the 3 experiments, and these values were tested for significant differences at the $P = 0.95$ level of significance. Percentage increases over 50 percent generally resulted in apparent fear responses involving movement away from the sound source and, on several occasions, attempts by the test animal to climb out of the small barred window at the rear of the holding cage. The level of increase diminished over the 3 days of tests, indicating a degree of habituation to the sounds, probably compounded by the inability of the bear to escape them and the lack of any reinforcement accompanying the aggressive vocalizations.

Fig. 3 presents a general summary of the effects of all of the sound types. In general, wild polar bears responded most strongly to their own and our synthesized aggressive sounds. Wild black bears also reacted strongly, whereas captive polar and brown bears appeared to be less affected by loud aggressive sounds. This result is understandable as they are always in close association with men and human sounds. Heart-rate increases correlated well with field observations. Some differences existed; however, these may have been due to the acoustics of the small room (introducing changes in the sound parameters) and the various factors associated with the confinement of the test bear. Replication in field experiments was possible in 4 instances. Bears so tested appeared to react more strongly in subsequent tests.

On-site Drilling Rig Tests

In late February 1976, a polar bear approached the Beaufort Sea drilling rig that had been fitted with our acoustical repellent system. The sounds were initiated when the bear was at least 800 m away. The animal hesitated, and then moved away after approximately 1 minute. Observations on the response of this bear were reported by several individuals, but the reports were not in general agreement. The bear was subsequently chased and shot and was reported to be in a semistarved condition, which is not uncommon in this region in the middle of winter. No distinction between known effective and ineffective sounds was made by rig personnel, and it is possible that a less effective sound may have been broadcast to the animal.

DISCUSSION

Initial studies of the responses of free-ranging and captive black, brown, and polar bears to biologically significant sounds suggest that these sounds may be effective in repelling nuisance bears. Comparison of response and sound type has allowed us to speculate on the required components of an effective bear-scaring sound. The frequency content should be within the range of 100-600 Hz, with frequency distribution in predominant bands at approximately 100, 125, 150, 200, 250, 400, and 600 Hz. These frequencies must fit within a frequency envelope that emphasizes those bands between 150 and 300 Hz. The amplitude-time plot, or amplitude envelope, must conform to a shape that is characterized by a relatively sharp *attack* (a near vertical slope), a plateau region of 2-4 seconds duration, and an attenuation of sound less severe than the attack. Finally, each roar, as described above, should be repeated 3 or 4 times in a series, at intervals of approximately 1-4 seconds.

The amplitude of the sounds in actual field use should be 100 dB, which is extremely loud at short

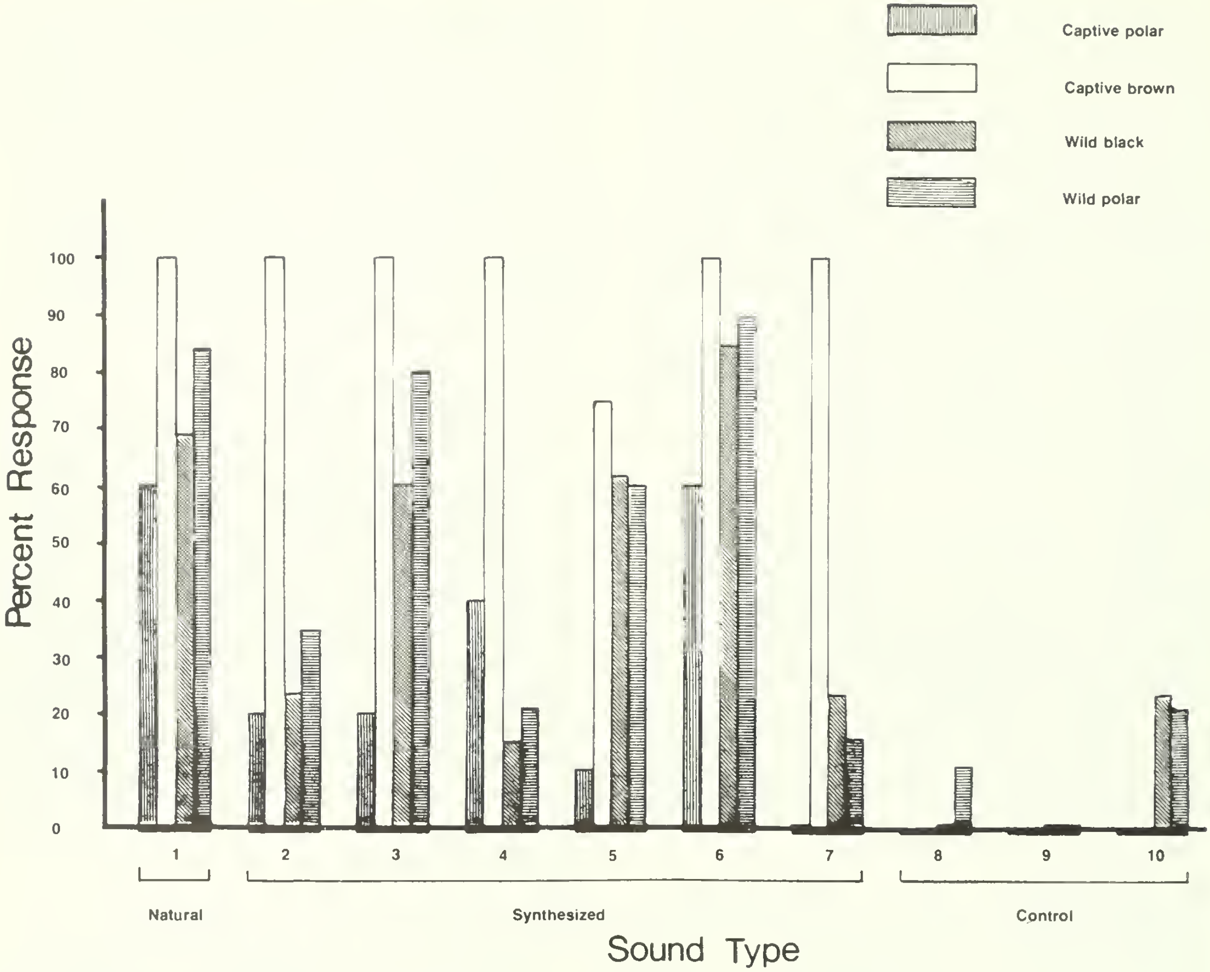

Fig. 3. Response vs. sound type. Frequency distribution of the total number of avoidance responses (expressed as a percentage) to each sound type, including the 3 control types (T_8, T_9, T_{10}) for captive polar and brown bears and for free-ranging black and polar bears.

Table 1. Effects of natural and synthesized sounds on the heart rate of a captive polar bear. Test 1, mean heart rate after sound = 129.0 bpm. Test 3, mean heart rate after sound = 110.6 bpm (14 percent decrease). One-tailed *t*-test for ($n_1 \pm n_2 - 2$) = 4 df at 0.05 level of probability is significant if $t > 2.13$.

Sound type	Test 1		Test 2		Test 3						
	Before sound	After sound	Before sound	After sound	Before sound	After sound	X_b	X_a	Percent increase	*t* value	Rank
1	105	170	110	168	100	150	105	163	54	8.26	2
2	120	135	105	110	100	98	108	114	5	0.48	
3	100	160	65	140	75	120	80	140	75	3.86	4
4	90	125	80	95	100	130	90	117	30	2.16	6
5	105	175	60	155	36	150	67	160	138	4.30	3
6	55	170	45	160	72	150	57	160	180	10.51	1
7	72	88	80	90	110	98	87	92	5	0.39	
8	60	72	85	87	95	100	80	86	8	0.48	
9	70	100	90	96	100	110	87	102	17	1.57	
10	70	95	95	120	80	110	82	108	31	2.60	5
Mean heart rates:		129.0				121.6					

distances from the speaker source and may in itself effect a retreat. At our test amplitude of 120 dB, we successfully rousted a bear at a distance of 250 m; continued application of the sounds resulted in the retreat of the bear to an estimated 500 m, at which point the test was discontinued.

Some positive responses by target bears were considered to be of minimal practical value in bear-man confrontations and were therefore disregarded in our observations. About 30 percent of our observed negative responses were in fact weak positive responses and were characterized by hesitation in an advance or by a slow retreat. No habituation was observed in the field. Four bears subjected to repeat tests at Churchill, Manitoba, appeared to respond more readily on second exposure to our test sounds. This readier response was probably due to the reinforcement that these animals sometimes receive from other, dominant animals. Such real aggressive encounters are often coupled with either a visual display or actual physical blows. Our sounds may act as releasers of responses that have been learned in the bears' daily life. Habituation appeared to be occurring in the responses of the captive polar bear fitted with an FM transmitter. His overall heart-rate increase for all sounds presented decreased from a mean of 129 beats per minute to 110.6 beats per minute, 14 percent over 3 days of tests. The conditions of his confinement and his continued exposure to the presence of people may have reduced his responsiveness to frightening sounds.

Repellent sounds offer advantages over conventional methods of bear control. They are nondestructive and require no actual contact between bear and equipment. They appear to be effective over moderately long ranges (250-500 m), probably because of their significance to the target animal. As a result of their electronic origins, they are easily interfaced with devices designed to detect the intrusion of bears. In the severe arctic environment, such detection devices may prove to be the only truly effective equipment capable of warning of the approach of an intruding polar bear.

Research is continuing at the time of writing. Field tests under arctic conditions, simulating actual field installations, should lead to definitive conclusions about the efficacy of this technique. Incorporation of repellent-sound devices offers the potential of reducing the numbers of dangerous bear-man encounters and of protecting polar bears in their home environment from destructive removal techniques in those instances where other alternatives exist.

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AGE DETERMINATION OF LIVE POLAR BEARS

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Abstract: The reliability of counting cementum annulations in premolar sections was evaluated for age determination in live polar bears (*Ursus maritimus*). Structural irregularities in cementum deposits decreased accuracy of age assignments. Displacements of the neonatal line toward the exterior margin of cementum growth resulted in erroneous aging for young animals. Striated, wavered, and doubled growth layers affected accuracy for older animals. Sixty-eight unlabeled tooth slides representing 57 known-age bears, examined by 3 independent investigators, revealed that only 32-45 percent were correctly aged. Analysis of age-related body measurements of 46 male and 63 female polar bears of known age showed that morphometric regression equations could be used as an age indicator. Reproductive status, general body size, and tooth replacement or wear used as criteria to tentatively age animals in the field, combined with subsequent cementum counts and growth regression analyses, provided reliable age determinations.

Differential growth in tooth cementum has been widely used to determine the age of individual animals (Klevezal and Kleinenberg 1969). Cementum annuli were confirmed in known-age brown (*Ursus arctos*) and black (*U. americanus*) bears (Rausch 1961, Sauer et al. 1966, Stoneberg and Jonkel 1966) and from teeth taken at different intervals from known-age grizzly bears (*U. arctos*) (Craighead et al. 1970). Legibility of cementum layers in brown and black bears appeared correlated to retarded growth zones formed during winter denning.

Chronological layers formed in cementum of polar bear teeth are much less consistent because activity patterns differ, particularly as related to winter denning. Lentfer (1976) noted that polar bears (except parturient females) were active, or at least intermittently so, throughout the entire year. Harington (1968) reported that the denning period of polar bears varied considerably by age, sex, and physiological state. Rausch (1969) observed structural irregularities in polar bear teeth and cited variation in annual activities as a plausible reason for cementum having little value for determining chronological age.

The Alaska Department of Fish and Game and the U.S. Fish and Wildlife Service conducted a polar bear mark-and-recovery program between 1967 and 1976. During this time, 809 polar bears including 286 known-age litter members were captured, marked, and released in the Alaska sector of the polar basin. Eighty-nine of these were recaptured 1 or more times. It became apparent early in this program that structural irregularities of cementum layering posed a serious problem in assigning ages to marked polar bears. The recovery of known-age polar bears led to a partial assessment of this problem.

This study was made between September and December 1977 to evaluate the reliability of counting cementum annulation and to ascertain whether this method, combined with age-related reproductive, growth, and tooth-wear characteristics, would improve the accuracy of age determination in marked polar bears.

METHODS

A vestigial premolar (Pm_1, Pm_2, or Pm_3) was extracted from captured animals, including those of known age. Known-age animals, first captured and marked as cubs, yearlings, or 2-year-olds, were aged accurately from postnatal features, especially the developmental stage of permanent teeth.

Lentfer (1968) described techniques to capture and immobilize polar bears. Experienced field crews tentatively estimated the ages of captured bears by tooth wear, relative body size, and reproductive status. Tooth wear was the most useful indication of age until about 12 years; annual changes then became imperceptible. Reproductive status as an indication of age was based on litter age, condition of the vulva (infantile, turgid, open) and mammaries (niple size and color, lactation in past or at present), and whether a mature female was accompanied by a mature male. Male characteristics considered were size and condition of genitalia. January was arbitrarily chosen as the birth month for all bears.

Teeth were prepared for examination by decalcifying for 24 hours in Decal® (Scientific Products D1208 or D1210) and then rinsing in running tap water for 1.5 hours. Longitudinal and some cross sections were cut at 24 microns in a cryostat at -20 to -30 C. Sections were stained by 3 methods during the ensuing years. The first method involved a dilute multiple stain for frozen sections (Steen and McIlroy 1971). The second was essentially the same except that Harris hematoxy-

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lin replaced the multiple stain. The third method was a modification of Johnson and Lucier's (1975) technique. With this technique, sections were overstained for 15 minutes in heated Harris hematoxylin for Papanicolaou staining. After rinsing 4 minutes in running tap water, sections were destained to desired contrast by dipping for approximately 4-6 seconds in an acid-alcohol solution (10 ml concentrated hydrochloric acid and 1,000 ml 70 percent ethyl alcohol). After an immediate rinse in tap water for 10-15 seconds, sections were immersed in lithium carbonate and water (20 grams lithium carbonate and 2,000 ml water) for 5-10 minutes to neutralize the acid. Rinsed sections floated on to glass slides were blotted and air-dried for 12-14 hours before affixing cover slips with Permount. In sectioning polar bear premolars, it was especially important to align the narrow root tip before mounting since it often curved laterally.

A variable-power miscroscope (14-60X) with a flourescent illuminator was used to view tooth sections. Structural characteristics were recorded by the tooth areas depicted in Fig. 1 so that investigators could trace annuli more accurately and compare teeth easily. Additional use of an overhead variable-power projector enabled 2 investigators to view sections simultaneously and discuss different interpretations. Cementum in C areas and the anterior A area was often damaged during tooth extraction and therefore did not provide discernible layering for counting.

Sixty-eight slides of teeth from known-age bears were analyzed. These teeth included 57 premolars from animals 1-10 years old and 11 lower third molars from hunter-killed animals 2-5 years old. To determine the magnitude of error and variation in reading tooth sections, slides were independently examined twice by each of 3 investigators. Investigator I had considerable experience in preparing and reading tooth sections of various mammals including brown, black, and grizzly bears. Investigators II and III were well versed in this technique but lacked recent experience. Slides were rearranged prior to a second examination; assigned ages were then compared with correct ages for analysis of error.

A series of body measurements of captured animals provided morphometric data. The series included total zoological length from nose tip, following dorsal curvature, to tail tip; total length in a straight line from nose to tail tip; body circumference directly behind forelegs; neck circumference; and hind-foot length from tip of mid-claw to heel. Linear and curvilinear multivariate regressions of these data were calculated for 46 known-age males 1-6 years old and 63 known-age females 1-10 years old.

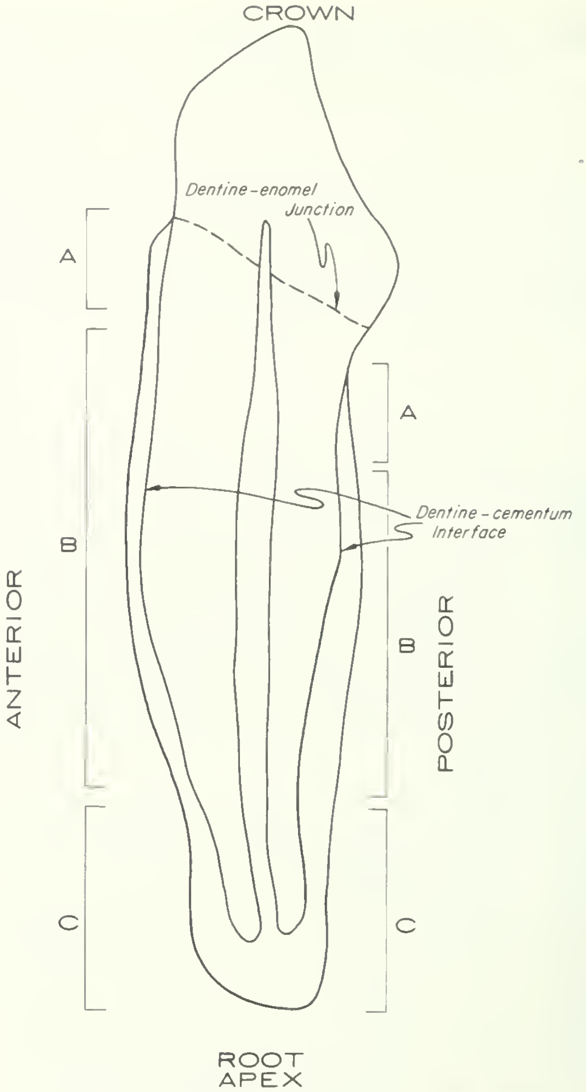

Fig. 1. Longitudinal section of polar bear Pm_1, showing cementum areas (A, B, C).

RESULTS AN DISCUSSION

Cementum Layering

Vestigial premolars apparently erupt as permanent teeth in polar bears as early as 2-3 months after birth. A fully erupted premolar of a 4-month-old cub disclosed a root length comparable to that of older bears. The root canal was open. Rausch (1961, 1969) found that because black and brown bear canines erupt between 9 and 12 months, there is 1 less cementum layer than the actual age. Similarly, the lower third molar was found in this study to erupt 9-12 months after birth and have 1 less annulation than the actual age.

Cementum deposited about the time premolar teeth erupt begins near the dentine-enamel junction and ends as a narrowing layer near the root apex. A thin, dark line extends the full length of the dentine-cementum interface, a structure described by Stoneberg and Jonkel (1966) as the neonatal line (Fig. 2).

Premolars from 14 polar bears 15-18 months old had completely or nearly closed root apices. The lightly stained growth layer was usually homogeneous except for C areas, where intense cellular activity adjacent to the dentine-cementum interface was believed to have displaced the neonatal line toward the exterior margin of the growth layer. This area stained lightly except for prominent dark spots probably comprised of interconnecting canaliculi and nuclei (Fullmer 1967). The active cellular area enlarged or invaded the root canal to thus obscure the first dark annulation. This obscurity persisted at all age levels in at least 90 percent of the teeth examined. Willey (1974) noted that the neonatal line became increasingly vague among older black bears.

Because cementum was deposited unevenly, the usual procedure was to select a counting area where annuli appeared as distinct layers. After identifying the neonatal line and the heavier band delineating the first growth layer, succeeding growth layers were counted from inside to outside. This procedure provided age estimates for premolars and for molars after adding another year to the total annuli.

Fig. 2. Lower third posterior surface of a known-age yearling polar bear premolar showing expanded neonatal zone (NZ) and single cementum layer. Neonatal line (N), dentine (D), periodontal membrane (PM), 100X.

The single growth layer typifying 14 yearling premolars was distinct except for distortion toward the root apex. Double lines, striations, and band displacement in the C area hindered correct interpretation.

Premolar sections of 13 2-year-olds exhibited the reverse; C and B areas, particularly along the posterior surface, provided the best place for interpretation. The line denoting the first year was indistinct and sometimes absent from the A area. Cementum layers were often moderately striated along the entire root surface. Less than 31 percent of the 13 2-year-old premolars had well-defined lines.

The 5 premolars from 3-year-olds also contained indistinct lines in the A area; however, their intensity increased just distal to the enamel junction. Legibility improved in the anterior C area despite supplemental streaks and striations along lower root surfaces. Less than 20 percent had well-defined lines, and all but the anterior A area contained multilayered lines (Fig. 3A).

Cementum characteristics differed markedly for premolars of 11 4-year-olds because annual layers were less distinct and uniform than in younger animals. This lack of clarity was most evident along the lower posterior surface, where bands frequently wavered, converged, and diverged. The A and B areas of the anterior surface were legible, although less than 25 percent had well-defined growth layers.

Cementum deposition in older animals appeared to have progressed from the dentine-enamel junction to the root apex. Teeth without new deposits over the entire root surface had more cementum in A areas than in C areas. New growth is apparent later in March and during April as evidenced by 80 percent of the teeth collected during this period. Dark-stained bands denoting periods of reduced growth appeared in December specimens, and a new, well-defined line appeared in specimens taken during February and later.

Anterior cementum on the first lower premolar was deposited nearer the dentine-enamel junction than on the posterior surface because this tooth erupts at an angle, causing the anterior protion to be embedded deeper in the mandible. Other vestigial premolars developed perpendicular to the mandible and contained equal cementum deposits on both surfaces.

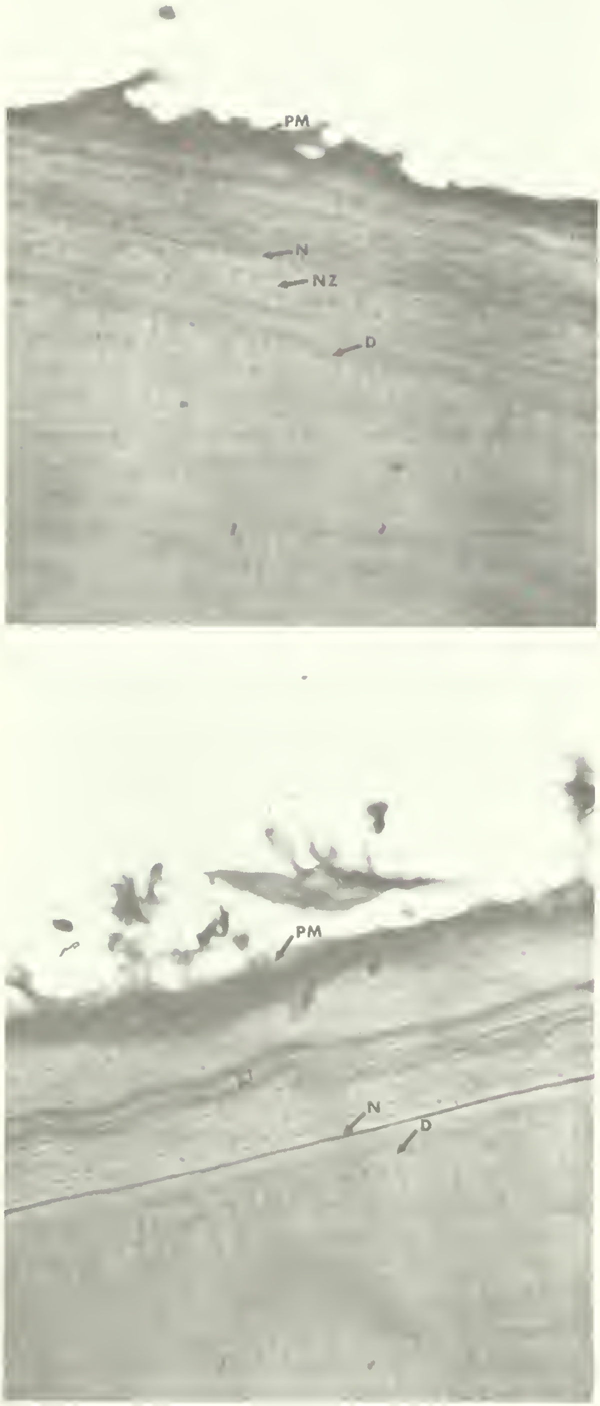

Fig. 3. Posterior surface of a known-age 3-year-old polar bear premolar showing (A) the neonatal zone (NZ) and multiple banding in Area C, and (B) double band of the first annual layer in Area B. Annual lines are numbered (A). Neonatal line (N), dentine (D), periodontal membrane (PM), 100X.

The first 2 growth layers were usually twice as wide as succeeding layers, with very narrow layers occurring after 5 or 6 years. Cementum deposits were widest along the posterior surface, particularly along the inward curved segment of B area. After the third or fourth layer had been deposited, succeeding annuli had uniform widths except near the exterior margin, where recent growth was sometimes narrowed. Double banding was prevalent, which may be described as the division of a single line into 2 dark lines bordering a lightly stained area (Fig. 3B). Because of double banding, dark-staining annuli often apeared as wide or wider than lightly stained growth layers; this occurred regularly in B and C areas of premolar sections.

In contrast to premolars of other bears as well as sea otters (*Enhydra lutris*) (Schneider 1973), harbor seals (*Phoca vitulina*), and sea lions (*Eumetopias jubatus*) (personal observation), polar bear premolars were without bulbous cementum deposits at the apex.

Growth layers were usually absent from the apex but, if present, were compacted toward the exterior margin. As well-defined lines approached the apex, they became discontinuous and illegible. Lines in the posterior segment of the C area were displaced and illegible. Lines in the posterior segment of the C area were displaced to the exterior margin in 20 percent of the premolars. Cellular activity associated with the neonatal line is believed to have caused the initial band to waver toward the exterior margin and to have compressed succeeding bands in these instances.

Lines along the posterior surface wavered along or distal to the inward curved segment of B area. This area is usually much wider than other areas, and wavering was more pronounced among premolars of immature polar bears but decreased in older specimens, particularly those with compact lines. As growth diminshed in older animals, cementum layers became more compact toward the outside surface. Lightly stained lines or striations appeared frequently among older specimens (Fig. 4). Irregularities such as swirls and indentions occurred among all ages.

Premolar specimens from 11 animals 5-10 years old exhibited characteristics similar to those of 4-year-old animals. These similarities included about the same legibility and better band definition in A and B areas of the posterior surface. Annuli compactness and a reduced incidence of multilayering constituted major differences.

Difficulties encountered in assigning ages to polar bears arise from indistinct annuli, double bands, multiple streaks, and striations. These irregularities are

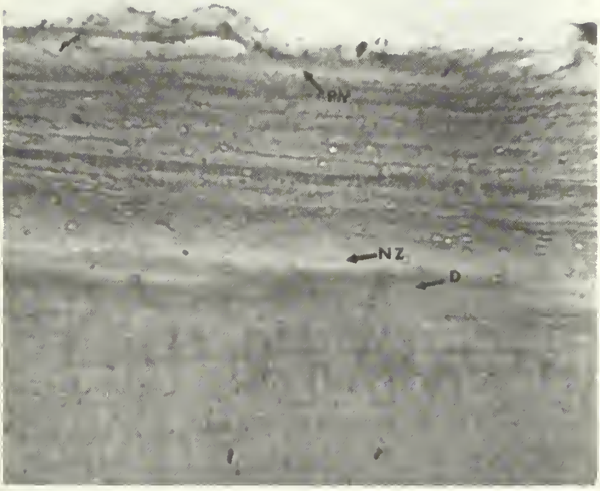

Fig. 4. Area C, anterior surface of a known-age 4-year-old polar bear premolar showing multiple striations. First growth layer obscured by neonatal zone (NZ). Dentine (D), periodontal membrane (PM), 100X.

probably associated with differences in food availability and other environmental conditions such as weather and breeding season. Protracted environmental conditions may cause intermittent denning throughout the long arctic winter and consequently disrupt the retarded growth layers and alter the legibility of cementum layers.

At present, the only way to determine whether lines are annual or not is to compare the relative width and numbers of growth layers. Although double lines occur frequently, they relate to a single annulation or to retarded growth layers. Double lines usually develop midway in root sections and converge or disappear toward the root apex. Interpretation can therefore be made near the dentine-enamel junction and above the root apex. Multiple streaks and striations often appeared in sections moderately stained with hematoxylin. With a certain amount of skill these structures can be distinguished from principal bands from which cementum layers are counted.

Age determination can be further complicated by compacted, uneven layers, particularly in outer growth layers. Under these circumstances any narrow, dark-staining lines can be equated with lighter or unstained growth layers to ascertain age. Low magnification often shows individual patterns that can be interpreted more easily than with greater magnifications. In teeth of older bears, annual layers may be more discernible if lightly stained. Future improvements in staining might resolve some of these problems.

Accuracy of Assigning Ages

A Student's t-test revealed no significant difference in accuracy of assigning ages to males and females ($t=0.86$, $P<0.1$), so data were combined to determine accuracy of assigning ages. Results of independent age assignments made by 3 persons for 57 unlabeled slides from known-age bears are diagramed in Fig. 5. An error of 2 years was considered to be unduly large.

The most experienced investigator (I) assigned correct ages to 45 percent of the 57 slides and made errors of 2 or more years for 2-, 4-, and 9-year-olds. For the less experienced investigators, only 32 and 37 percent were correct, with errors of 2 or more years made in all age-classes. All 3 investigators erred most frequently at the 3- and 4-year age levels. Repeating the examination for the second time, accuracy at the younger age level

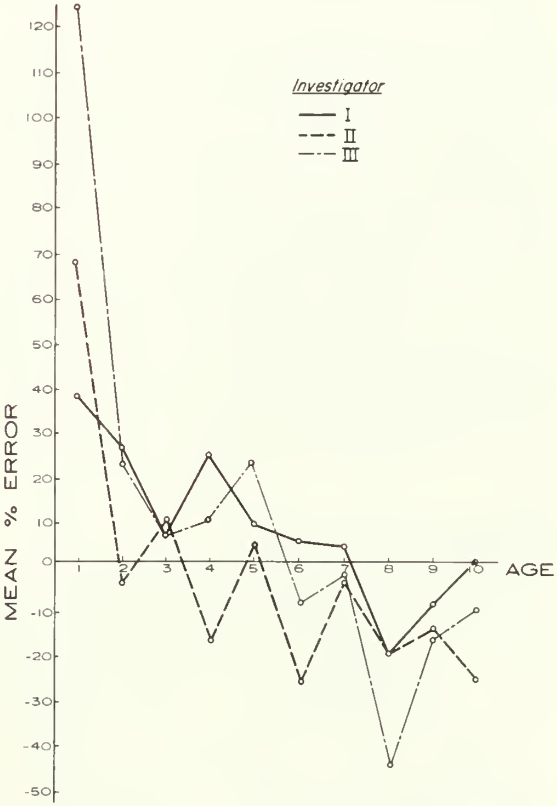

Fig. 5. Mean percentage error of ages assigned by 3 investigators from cementum annuli counts of polar bears.

improved for Investigator III but slightly decreased for the other investigators. These percentages are less meaningful because of the few specimens 5 or more years old.

The results of both examinations were combined to calculate a mean percentage error using the following equation:

$$\text{Mean \% error} = \frac{\frac{\Sigma A}{N} - K\ (100)}{K},$$

where A=assigned age, K=known age, and N=sample size.

Each investigator consistently overestimated ages of younger bears and underestimated ages of older bears (Fig. 5). Age assignments made by Investigator II varied from low to high until the 5-year level. The same individual tended to underestimate even ages and overestimated odd ages; the others began at 6 and 7 years to underestimate all ages. Similar inaccuracies were realized with molar sections.

Although differences in staining techniques have biased the results, this accuracy examination illustrated the magnitude of error inherent in counting cementum annulations in polar bear teeth. Double lines were a primary source of error, a situation that evidently persists throughout the life-span of most polar bears. Errors of 2+ years increased during even years as shown in Fig. 5. This increase may be partly attributed to a higher probability of misinterpreting an even number rather than an odd number of lines. The frequency and the magnitude of error present a serious problem, particularly among younger animals, the largest segment of the marked populations. For example, a 2-year error for a actual 4-year-old bear constitutes a 50 percent error. The width of growth layers in younger animals, however, reduces the probability of a miscount attributed to double lines. Compressed lines increased the probability of errors of 2+ years in older animals.

Age-related Morphometrics

Linear and curvilinear regression analyses of age-related body measurements were calculated for 46 known-age males, ages 1-6, and 63 known-age females, ages 1-10. Because growth diminishes after sexual maturity, at approximately 5 years for females especially (Manning 1964), 2 regressions were calculated using females 1-4 and 1-10 years old. The female sample contained all ages except 5- and 6-year-olds and the mark-recapture program has yet to provide known-age animals older than 10 years for study. Curvilinear regression provided higher correlation coefficients than linear regression. Table 1 presents curvilinear correlation coefficients. The highest age correlations in males and females were neck circumference, total length, and straight-line length. Correlation between age and size was greater for males than females. The lowest correlation in both sexes was between age and hind-foot length. Females had a greater correlation for ages 1-4 than when all ages were combined.

A standard forward stepwise regression was applied to determine the best combination of measurements. Equations for ages 1-4 are more meaningful than for ages 1-10 because of the small sample beyond 5 years (2 males, 5 females). These equations are:

$$\text{Males age 1-6} = 9.25\text{-}0.558(N)+0.015(N^2) +0.00165(SL^2)-0.163(SL)+0.00024(TL^2)$$
$$r^2=0.93$$
$$\text{Females ages 1-10} = 31.92\text{-}3.446(N) +0.091(N^2)+0.0007(SL^2)$$
$$r=0.70$$
$$\text{Females age 1-4} = 11.58\text{-}0.819(N)+0.0237(N^2) +0.0022(SL^2)-0.1799(SL)$$
$$r^2=0.78,$$

where N=neck circumference, SL=straight-line length, TL=total length (spinal curve), and r_2=coefficient of determination.

The coefficient of determination (r_3) identified only 78 percent of the variable for females ages 1-4 but 93 percent of the variability for males ages 1-6. The data for each known-age bear sampled were used in the corresponding equation to compare these results with the known age. Mean errors for ages calculated by regression equations are given in Table 2. Assuming a January birth date, most bears captured between March and May would have grown for 0.25-0.42 year, so errors less than 0.50 are acceptable.

The mean error for all males is within 0.3 year except for age 6, which is underestimated. The males were aged accurately by the above equation (e.g., a 4-year-old bear in March would be 4.25 years, and 4.18 years by the equation). The age equation for 1-to 4-year-old females alternated between over- and under-estimation and, except for age 4, mean error for each group was within ±0.3 year.

Generally, equations became inaccurate at the upper limit as evidenced by the female equation for ages 1-10. For ages 8, 9, and 10, the equation underestimated the actual age by about 3 years. The small sample of older bears biased the equations toward younger animals and also slightly increased their ages.

The possibility that polar bears form discrete popu-

Table 1. Correlation coefficients for body measurements and ages of 109 known-age polar bears. *TL* = total length, *SL* = straight-line length, *G* = girth circumference, *N* = neck circumference, *HF* = hind-foot length.

Sex and age (years)	TL	TL^2	SL	SL^2	G	G^2	N	N^2	HF	HF^2
Males										
1-6	0.88	0.91	0.87	0.89	0.87	0.89	0.90	0.91	0.84	0.85
Females										
1-4	0.75	0.76	0.73	0.77	0.72	0.72	0.77	0.78	0.56	0.57
1-10	0.69	0.71	0.63	0.67	0.66	0.67	0.74	0.76	0.49	0.51

Table 2. Mean error in years calculated from regression equation. Sample sizes are in parentheses.

Regression equation	Known age									
	1	2	3	4	5	6	7	8	9	10
Males										
1-6	0.15(27)	0.14(8)	0.05(1)	0.18(7)	0.08(1)	−0.30(2)	-	-	-	-
Females										
1-4	0.04(29)	−0.10(24)	0.29(1)	−0.86(4)	-	-	-	-	-	-
1-10	0.12(29)	0.26(24)	1.68(1)	0.66(4)	-	-	1.45(1)	−3.38(2)	−3.31(1)	−2.83(1)

lations (Jonkel 1970; Larson 1971; Manning 1971; Lønø 1972; Lentfer 1974, 1975; Stirling 1974) would require separate regression equations for each population. At this time it would be difficult to obtain large enough samples, especially for older animals, to evaluate this relationship.

Evaluation of Aging Criteria

Age estimates based on cementum annuli combined with individual regressions of age-related body measurements and with teeth and reproductive characteristics were used to evaluate the individual ages tentatively assigned to 546 polar bears of unknown age. Ninety percent of the bears were believed to be less than 11 years old when first captured.

Of 546 animals, 70 percent of the assigned ages required no adjustment, whereas 20 and 10 percent had to be adjusted by 1 and 2 years, respectively. Bears older than 11 years exhibited less conformity; 17 percent required 1-year and 25 percent required 2-year adjustments. The same tendency to age younger animals as older animals and vice versa prevailed, however.

Tentative age estimates made in the field proved remarkably close to age estimates derived from cementum annuli. This close agreement reflected the quality of observations made on age-related tooth wear, reproductive, and growth characteristics of each immobilized bear. Age assignments were finalized if field estimates corresponded to those obtained from discernible tooth sections. Illegible or questionable tooth sections, on the other hand, prompted greater reliance upon age-related regression equations, reproductive parameters, and tentative age estimates.

A mean breeding interval of 3.4 years and a 3-year minimum breeding age (Lentfer et al. 1979) permitted age extrapolation for some females. Any disparity in litter age or frequency related to these parameters indicated the necessity to adjust ages for maternal females. Growth regression equations provided a reliable method for age determination of females up to 4 years and of males up to 6 years. As additional known-age material becomes available these processes will be refined and perhaps augmented by other criteria such as skull measurements following the technique outlined by Manning (1964).

An accurate method of age determination is prerequisite to understanding the periodicity of reproduction, age composition, and age-specific mortality in Alaska's polar bear populations. This preliminary study suggested that exclusive use of cementum annuli for age determination would adversely affect the credibility of population studies. As this age determination study continues, compensatory steps to alleviate this problem include (1) assuring that tentative age estimates of captured animals be carefully considered; (2) taking consistent and accurate body measurements; (3) improving techniques for preparing and analyzing tooth sections; and (4) combining all age-related data to arrive at the best possible age estimate.

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ALASKAN POLAR BEAR DENNING

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Abstract: Information on 35 overwinter maternity dens of Alaskan polar bears (*Ursus maritimus* Phipps) and on 101 female polar bears with cubs, recently emerged from dens, was obtained by aerial and ground surveys, interviews with Arctic coast residents, and literature review. Pregnant females form snow dens in October and November and give birth in December and January. Females and cubs emerge from dens in late March and April. Factors necessary for continued successful denning in an area include ice movements that enable bears to reach the area in the fall; the availability of seals as a food source and ice conditions facilitating their capture during the predenning and postdenning periods; and suitable weather conditions (snowfall, wind, and ambient temperatures) and topography that combine to produce snowdrifts that do not thaw during the denning period. Dens consist of 1 or more chambers, connecting tunnels, and entrance-exit tunnels. Alaskan dens were found as far inland as 48 km from the coast, along the coast, on offshore islands, on shorefast ice, and on drifting sea ice. Bears denning in the coastal zone are subject to human disturbance and should receive protection.

Parturient female polar bears give birth in winter snow dens occupied from late October or November to late March or April. For their first 3 months, cubs born in December or January require a den for protection from the harsh arctic environment. Thus, good denning conditions are essential for maintenance of populations.

Land areas where bears concentrate for denning have been described by Uspenski and Chernyavski (1965), Harington (1968), Jonkel et al. (1972), Uspenski and Kistchinski (1972), and Larsen (1976). Bears do not concentrate for denning on the Alaskan coast, and it was formerly thought that recruitment to the Alaskan populations was from the Soviet Union and Canada.

An objective of this study was to determine if denning occurs on or offshore from Alaska's coast, and if so, where and to what extent. Another objective was to obtain information on which to base recommendations for protection of denning polar bears from the impacts of energy exploration and extraction in the Alaskan Arctic. The need for protection is especially critical because the Marine Mammal Protection Act of 1972 removed all restrictions on harvest of polar bears by Natives; therefore, denning females are no longer protected.

We gratefully acknowledge the Alaska Department of Fish and Game for providing data obtained before 1973, the Naval Arctic Research Laboratory and DEW-line stations for logistics support, numerous residents of the north coast for information and hospitality, and many members of the Alaska Department of Fish and Game and the U.S. Fish and Wildlife Service for assistance with mark and recapture studies. The following people deserve special recognition for assisting with den searches: G. Hall, A. Thayer, D. Frickie, T. Schmidt, and D. Ross of the U.S. Fish and Wildlife Service, C. Evans of the University of Alaska; R. Quimby and G. Moore of Renewable Resources Consulting Services; and W. Overway of Interior Department Office of Aircraft Services. F. Sorensen assisted with data compilation.

METHODS

Interviews to obtain denning information were conducted with residents of northern Alaska coastal villages and Prudhoe Bay oil camps. Pilot-guides were queried after hunting flights. Of particular value were detailed records of H. Helmericks, who has lived on the Colville Delta for more than 20 years and guided polar bear hunters until 1973. Files of the Naval Arctic Research Laboratory at Barrow and literature review provided additional information.

In a well-publicized program started in 1973, the U.S. Fish and Wildlife Service offered $50 to anyone reporting an overwinter maternity den and leading a biologist to it to verify the report and inspect the den. Payment was increased to $200 in 1974.

After freeze-ups in the falls of 1965, 1967, 1971, 1973, 1974, and 1976, surveys were flown (Cessna 180 and 185) along the coast and offshore islands between Point Barrow and the Canadian border. Objectives were to track bears inland to denning sites, determine from tracks the relative densities of bears at different locations, and record ice conditions and relative abundance of ringed seals (*Phoca hispida*). Flights and observations were hampered by adverse flying conditions, and only 1 den was found during fall surveys.

Fish and Wildlife Service personnel using light aircraft searched for dens in late March and early April 1973, 1974, and 1975, when females with cubs were emerging from dens. Renewable Resources Consulting

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Services, obtaining data for a proposed natural gas pipeline from Prudhoe Bay to the Mackenzie Delta, also searched for dens from aircraft in 1974 and 1975. Areas searched were shorefast ice, offshore islands, the mainland beach, and inland for approximately 50 km. Search efforts were concentrated in areas where drifting snow had accumulated in the lee of pressure ridges and cutbanks and in river and stream bottoms. It was assumed that tracks of bears leaving dens could be followed back to dens, as was done in Manitoba, Canada (Jonkel et al. 1972). Snow was so hard-packed in many areas, however, that Alaska observers could not see tracks from aircraft. Windblown snow also covered some tracks and den exits.

Two 2-man teams hired from the village of Kaktovik in the Arctic National Wildlife Range searched between the Hulahula and Katakturuk rivers and the Jago and Kongakut rivers in April 1975 but found no dens.

Polar bear mark and recapture studies based at Lisburne, Barrow, and Barter Island provided incidental information on denning (Lentfer 1975).

RESULTS

The general characteristics of maternity dens and their use in the Alaska coastal zone were similar to those reported previously for other areas (Uspenski and Chernyavski 1965, Harington 1968, Lønø 1970, Uspenski and Kistchinski 1972, and Larsen 1976). Pregnant females came to the coastal zone in late October or early November; exact times and locations depended on ice movement and freezing. First observations were east of Point Barrow and then southwest of Point Barrow in the same sequence that shorefast ice forms. Bears were more numerous in years when winds from the north and west brought old ice to the coast than when new ice drifted in (Lentfer 1972).

Parturition occurred in midwinter, and females and cubs broke out from dens in late March or early April. After emergence, family groups continued to use their dens intermittently for several days before abandoning them.

Dens were sparsely distributed on the mainland, on offshore islands, on fast ice, and on drifting ice (Table

Table 1. Search effort (whole or part crew-days), number, and mean distance from mainland coast (km) of polar bear maternity dens and cub litters, northern Alaska. A, B, C, and D refer to map (Fig. 1). Numbers in parentheses are ranges.

	Land	Offshore island	Shorefast ice	Drifting ice
A. *Point Hope-Lisburne-Northeastern Siberia area*				
Search effort	25	25	50	100
Number of dens	1	0	1	1
Distance from coast	9	-	6	93
Number of cub litters	0	1	0	16
Distance from coast	-	26	-	96(37-204)
B. *Barrow area*				
Search effort	50	50	75	400
Number of dens	6	0	0	2
Distance from coast	8(0-24)	-	-	117(65-169)
Number of cub litters	0	0	2	58
Distance from coast	-	-	4(2-6)	77(7-204)
C. *Oliktok area*				
Search effort	60	100	150	100
Number of dens	5	2	3	1
Distance from coast	30(19-48)	13(7-19)	6(2-9)	21
Number of cub litters	2	0	3	15
Distance from coast	10(2-19)	-	15(9-19)	43(9-111)
D. *Barter Island area*				
Search effort	65	65	65	30
Number of dens	7	1	4	1
Distance from coast	15(4-22)	4	7(2-9)	28
Number of cub litters	0	0	0	4
Distance from coast	-	-	-	127(28-278)
Total				
Search effort	200	240	340	630
Number of dens	19	3	8	5
Distance from coast	16(0-48)	10(4-19)	6(2-9)	75(21-169)
Number of cub litters	2	1	5	93
Distance from coast	10(2-19)	26	11(2-9)	77(7-278)

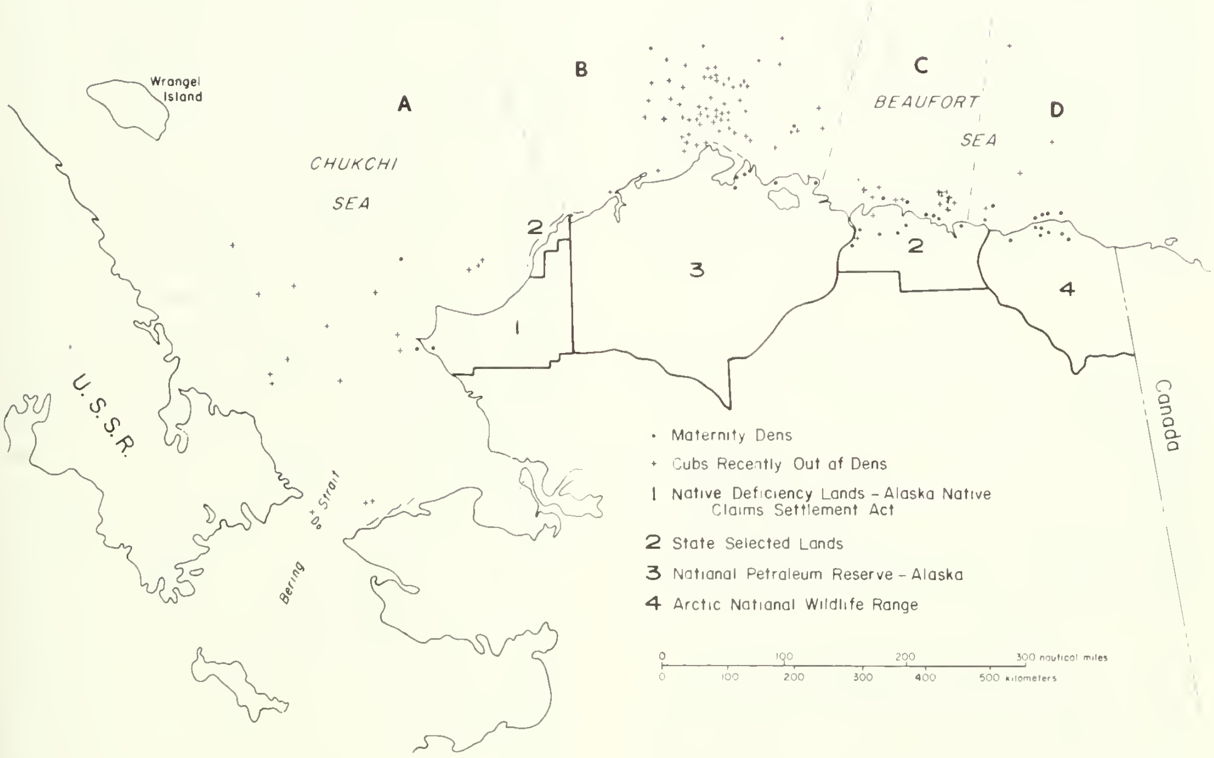

Fig. 1. Northern Alaska, showing distribution of polar bear maternity dens and of cubs recently out of dens, and land status along coast. A, B, C, and D refer to areas of search effort (Table 1).

1, Fig. 1). The den farthest offshore was 169 km from the coast, and the den farthest inland was 48 km from the coast. More dens were found on land and on shorefast ice between the Colville River and the Canadian border than on other areas searched. A large number of cubs were observed on drifting ice north of Point Barrow. The greatest distance from shore that a cub was sighted was 278 km.

Inspection of 10 dens (Table 2) revealed 7 with 1 denning chamber and 3 with 2-3 chambers. Two dens had additional chambers 50 cm or less in height that had probably been formed by cubs. Surfaces of ceilings, walls, and floors varied from hard-packed snow showing recent signs of digging to ice layers 2-7 cm thick. In dens with more than 1 chamber, chambers with the least amount of ice had been used most recently. Two dens had vents to the surface, 38 and 45 cm in diameter. Five dens contained fecal material and 5 (not all the same dens) contained urine. In 3 dens, feces were from the adult only and in 2 dens from cubs only. No attempt was made to examine the snow beneath den floors for feces or urine that might have been covered by snow.

As females and cubs traveled from denning areas to leads in the sea ice, where they fed on seals, they sometimes formed temporary resting shelters consisting of simple depressions in the snow, generally in the lee of the wind. No dens used over long periods were observed or reported, except those of parturient females. Observations and kill reports by Alaskan Eskimos indicate that all age/sex-classes of bears except parturient females and cubs live outside of dens throughout the winter. Denning for extended periods by polar bears other than parturient females has been reported in Canada (Van de Velde 1957, 1971; Harington 1968) and in northern Taimyr and northern Greenland (Uspenski and Chernyavski 1965). Earth dens like those used in the Hudson Bay and James Bay areas of Canada (Kolenosky and Stanfield 1966, Doutt 1967, Jonkel et al. 1972) have not been reported along the Alaskan coast. Alaskan bears need not spend summers on land as bears do at Hudson Bay, where sea ice melts completely, leaving no permanent pack ice on which bears can summer.

Table 2. Measurements (cm) of 10 polar bear dens, Alaska, 1972-74.

	N	Mean	Range
Main chambers			
Number	14	1.4	1-3
Height	13	78	51-109
Width	14	162	81-229
Length	14	180	81-508
Exit tunnel length	10	257	0-732
Exit-entrance height	9	62	32-81
Exit-entrance width	9	87	61-109
Snow depth above chambers	9	67	13-137

DISCUSSION

Distribution of Denning

One reason that more dens were found on land and on shorefast ice between the Colville River and Canadian border than elsewhere along the northern Alaskan coast is that ice first forms in the fall between Point Barrow and the Canadian border, and therefore pregnant females may come ashore in that area earlier than in others. Another reason is that oil and gas development started east of the Colville River, prompting searches for dens.

Like many other mammals, female adult polar bears may show fidelity to parturition sites and therefore try to reach specific denning areas. Return of females to previously used denning areas could help maintain subpopulation of bears (Manning 1971, Lentfer 1974, Wilson 1976). The number of bears returning to specific coastal areas to den may vary from year to year, however, depending on the type of ice and the time it forms. As mentioned, bears are more abundant along the coast in years when winds bring heavy ice to the coast early in winter than in years when newly frozen ice drifts in to shore or freezes in place a considerable distance offshore (Bailey and Hendee 1926, Lentfer 1972). The numbers of bears in denning areas elsewhere in the polar basin also vary from year to year, depending on ice conditions (Harington 1968, Kistchinski 1969, Lønø 1970, Uspenski et al. 1978).

Snowfall, ambient temperatures, wind, and topography, all occurring in such a manner as to result in snowdrifts that do not thaw during the denning period, are necessary for continued successful denning in an area. Another requirement is the availability of seals nearby and ice conditions enabling bears to catch them during predenning and postdenning periods.

Bears that do not reach offshore islands, fast ice, or the mainland may den on drifting sea ice. Drifting ice can transport denned bears through areas where ice movement is a threat to dens or to areas where feeding conditions are poor when bears emerge from their dens.

The best method for determining the area where bears emerging from dens on sea ice may have entered the dens 5 months earlier is to refer to long-term mean ice drift calculated from many years' data collected at drifting stations (R. Colony and D. Rothrock, AIDJEX, University of Washington, personal communication). The method is not precise because winds causing ice drift vary considerably from year to year. Stresses transmitted between floes also affect drift, and maps of surface pressure, which determines the wind, do not give exact estimates. Along the Beaufort Sea coast, ice drifts from the Canadian border toward Point Barrow at a mean speed of 2-5 km per day. It moves away from the coast as it passes Point Barrow. It would be useful to be able to predict with some degree of certainty the drift patterns from dens originating in various locations. Data from the Arctic Ice Dynamics Joint Experiment (AIDJEX), a United States-Canadian study of Beaufort Sea ice, could be used to refine existing data obtained from ice stations.

From long-term data on mean drift, it was calculated that a den on drifting ice 169 km northwest of Point Barrow, when bears emerged 1 April, had been less than 20 km offshore in the vicinity of Barter Island when first occupied about 1 November (drift calculated by D. Rothrock, AIDJEX, University of Washington). The den had drifted about 650 km.

Several circumstances may explain why more dens, and cubs recently out of dens, were reported offshore from Alaska then from other offshore areas. Ice may not be suitable for denning in some other locations, as Lønø (1970) reported for Spitsbergen. Also, there was more opportunity to record cubs recently out of dens in the Alaska sector during the 15-year period before 1972, when hunting guides searched for bears with airplanes and reported sightings. An intensive offshore research program by federal and state biologists has also provided data. We do not know if the large number of cubs reported and tagged north of Point Barrow indicates that denning is concentrated in this region or if cubs occur at about the same density over a large portion of the sea ice north of Alaska. Cubs observed on sea ice in March or early April are probably born fairly close to where they are observed, but by late April cubs may have traveled considerable distances.

Dens are more sparsely distributed in the Alaska coastal zone than in core denning areas in other countries (Uspenski and Chernyavski 1965, Harington 1968, Jonkel et al. 1972, Uspenski and Kistchinski 1972, Larsen 1976). A comparison of the Alaskan coastal zone with Wrangel Island off the eastern Siberian coast, where 150-200 females produce cubs each year, suggests an explanation. A primary requisite for successful denning is deep snow. Wrangel Island has hills up to 1,100 m above sea level, where drifted snow collects on open slopes. These hills may provide many more suitable denning sites per unit of area than the flat Alaskan coastal zone, where snow collects only along drainages, cutbanks, and rough ice. Also, Stirling et al. (1975) suggested that intensive hunting along the Alaskan coast, since whalers introduced firearms more than 80 years ago, may have reduced the stock of bears that traditionally came ashore to den. This suggestion is based on the premise that adult female polar bears show a fairly high degree of fidelity to parturition sites.

Climatic changes may also affect distribution of dens. Long-term warming and cooling trends in the Arctic have been demonstrated (Budyko 1966, Vibe 1967). As warming trends cause ice to form later in the fall, bears may be unable to reach areas that formerly supported denning. A warming trend would also impair the snow conditions necessary for successful denning. Conversely, cold trends would increase numbers and sizes of areas suitable for denning. Snow depth is also related to climate. In years when little snow accumulates, bears may den later, emerge from dens temporarily in midwinter, or leave their dens earlier than when normal snow depths provide satisfactory denning situations. Such activity causes an energy drain that could directly or indirectly increase mortality. The IUCN Polar Bear Specialist Group (1978) pointed out that managers should be particularly aware of the vulnerability of polar bear populations during periods when detrimental human activities coincide with unfavorable climatic conditions.

Den Structure

Alaskan dens are similar in structure to dens described for other areas (Harington 1968, Uspenski and Kistchinski 1972, Larsen 1976), but several points merit discussion. Den site and configuration may affect physiology of bears, especially thermoregulation and energetics. They are especially critical for females, which do not feed for a 5-month period that includes the last term of pregnancy, parturition, and lactation. They are also critical for cubs, which have only short hair and no fat layer to aid in thermoregulation.

Not all dens had vent holes to the outside. Bears may control temperature by blocking or enlarging vents, actions observed for a denning zoo bear (Mitchell 1921). Adjusting the size of vent holes may help maintain the insulating quality of snow by keeping temperatures in dens low enough to prevent thawing and subsequent ice layering. Vent holes may also allow gas exchange between the dens and outside if snow conditions or ice layers on the den ceilings reduce this exchange. Heavy ice layers in some denning chambers indicated that temperatures sometimes rose above freezing. Bears may dig other chambers when ice decreases the insulating value of snow and the gas exchange through the snow.

Tunnels showed varying degrees of use. A portion of a tunnel formed in the fall may be used for the entire denning period. A new tunnel may be formed to lead to a new chamber, and an exit tunnel to the outside may be formed in the spring. Some tunnels were long, possibly to conserve heat in the denning chamber.

Evidently some bears claw at the ceiling, as snow drifts over the den, to maintain a fairly constant snow depth above the den and perhaps to eliminate an ice layer as it forms. The snow from the ceiling falls to the floor, so the height of the denning chamber remains about the same. In some instances, however, bears tolerate deep snow over a den. Harington (1968) reported snow depths of more than 2.25 m over dens. Dens with floors on or close to the ground or ice may receive more heat dissipated from the ground or from the water beneath the ice then dens with thick layers of snow beneath them (Elsner and Pruitt 1959). Depth and density of snow over dens may also affect den temperatures. Some of these physiological aspects of denning have been studied on Wrangel Island (S. Belikov, personal communication) and will be studied in the Churchill, Manitoba, denning area (N. Oritsland and P. Watts, personal communication).

Management Considerations

Alaskan polar bears that den on shore and fast ice can be hunted or subjected to other human disturbance for several months each year. Therefore, denning requires special management consideration.

The Marine Mammal Protection Act of 1972 transferred management authority for polar bears from the State of Alaska to the U.S. Department of the Interior and removed all restrictions on taking of polar bears by Natives, provided waste does not occur. Females accompanied by young, and their young, were protected even from subsistence hunters before the Marine Mammal Act. The State of Alaska has requested return of management with a proposed program that would protect the young and females with young throughout the year and would protect pregnant females coming ashore to den by establishing a closed season from 1 June through 31 December.

Increasing human activity associated with oil, gas, and coal exploration and development could also adversely affect denning. Human activity might cause females coming to shore to den in October and November to move back onto drifting sea ice and den there. Drifting ice may provide a less stable platform than land or shorefast ice and thereby reduce denning success. Drifting ice may also transport bears to areas where they cannot find adequate food when they emerge from their dens. Human activity might interfere with bears that had selected sites for denning. Shereshevskii and Petriaev (1949) stated that females were easily frightened away from dens before parturition. Belikov (1976) reported that several bears deserted dens on Wrangel Island shortly after forming them in October and November because of the presence of investigators. Belikov (1976:37) further stated: "Contact of breeding females with man leads to a disturbance of the normal rhythm of breeding and rearing of young. Consequences are still unclear but undoubltedly there is a negative influence on the life cycle of the polar bear." Disturbances could also affect bears later in the denning period. Bears in zoos produce cubs successfully only if shielded from noise and visual disturbances during denning and for several months thereafter. There is some evidence that bears in the wild, when disturbed in their dens, neglect the cubs or lead their cubs out of dens before the young are sufficiently developed to withstand the severe midwinter environment. On 2 and 3 March 1974, a seismic crew observed a female with a new cub traveling northeast across Prudhoe Bay, Alaska. The bears had left their den a month earlier then normal, possibly because of seismic or other human activity. The cub was extremely small, had difficulty in traveling, and may not have survived. In contrast, however, oil company personnel observed a den with a female and 2 cubs for several weeks on Niakuk Island in Prudhoe Bay during the winter of 1973-74, and the bears did not abandon the den (C. Knowles, personal communication). Belikov (1976) observed a den throughout the denning period from October to April at fairly close range, and these bears did not abandon the den prematurely.

Possible effects of disturbance to denning bears appear serious in view of the potential for industrial development along much of Alaska's north coast. The Beaufort Sea outer continental shelf and the coastal plain from northwest Alaska to the Canadian border has high potential for oil and gas, and the coastal plain has extensive coal deposits. Extraction of these resources will likely be a major goal on state lands, Native lands, National Petroleum Reserve — Alaska, and the Beaufort Sea Outer continental shelf, and could occur in the Arctic National Wildlife Range (Fig. 1). A number of actions can be taken to protect bears and their habitat. An ecosystem approach over large areas should be followed rather than a species-by-species approach in restricted zones. The ecosystem approach would require cooperative land and offshore management by federal, state, and local governments and holders of oil and gas leases and, if possible, by Soviet and Canadian governments. The concept of fairly large zones of minimal activity between developmental zones should be considered.

The coastal area of National Petroleum Reserve — Alaska should receive special area designation for protection of wildlife values as provided for in the National Petroleum Reserves Production Act of 1976. Jurisdiction over this area should be clearly established so that the agency responsible for environmental protection can implement protective measures in the near future (Skladel 1974).

There should be one-time-only seismic exploration on public lands, accomplished by treating information from seismic surveys as public property and making it available to all who might wish to evaluate oil potential on public lands. Near shore seismic exploration should be conducted with reduced charges from boats during summer rather than from fast ice during late winter.

Activity should be reduced along the coast during the late October-early November period, when bears come ashore to den, and also from late December through mid-April, when disturbance could cause bears to desert their dens after the cubs are born. Seismic lines, pipelines, and roads should be routed at right angles to the coast rather than parallel and adjacent to it. Specific proposals for development, including plans for removal of snow from drift areas for roads and pads, should be reviewed by wildlife specialists to minimize impact on denning bears. *No-activity* zones should be established around active polar bear dens.

Camps to support oil and gas activities should be established inland rather than on routes that bears normally travel along the coast. Studies to develop scaring devices and deterrents to keep bears away from camps should be continued (Wooldridge 1980, Wooldridge and Belton 1980). Garbage should be incinerated properly. Spilled oil, fuel, chemicals, and drilling muds should be contained in lined, bermed sumps and storage areas.

Studies to delineate areas of critical polar bear habitat, especially denning areas, should be continued. The relative importance of coastal areas and sea ice for denning should be determined. Effects of disturbance on individual bears, particularly denning females, should be quantified. These determinations would require observations of the effects of disturbance, either artificial or actual, during the predenning, denning, and postdenning periods. Effects of human activity and of oil spills on ringed seals and other organisms in the food chain supporting polar bears should also be determined.

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POPULATION CHARACTERISTICS OF ALASKAN POLAR BEARS

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Abstract: A mark-recapture study of Alaskan polar bears (*Ursus maritimus*) was conducted between 1967 and 1976. Of 809 bears tagged, 147 were recaptured 1 or more times or killed by hunters. Three-year-old males and 6- and 7-year-old females were underrepresented in the captured sample. Analyses of cohort age composition over time indicated male (age 6+) and female (age 8+) annual survival rate of 0.84. Average litter size was 1.63 and breeding interval was 3.6 years. The age of first successful breeding for females was 5.4 years. For adult females, the average number of young per year was 0.45. With these fecundity estimates, the annual juvenile survival rate of 0.97 calculated from cohort data is that which is required to maintain population size.

The purpose of this study was to define population characteristics of Alaskan polar bears as a basis for developing sound management programs. Objectives were to determine population composition, reproductive rates, survival rates, and numbers and trends.

It is especially important at the present time that wildlife managers understand population dynamics of Alaskan polar bears because land ownership and land management policies in northern Alaska are changing and demand for fossil fuel located along and offshore from Alaska's north coast is increasing. Regulatory agencies also need to know population characteristics in order to assess existing regulations and proposed changes.

This paper is a report of population data, mostly from a polar bear mark and recovery program conducted by the Alaska Department of Fish and Game and the U.S. Fish and Wildlife Service for the 10 years from 1967 through 1976.

We gratefully acknowledge the Alaska Department of Fish and Game for providing data obtained before 1973, the Naval Arctic Research Laboratory and DEW line stations for logistics support, and numerous members of the Alaska Department of Fish and Game and the U.S. Fish and Wildlife Service for assistance with mark and recapture studies.

METHODS

Polar bears located on sea ice from aircraft between 1 March and 10 May were immobilized for examination and marking by injecting phencyclidine hydrochloride (Sernylan) with a syringe gun from a helicopter. They were marked with ear tags, lip tattoos, and large numerals dyed on the fur (Lentfer 1968). Of a total of 809 bears captured for the first time (Table 1, Fig. 1), 94 were recaptured 1 or more times and 53 were taken by hunters. An intensive effort was made to resight marked animals during the 1976 study period.

Table 1. Distribution of 809 Alaskan polar bears captured for the first time for marking.

	Area								
	Bering Strait		Lisburne		Barrow			Barter Island	
	M	F	M	F	M	F	Unknown	M	F
1967	0	0	0	0	13	18	0	0	0
1968	5	5	20	30	24	56	0	0	0
1969	0	0	5	2	4	16	2	1	1
1970	0	0	7	20	19	34	1	0	0
1971	0	0	13	9	19	33	0	0	0
1972	0	0	25	34	33	63	0	0	0
1974	0	0	0	0	51	66	1	0	0
1975	0	0	0	0	18	20	0	19	16
1976	0	0	24	25	23	34	0	0	0
Total	5	5	94	120	204	340	4	20	17

Ages of cubs, yearlings, and 2-year-olds were usually determined by body size. Occasionally, degree of canine tooth eruption was used to distinguish yearling males from 2-year-old females. Older bears were assigned ages based on tooth cementum layering, tooth wear, body measurements, and indicators of reproductive status (Hensel and Sorensen 1980). In a few instances, not enough information was obtained to assign an age.

Reproductive status of females was determined from the condition of the vulva (infantile, turgid, open) and the mammae (nipple size and color, lactation in past or in present).

Before passage of the Marine Mammal Protection Act of 1972, Department of Fish and Game personnel

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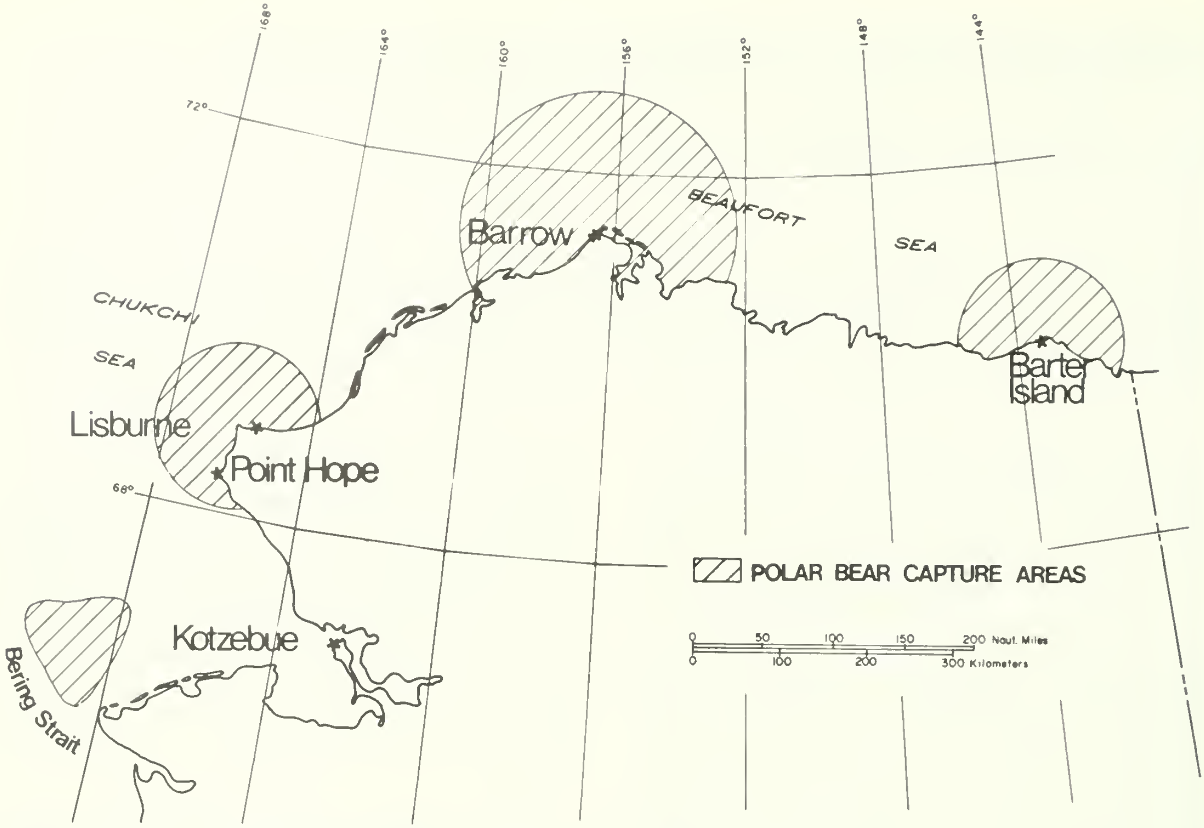

Fig. 1. Map of northern Alaska showing where polar bears were captured, 1967-76.

stationed in coastal villages to monitor hunting activity obtained polar bear testes, female reproductive tracts, teeth for sectioning, and skull measurements to relate reproductive status of individual animals to age. Incidental to Alaskan studies, testes were also obtained from bears taken on sea ice near Spitsbergen (north of Norway) during August 1967. Sections of selected testes and epididymides were examined for sperm (Lentfer and Miller 1969). Female tracts were measured and examined for placental scars and ovarian bodies.

The length of the reproductive cycle (interval between fertile breedings) was obtained by recapturing females with second litters or recapturing females without young who state in the reproductive cycle could almost definitely be determined by other means (e.g., a postlactating female paired with a mature male and in estrus when captured would be assumed to be entering another breeding cycle). A reproductive rate (average number of young produced per year per adult female) was obtained by dividing average cub litter size by length of breeding cycle.

RESULTS AND DISCUSSION

Population Composition

The best indication of polar bear population composition is a composite age structure from known or estimated ages of 378 males and 555 females captured between 1 March and 10 May from 1967 through 1976 (Table 2). That sample consisted of 32 percent litter members (cubs, yearlings, and 2-year-olds), 43 percent females 3 years old and older, and 25 percent males 3 years old and older. The data may not adequately represent some population segments, however, for the following reasons.

Relatively few cubs, compared with yearlings, were recorded because new family groups were in maternity dens during the first part of study periods. The low number of 6- and 7-year-old females is additional evidence that females with cubs were underrepresented, since at these ages substantial numbers of females have their first litters. The small number of 3-year-old males perhaps indicates dispersion of subadult males from sampling areas after family breakup. There is no reason

Table 2. Composite age structure of 933 Alaskan polar bears marked or recovered after marking, 1967-76.

Age	Male		Female		Total	
	Number	Percent	Number	Percent	Number	Percent
0	22	2.4	28	3.0	50	5.4
1	65	7.0	65	7.0	130	14.0
2	49	5.3	65	7.0	114	12.2
3	25	2.7	51	5.5	76	8.1
4	53	5.7	51	5.5	104	11.1
5	55	5.9	51	5.5	106	11.4
6	39	4.2	34	3.6	73	7.9
7	25	2.7	36	3.9	61	6.5
8	11	1.2	53	5.7	64	6.9
9	9	1.0	32	3.4	41	4.4
10	11	1.2	24	2.6	35	3.8
11	1	0.1	18	1.9	19	2.0
12	3	0.3	12	1.3	15	1.6
13	3	0.3	13	1.4	16	1.7
14	1	0.1	5	0.5	6	0.6
15+	6	0.6	17	1.9	23	2.5
Total	378	40.3	555	59.7	933	100.0

to believe that 3-year-old males were less susceptible to capture than older males. Females predominated in older age-classes because mature males tended to range farther offshore and out of sampling areas early in sampling periods, females with cubs and yearlings were protected from hunting through 1972, and hunters selected the larger males at an earlier age than females (225 males compared with 137 females killed in the Barrow area, 1967-72). Mature females and young may be slightly overrepresented in samples because family groups rather than single bears were captured for marking if the option existed.

Survival Rates

Composite annual survival rates were calculated from segments of the age structure data for each sex by using regression estimates (Seber 1973:414) and Chapman-Robson estimates (Chapman and Robson 1960). For males, these estimates were made for survival for ages 2-6 and for older than age 6. Information for males of age-class 3 was eliminated because this group was underrepresented in the samples (Table 2). For females, estimates were made of survival for ages 2-8 and for older than age 8. Information for female age-classes 6 and 7 was eliminated because they were underrepresented in the sample (Table 2). The age 6 separation point for males and age 8 separation point for females were chosen after examination of the age structures (Table 2).

Table 3. Estimates of annual survival rates for male and female polar bears.

	Males		Females	
	Age (years) 2-6	>6	Age (years) 2-8	>8
Composite age structure estimates				
Regression	0.90	0.70	0.98	0.73
Chapman-Robson	0.69	0.63	0.70	0.64
Cohort estimates	0.97	0.84	0.99	0.84

The regression estimates were higher than the Chapman-Robson estimates of survival (Table 3). The estimate indicated that younger animals had a higher probability of survival, possibly because older age-classes were subjected to heavier hunting pressure. Males had lower annual survival rates than females in any age-class.

Both the regression and Chapman-Robson techniques assume a constant population size during the years of study. If size were not constant, the estimates would be biased. One method not subject to this bias is to calculate survival rates from cohort data. This calculation was accomplished for each sex by arranging the numbers in each age-class captured or recaptured in each year into cohorts and then calculating regression estimates of survival, using the actual number in each age-class in each year as a sample, and then calculating an average survival rate over all cohorts. This method eliminated the assumption of constant population and smoothed the data for variation in effort from year to year. For males, these estimates of survival rates were 0.97 for ages 2-6 and 0.84 for older than age 6. For females, the estimates were 0.99 for ages 2-8 and 0.84 for older than age 8 (Table 3).

Survival of young with the female is the product of the female's survival probability and the probability of loss of young from the female. Mean litter sizes of cubs, yearlings, and 2-year-olds (1.58, 1.65, and 1.47, respectively) indicated little loss of young. It is recognized that loss of entire litters would not be evident with this type of comparison. Recapture information provided 2 records of loss of young between 5 and 17 months of age; 1 was a single young and 1 was a twin. No information is yet available on cub loss from birth until cubs are first observed in April.

If the age of self-sufficiency for polar bears is assumed to be 28 months, then the annual survival rate for both male and female young would be slightly less than that of an adult female, i.e., 0.84. The resulting cohort life tables for males and females, using an equal sex ratio at birth, are given in Table 4.

Reproduction

Obtaining the number of young per adult female per

Table 4. Cohort life table for male and female polar bears from calculated annual survival rates in Table 3.

Age x	lx males	lx females	Age x	lx males	lx females
0	1000	1000	19	65	93
1	840	840	20	54	77
2	706	706	21	46	65
3	684	699	22	38	54
4	664	692	23	32	45
5	644	685	24	27	38
6	625	678	25	22	32
7	525	671	26	19	26
8	441	664	27	16	22
9	370	556	28	13	18
10	311	464	29	11	15
11	261	388	30	9	13
12	219	324	31	8	11
13	184	271	32	7	9
14	155	226	33	6	8
15	130	190	34	5	6
16	109	159	35	4	5
17	91	133	36	3	4
18	77	111			

year requires an estimate of cub litter size and of the average length of the breeding interval.

Mean litter size. — Numbers of young in litters at birth or in maternity dens have not been obtained during Alaskan studies. Litter size data for family groups captured in March, April, and early May are presented in Table 5. Mean litter sizes of cubs, yearlings, and 2-year-olds were 1.58, 1.66, and 1.47, respectively. These litter sizes are not significantly differnt ($p<0.05$). Litter size was most commonly 1 or 2, but 2 family groups with 3 yearlings were observed (Table 5).

Table 5. Age-specific reproductive data for female Alaskan polar bears, 1967-76.

Age of female	Total females	Without young	With young — Age and size of litter							Vulva swollen[a]	Paired with male[a]
			Cub		1-year-old			2-year-old			
			1	2	1	2	3	1	2		
3	51	51	0	0	0	0	0	0	0	3	2
4	51	50	0	1	0	0	0	0	0	12	5
5	51	49	2	0	0	0	0	0	0	27	10
6	34	18	5	2	5	2	0	1	1	11	5
7	36	15	3	3	4	7	0	2	2	16	6
8	53	14	4	3	8	9	0	7	8	19	6
9	32	6	1	1	1	11	0	5	7	6	1
10	24	6	1	4	5	4	1	1	2	3	3
11	18	4	0	2	0	4	0	3	5	6	1
12	12	4	0	1	2	1	0	3	1	7	0
13	13	3	0	2	1	0	1	5	1	5	0
14	5	2	0	1	0	2	0	0	0	2	0
15+	17	3	0	2	2	7	0	3	0	7	2
Total	397	225	16	22	28	47	2	30	27	124	41

[a] Some females with swollen vulvas were also paired with males.

Mean litter size for each age of female is shown in Table 6. This age-specific mean litter size had some tendency to increase with age of the female, although the increase was not as uniform as that noted by Stirling et al. (1975) in polar bears of the eastern Canadian Arctic. An overall mean litter size of 1.63 can be calculated from the litter size data for cubs and yearlings (Table 5).

Table 6. Age-specific litter sizes, conception rates, and production of female polar bears. Figures in parentheses are cub and yearling sample sizes.

Age of female	Mean litter size at birth	Fraction of all females successfully bred	Probability of conception[a]	Number of young per adult female per year
3		0.03	0.03	-
4	2.00 (1)	0.12	0.12	0.06
5	1.22 (9)	0.26	0.30	0.15
6	1.50 (18)	0.29	0.37	0.39
7	1.52 (23)	0.21	0.35	0.44
8	1.74 (19)	0.29	0.41	0.37
9	1.58 (12)	0.26	0.40	0.46
10	1.89 (9)	0.27	0.39	0.49
11	1.60 (5)	0.08	0.16	0.43
12	2.00 (3)	0.28	0.37	0.16
13	2.00 (4)	-	-	0.56
14+	1.92 (13)	-	-	-

[a] An estimate of the fraction of *available* females that actually bred.

Average length of breeding interval. — Sufficient data were obtained from 8 recaptured females to provide direct information on breeding intervals. Three had 3-year breeding cycles, 3 had 4-year breeding cycles, and 2 had at least 4-year breeding cycles. Sequential events in a normal 3-year breeding cycle, using 1970 as the year of first breeding, would consist of breeding between April and June of 1970, parturition in December 1970 or January 1971, separation from young in April 1973 when the young are about 28 months old, and breeding again that same spring. From the recapture histories of the 8 marked females, age 7 or older, an approximate mean breeding interval of 3.6 years can be calculated.

There is no evidence from Alaskan studies that young remain with the female for more than 28 months, and in a 4-year cycle the female presumably remains unbred for a year after separating from her young. Stirling et al. (1975), from studies in the Canadian section of the Beaufort Sea, cited 2 instances of 3-year-olds still with the females but stated that a 3-year breeding cycle is probably the most common. Lonø (1970) stated that in Spitsbergen, young normally separate from the female at 17 months, and a 2-year breeding cycle is the most common.

Because direct information on the breeding interval was available from only 8 females, we examined 2 other measures of the breeding interval. One measure of the breeding interval is the inverse of the fraction of all females of each age-class that were successfully bred. For a particular age-class, 3 estimates of the fraction successfully breeding are available from the reproductive data in Table 5. For example, the fraction that successfully bred at age 5 is estimated by the fraction with cubs at age 6 (7 of 34), the fraction with yearlings at age 7 (11 of 36), and the fraction with 2-year-olds at age 8 (15 of 53). The mean of these 3 fractions, 0.26, is an estimate of the fraction of all females at age 5 that successfully bred. This fraction was calculated for each age-class (Table 6). For females at age 5 and above, this fraction varies generally in the range between 0.26 and 0.29. The inverse, or mean breeding interval, would then be between 3.85 and 3.45 years. The direct estimate from the 8 females (3.6 years) is within this range.

A second indirect measure of the breeding interval can be calculated from the probability of a female with 2-year-olds or without young conceiving in any particular year. From this probability, the fraction that conceive during the first and subsequent years that they are available for breeding can be calculated. For example, if this probability of conception was 0.40, then 40 percent of the females would have a 3-year cycle, 24 percent would have a 4-year cycle, and 14 percent would have a 5-year cycle, etc., implying a mean breeding cycle of 4.15 years. If, however, it was assumed that all females that did not breed in the first year that they were available for breeding successfully bred the next year, a 3.6-year cycle would be implied.

The probability of conception was calculated from the data in Table 5 by using the numbers of females with litters of different ages as 3 samples. For example, the probability of a female of age 5 conceiving at that age was estimated from the mean of the following fractions: females of age 6 with cubs divided by the total females of age 6 less those with yearlings or 2-year-olds (7 of 25), females of age 7 with yearlings divided by the total females of age 7 less those with 2-year-olds (22 of 32), and females of age 8 with 2-year-olds divided by the total females of age 8 (15 of 53). The mean of these fractions is 0.30, the probability of a female conceiving in her fifth year if she was single or had 2-year-old young. These probabilities of conception are present in Table 6.

For females of age 6 and above, this probability of conception ranged generally between 0.35 and 0.41. This range would imply a mean breeding interval between 4.12 and 4.42 years, or, assuming all females breed in either the first or second year that they are available for breeding, between 3.59 and 3.65 years. These figures also confirm a mean breeding interval of approximately 3.6 years.

Mean number of young per adult female per year. — The mean number of young per adult female per year is calculated by dividing mean litter size by breeding interval. Given a range in litter size from 1.58 to 1.70 young and a range in breeding interval from 3.5 to 3.8 years, the range in number of young per adult female per year is between 0.42 and 0.49. When the best estimates of a litter size of 1.65 and a breeding interval of 3.6 years are used, the most likely number of young per adult female per year is 0.46.

Age-specific numbers of young per female are presented in Table 6. Since the fraction of all females successfully bred is the inverse of the breeding interval, the age-specific number of young per adult female is the product of litter size and the fraction of all females successfully bred in the previous age-class.

Reproductive potential of polar bears is lower than for grizzly bears (*Ursus arctos*) in Yellowstone National Park, where an average litter size of 2.24 and an average breeding interval of 3.40 years gave an average of 0.66 young per adult female (Craighead et al. 1976).

Breeding Age

Minimum breeding age for females was determined by noting their vulval condition and whether they were accompanied by young or were paired with mature males. All three criteria indicate a minimum breeding age of 3 years (Table 5).

The average minimum breeding age may be calculated from the distribution of ages of first conception that may be calculated from age-specific reproductive data in Table 5. One approach is to subtract from the number of females bred in each year of life those that were probably breeding a second time. The sum of the percentage of total first breeding at each age, times the age, results in an average age of first breeding of 5.4 years, with a distribution of ages of first breeding as indicated in Table 7.

This mean age of first breeding is substantiated by calculating age-specific rates of conception. The proportion of females with cubs, with yearlings, and with 2-year-olds constitute independent estimates of the proportion of available females that actually bred (Table 6). The mean conception rates for age-classes 3 through 6 correlate fairly closely with the percentage of females that first breed at these ages (Table 7).

Further information on the range of age of first

Table 7. Calculation of the distribution of ages of first breeding of female polar bears from Table 5.

	Age (years)						
	3	4	5	6	7	8	9
(1) Number successfully bred	3	13	33	35	22	20	13
(2) Correction for number bred second time[a]							
First bred at age 3	-	0	0	1	2	0	0
First bred at age 4	-	-	0	0	6	7	0
First bred at age 5	-	-	-	0	0	16	17
(3) Number first bred successfully [(1) minus (2)]	3	13	33	34	14	0	0
Percent of total	3	14	34	35	14	0	0

[a] Approximately 50 percent of the females breed the same spring in which their cubs are 2 years old; the remainder delay 1 or more years.

breeding comes from histories of individual bears captured several times. The oldest age of first breeding thus documented was 7 years.

Maximum breeding age is not as well defined as minimum breeding age because fewer old animals remain in the population to provide a data base. One female estimated to be 21 years old and 2 estimated to be 18 years old were the oldest reproductively active females captured. The 21-year-old had prominent mammae and external genitalia, indicating estrus, when examined on 2 May. Both 18-year-olds had cubs, and if they bred again, could do so at age 20 after weaning 2-year-olds. Females at this age are probably approaching maximum breeding age. The oldest Alaskan polar bear captured or killed was estimated to be 25 years old.

Other workers have reported on minimum and maximum breeding ages of bears. Erickson and Somerville (1967) speculated that polar bears, like brown and grizzly bears, achieve sexual maturity when approximately 3 years old. Lønø (1970) stated that 3.5 years was the probable age of sexual maturity for female polar bears, although some do not mate until 4.5 years of age. Stirling et al. (1975), with a good data base from northwestern Canada, found a low conception rate for 3- and 4-year-old female polar bears, suggesting that sexual maturity for most females occurs at 5 years. Craighead et al. (1969) stated that female grizzly bears are not sexually mature until 4.5 years old. Hensel et al. (1969) said that female brown bears become sexually mature at 3-6 years but usually at 4 years of age.

The maximum breeding age reported by Stirling et al. (1975) for female polar bears in northwestern Canada was 18 years. Craighead et al. (1976) reported a grizzly bear that gave birth when 22 years old and weaned young when 24 years old. They also noted that 2 females produced litters when 19 years old and stated that reproductive longevity approximates physical longevity.

Presence of mature sperm in testes and epididymides indicates that minimum and maximum ages at which males may be capable of breeding are 3 and 19 years, respectively (Lentfer and Miller 1969). Although presence of sperm indicates breeding capability, it does not show that bears as young as 3 and as old as 19 are successful breeders. An understanding of the significance of breeding by young and old animals requires study of social interactions and behavior. Male paired with mature females when captured ranged in age from 3 to 11 years.

Numbers and Trends

An attempt was made to estimate population size of polar bears in the Barrow area by using the Seber-Jolly mark-recapture procedure (Seber 1973:204). This procedure was unacceptable, however, because permanent emigration could not be assumed. Whether killed bears were included made little difference; survival rates were sometimes greater than 1.0 and birthrates were sometimes negative.

Single season mark-resighting estimates of population size in the Barrow area in 1976 were more consistent. Using a Seber-Jolly procedure, we estimated that 320 polar bears were in the study area (110 km × 110 km) between 17 March and 28 April. Estimates of the number of bears in the area in any 3-day period ranged from 15 to 57. The mark-resighting estimates indicated a rapid turnover in bears available to be captured and much movement of polar bears through the area at this time. The estimated 320 polar bears do not represent the entire population in the Barrow area, because the sample area was small and some bears probably moved through the area after 28 April.

Population trends during the sampling period from 1967 to 1976 may be inferred from comparisons of survival rate estimates derived from cohort data and age structure. Survival rate estimates calculated from cohort data are higher than those calculated from the composite age structure, indicating that the population was increasing slightly throughout the years of study.

If the survival rates given for females in Table 3 are correct, and if it is assumed that female polar bears can reproduce to at least age 21, the number of female young per mature female per year required to maintain a constant population size would be 0.213. Given an equal sex ratio at birth, the number of young required per adult female per year would be 0.426, less than the estimated production rate of 0.48 young per adult female. Again, this calculation implied that the population was increasing.

Breeding Season

Pilot guides and tagging crews observed mature male bears starting to move south in late March, presumably for breeding, in the area north of Point Barrow. These observations are borne out by kill figures showing that the percentage of males taken north of Barrow began increasing in early April (data in Alaska Federal Aid in Wildlife Restoration polar bear reports, 1967-73).

Field observations by tagging crews between 2 March and 13 May revealed the earliest pairing of a male with a female, indicative of breeding activity, on 21 March and the latest on 10 May. Seven pairings were recorded the last week of March, 13 in April, and 1 each on 5 May and 10 May. Copulation was never observed, possibly because the observations occurred after bears had been disturbed by aircraft. The earliest and latest dates that turgid vulvas, indicative of estrus, were noted were 21 March and 10 May. However, field work was most intensive in late March and April, and there was therefore more opportunity to make observations during this period. Breeding is believed to have continued after 10 May but related activities were not observed.

In Spitsbergen, Lønø (1970) cited instances of breeding behavior by males but without copulation on 8, 10, and 26 March and observations of mating or attempted mating on 27 and 30 April, 7 May, and 20 June.

Variability in weight of testes and presence of mature sperm in testes and epididymides also aid in delineating the breeding season. Erickson (1962) weighed testes from 69 Alaskan male bears killed between 13 February and 29 April. There were no definite trends of increasing or decreasing weight during this period, and he concluded that throughout this period some males are capable of breeding. Lønø (1970) examined testes from 88 mature Spitsbergen bears, some of which were taken in most months of the year. Weights were lowest in October, November, and December. Testes increased in weights from December to March and were at about the same high level in April as in March. There were no May specimens. Weights in June had started a decline that continued to the October-December low. Weights varied considerably in both Lønø's (1970) and Erickson's (1962) samples. Specimens from 43 polar bears examined by Lentfer and Miller (1969) revealed sperm in testes and epididymides in February, March, and April, but not in August.

These observations indicate that prebreeding physiological changes begin before March and that males and females begin to pair in March. The amount of pairing increases in April. The few observations in May and a lack of observations in June and July preclude conclusions from Alaska data about the latter part of the breeding season. From histological examination of testes and ovaries from Spitsbergen bears, Lønø (1970) concluded that breeding continues through mid-July.

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DISTRIBUTION AND STRUCTURE OF DENS OF FEMALE POLAR BEARS IN WRANGEL ISLAND

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Abstract: During the period 1971-76, the number of dens of female polar bears (*Ursus maritimus*) in the Drem-Head Mountains (25 km^2 on the northwest side of Wrangel Island) underwent radical changes, ranging from a maximum of 63 dens noted in 1975 to a minimum of 17 dens in 1976. The number of dens was not directly related to spring snow depth.

The topography of the snow cover is very specific each year, depending on the direction of prevailing winds, slope exposure, absolute and relative elevation, and steepness. This results in uneven distribution of dens. More than half of the dens were found at middle elevations (101-300 m); snow depth here (average 137 cm) was 1.5 times less than at lower elevations and 1.35 times greater than at higher elevations. It is possible that females avoid areas of both too deep and too shallow snow cover.

Slopes with terraces which are not relatively high (up to 50 m) and with average steepness of 10-30° are especially favorable for the accumulation of snow, and it is here where most dens are found.

While bears are in their dens, changes in wind direction cause redistribution of snow, resulting in many dens becoming unsuitable (half-opened dens and dens with thin roofs). Females often leave such dens and dig temporary dens or occasionally reoccupy deserted ones. The proportion of temporary dens is higher in years with little snow.

Many dens show signs of the digging activity of the female; this is very conspicuous in dens with several chambers. The digging activity of the female brings about changes in the thermal and gas regimes in the den. If the female does not dig out a new chamber upward but digs it along or down the slope, the ''igloo'' principle — that the chamber of the den should be located higher than the entrance hole for preservation of heat in the den — may be violated. In dens located in areas with little snow where the snow cover upslope becomes thinner, the igloo principle may be easily violated.

Of 131 dens examined, 85 (65 percent) were maternal, 19 (15 percent) were temporary, and 27 (20 percent) were of unknown character. The relative proportions of maternal and temporary dens enables us to more precisely define the number of breeding females in the population.

DATA ON THE WINTER ECOLOGY OF THE POLAR BEAR IN WRANGEL ISLAND

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Abstract: Analysis of the reproductive segment of the polar bear (*Ursus maritimus*) population on the study area in the Drem-Head Mountains of western Wrangel Island indicated that the distribution and, to some extent, the number of dens in specific areas of Wrangel Island are dependent on characteristics of the autumn snow accumulation which, in turn, is subject to the prevailing winds and amount of precipitation. With drastic changes in snow cover, females may change the location of their dens, particularly during years with little snow.

One hundred thirty-one dens located in snow of the current winter were thoroughly examined and partly dug out. Some pregnant females had used dens preserved in the last season's snow. Bear families remained in the opened dens for 1 day to 2-3 weeks; dens with thin roofs were the first to be left. Occasionally, the female stayed near the den and made a temporary den. The number of temporary dens grew in years with little snow. Temporary dens were usually occupied only for several days, but in one case a female with cubs stayed in the temporary den for more than 30 days.

Temperatures in the inhabited dens were found to fluctuate less than temperatures outside the dens, and the temperature inside the dens was 5-17C higher than that outside the dens.

Average litter size at the end of the denning period was 1.80 ($N=136$); this does not differ considerably from litter sizes in other parts of polar bear range. Twenty-eight percent of the litters had 1 cub, 68 percent had 2 cubs, and 4 percent had 3 cubs. The male:female ratio in litters in the western areas of Wrangel Island was 61:39; in eastern areas, it was 44:56.

Average weights of females and cubs, den numbers, and average snow depth on the study area in 1973-76 were continually changing, indicating that the population goes through certain difficulties. This may be related to unknown changes in the distribution and number of seals, the main prey of the polar bear.

Counts of dens opened in the springs of 1964, 1970, 1973, and 1976 indicate an increase in the number of breeding female polar bears in the Wrangel Island area.

DENNING AND RELATED ACTIVITIES OF BLACK BEARS IN THE COASTAL PLAIN OF NORTH CAROLINA[1]

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Abstract: Black bear (*Ursus americanus*) activities in southeastern North Carolina were determined by radiotelemetry, trapping success, track counts, scat collections, and hunter harvests from May 1974 to January 1977. All data indicated that bear activity decreased progressively in autumn. The only significant winter movement was by males, 3 years old and younger. Four bears denned on the ground in dense Carolina bay vegetation. One adult female denned in a bald cypress (*Taxodium distichum*) with an entrance cavity approximately 25 m above the water. The earliest date for denning by radio-monitored bears was 5 December and latest emergence was 22 April. five bears remained inactive for periods ranging from 85 to 113 days, averaging 102. An adult male had the shortest period of inactivity. Two subadult males remained active throughout the midwinter. Postdenning movements gradually increased and reached a peak during breeding season in June and July.

Black bears are most often associated with mountainous areas of the western and eastern United States, but there are also well-established populations in swampy areas throughout the Coastal Plain of the Southeast. A black bear study in the North Carolina Coastal Plain was conducted from May 1974 to January 1977. Information on behavior and ecology associated with denning in a relatively mild climate is presented in this paper. Our study is the first documented report of native black bears denning in the southeastern coastal region.

We are grateful to private landowners, personnel of the North Carolina Wildlife Resources Commission and Bladen Lakes State Forest, and to many friends and sportsmen for their cooperation and assistance throughout this study.

STUDY AREA

The study area, located in Bladen County, North Carolina, consisted of about 55,930 ha, including 13,051 ha in Bladen Lakes State forest (Fig. 1). Elevation varies from 9 to 30 m above sea level, and local relief averages less than 1 percent fall over the 45-km-long study area. Annual rainfall averages approximately 135 cm and the growing season averages about 220 days per year. Snowfall is uncommon and did not occur during the study period. The climate is mild and pleasant with temperatures seldom reaching 38 C in summer and below -12 C in winter.

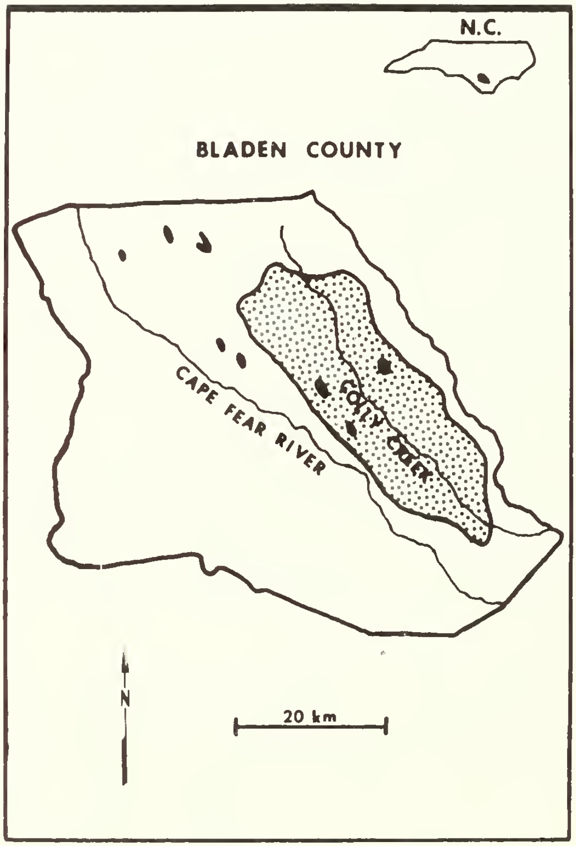

Fig. 1. Location of the 55,930-ha study area in Bladen County, North Carolina. Illustration shows 8 of the many Carolina bay lakes characteristic of this region.

The largest single habitat component (41 percent) was Carolina *bays*. These elliptical craters commonly occur from north-central Georgia to southeastern North Carolina (Murray 1961:512-519). Bays contain extremely dense thickets of evergreen woody plants matted with laurel-leaf greenbrier (*Smilax laurifolia*) and related species. The name *bay* apparently was derived from the bay trees (e.g., loblolly bay, *Gordonia lasianthus;* sweet bay, *Magnolia virginiana;* and redbay, *Persea borbonia*) frequently scattered throughout

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the oval depressions (Johnson 1944:1). Other common trees were red maple (*Acer rubrum*), white cedar (*Chamaecyparis thyoides*), and pond pine (*Pinus serotina*). The shrub layer grew from a peat bog floor and contained fetterbush (*Lyonia lucida*) and various berry-producing shrubs such as huckleberries (*Gaylussacia* spp.), sweet gallberry (*Ilex coriacea*), winterberry (*I. verticillata*), and blueberries (*Vaccinium* spp.). Occurring in association with bays and having an elliptical shape, bay lakes covered 3 percent of the area (Fig. 1).

Ridges of fine-grained, sandy loam soals, constituting 33 percent of the study area, partially surrounded the bays. These sand ridges were dominated by longleaf pine (*Pinus palustris*) and scrub oaks (*Quercus* spp.). Persimmon trees (*Diospyros virginiana*) were common. Shrubs such as small gallberry (*Ilex glabra*), wax myrtle (*Myrica crifera*), and blackberry (*Rubus cuneifolius*) were sparse. Ground story vegetation included clumps of legumes (e.g., *Baptisia* sp., *Lupinus* spp.) and grasses (e.g., *Aristida stricta*, *Panicum* spp., *Sporobolus* spp.).

Colly Creek and an 8,000-ha swamp system, over 2 km wide in places, comprising 14 percent of the study area, bisected the area. A dense canopy formed by red maple, yellow popular (*Liriodendron tulipifera*), blackgum (*Nyssa sylvatica*), red bay, and bald cypress shaded such common shrubs as pepperbush (*Clethra alnifolia*), titi (*Cyrilla racemiflora*), and fetterbush. Greenbrier vines were common and usually occurred with patches of shrubs. The organic, black, mucky loam soil was covered by decaying plant matter on sites above water, while some openings, associated with timber harvests on wet sites, supported stands of emergents.

Residential areas (2 percent) and farmlands (7 percent) composed the remainder of the study area. Major crops produced were corn, soybeans, and blueberries. Approximately 45 percent of the private land (42,600 ha) was owned by timber companies practicing short-rotation even-age management with clearcutting followed by replanting of slash pine (*Pinus elliottii*). During a 20-year span from the mid-1930s to the mid-1950s, sawtimber was harvested from the Colly Swamp system.

METHODS

Bears were captured in box-type traps constructed of a metal frame covered with chain-link wire. Traps were permanently mounted on trailers to aid in transportation. All captured bears were immobilized with M99 (Etorphine) injected intramuscularly by a dart from a CO_2-powered gun. The antidote used was M50-50 (Diprenorhine). Each bear was ear-tagged, lip-tattooed, weighed, and measured. An upper first premolar was extracted for age determination by counts of tooth cementum layers (Stoneberg and Jonkel 1966).

Selected animals were fitted with collars containing radio transmitters with a frequency range of 150.850-151.125 MHz. Radio-tagged bears were located daily, if possible, by triangulation with a 12-channel receiver and directional 4-element, hand-held yagi antenna. Sudden changes in location or movement into an inaccessible area often resulted in unsuccessful attempts to locate bears from the ground. A Piper Supercub with a 4-element yagi antenna attached to a wing strut was invaluable in locating "missing" bears. Seasonal activity patterns, habitat preferences, and range sizes were determined by repeatedly radiotracking individual bears during 24-hour periods.

A 55-km track census route was traveled 1-3 times each month for 2 years as an aid in determining seasonal activity patterns. Weather permitting, track counts were conducted at least 3 days after a rain. The number of tracks observed was divided by the number of 24-hour periods since the last rain. Results expressed in tracks/track-night gave an overall view of monthly activity. Scats were collected daily throughout the study period and the monthly totals were used to indicate activity patterns. Data were collected from legal harvests during 3 bear-hunting seasons to gain insight into sex ratio, age structure, and population density. Changing sex ratio and age structure throughout each hunting season were used to estimate vulnerability resulting from differential activity patterns between sexes and between age-classes (adults, >3 years old; subadults, <3 years old).

RESULTS

Twenty-one different bears were captured 38 times. Ten animals (6 males, 4 females) were selected for radio-monitoring. Seasonal activity patterns and denning behavior were determined by daily locations and by monitoring individual bears during 68 complete 24-hour periods. Telemetry provided information on the activities of specific animals whereas trapping success, monthly track counts, scat collections, and harvest data served as indicators of activities at the population level.

Winter Inactivity

The scarcity of tracks and scats indicated that most bears were inactive during the winter (Fig. 2). No

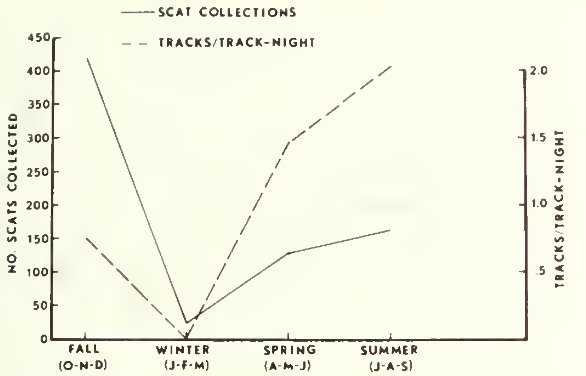


Fig. 2. Predenning, denning, and postdenning activity indicated by track count and scat collection data compiled on a season basis for a 2-year period.

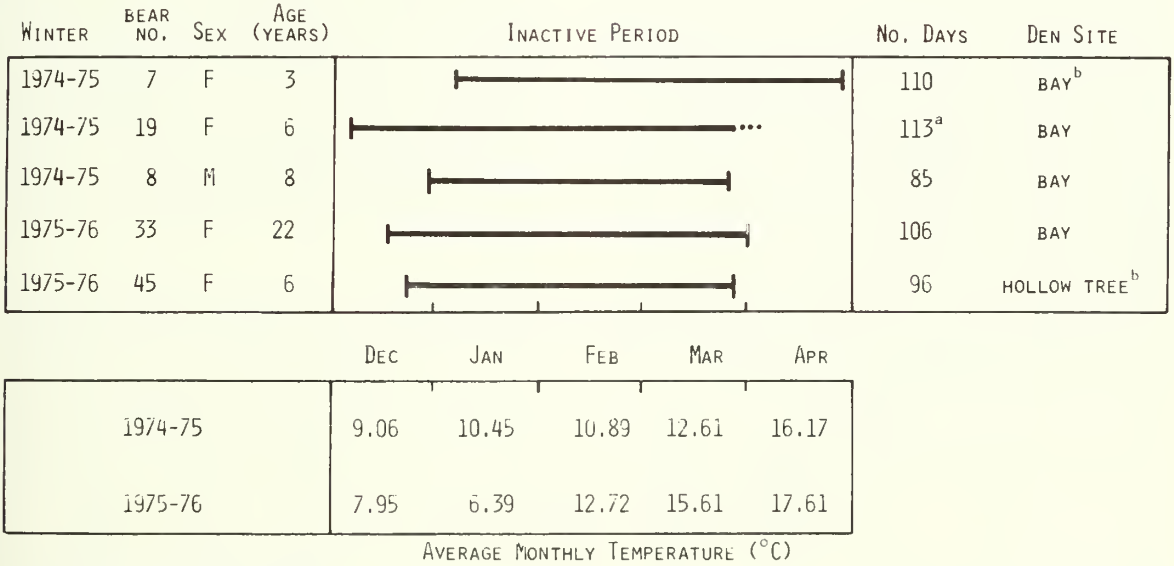
tracks were observed on the regular census route during winter although several small tracks (apparently those of young bears) were found in other parts of the study area. Three subadult males were the only bears trapped from January through March during both winters.

The 3 bears radio-monitored through the winter of 1974-75 and 2 of the 4 monitored the next winter remained inactive for extended periods despite relatively mild temperatures (Fig. 3). The earliest date for denning of radio-tagged bears was 5 December and the latest emergence was 22 April. Periods of inactivity ranged from 85 to 113 days, averaging 102 (Fig. 3).

Three adult females began denning between 5 December and 21 December. An adult male became inactive by 28 December and a young female bedded down for the winter on 3 January. Two young males (2 and 3 years old), tracked for only short periods during midwinter (6 January — 28 January, and 15 January — 9 February 1976, respectively), remained active during those periods. None of the 4 females were lactating or accompanied by cubs when trapped, and there was no evidence that any bore cubs during the radio tracking period.

Den Site Selection and Related Activity

No movement by denning bears was detected during any of 41 complete 24-hour monitoring periods, indicating that bears rarely ventured from their den sites during the day or night. Several bears were forced from their dens for short periods in midwinter, apparently by rising water or other disturbances. An adult male (No. 8), located in a 1,040-ha bay, vacated his den on 17 February 1975 after several days of heavy rain. He returned to the same location on 21 February and remained there until 23 March 1975. In late January 1976, the same conditions evidently caused a 22-year-old female (No. 33) to leave her den site in a 115-ha bay. Two days later, she settled in the northwestern end



WINTER	BEAR NO.	SEX	AGE (YEARS)	INACTIVE PERIOD	NO. DAYS	DEN SITE
1974-75	7	F	3		110	BAY[b]
1974-75	19	F	6		113[a]	BAY
1974-75	8	M	8		85	BAY
1975-76	33	F	22		106	BAY
1975-76	45	F	6		96	HOLLOW TREE[b]

	DEC	JAN	FEB	MAR	APR
1974-75	9.06	10.45	10.89	12.61	16.17
1975-76	7.95	6.39	12.72	15.61	17.61

AVERAGE MONTHLY TEMPERATURE (°C)

[a] SIGNAL LOST 27 MARCH 1975

[b] DEN SITE OBSERVED

Fig. 3. Periods of inactivity of 5 radio-monitored black bears and relatively mild average monthly temperatures in Bladen County, North Carolina, during the winters of 1974-76. Temperatures were recorded at the U.S. Army Corps of Engineers Lock and Dam No. 2 on the Cape Fear River approximately 16 km from our study area.

of the same bay, 966 m from the original den site, and remained inactive until 29 March 1976.

A 6-year-old female (No. 45) began denning in a 4-ha bay on 21 December 1975. Disturbance by a pack of deer dogs on 1 January 1976 apparently made her move into nearby Colly Swamp, where she was found in a hollow bald cypress tree on 3 January. The den tree measured 1.1 m in diameter above the butt swell, was approximately 37 m tall, and was surrounded by standing water 1 m deep. The base was not hollow and the cavity entrance was about 25 m above the water. Telemetric signals indicated that the bear was no more than a few meters below the cavity entrance. She removed her collar on 9 April 1976, 2 weeks after leaving the den tree.

A 6-year-old female (No. 19), located in a 910-ha bay, moved 332 m when an unsuccessful attempt was made to find her den. She was still at a "new" location in the same bay when her radio transmitter ceased functioning on 27 March 1975.

On 12 March 1975, we examined the den of a 3-year-old female (No. 7). Vegetation in the 36-ha bay was very dense and we used a machete to open a trail to her location. This disturbance caused her to withdraw when we approached within 15 m. She returned shortly thereafter and did not leave again until 22 April 1975. This animal's "den" was a shallow depression measuring 61 cm x 56 cm with an 11-cm rim of litter and was located at the base of a pond pine approximately 10 m tall. Bedding material consisted of pond pine needles and leaves from surrounding fetterbushes. Instead of using a site with a protective canopy of vegetation, as may have been expected, the female had removed the overhead fetterbush branches evidently by clipping them with her teeth. This open-ground nest is assumed to be representative of the dens located in Carolina bays, because the bays have homogeneous vegetation and terrain and lack large trees or logs.

A fecal plug expelled as the bear fled was dark green and encased in a sheath of mucus. It weighed 139 g and measured approximately 10 cm long. Contents of the plug measured by volume included leaves of fetterbush (53.8 percent) and laurel-leaf greenbrier (46.1 percent). Occuring in trace amounts (<0.1 percent volume) were sericea lespedeza (*Lespedeza cuneata*), pokeberry (*Phytolacca americana*) seeds, intestinal lining, and unidentified dead leaves and stems.

Predenning and Postdenning Activity

Telemetric data suggested a steady decrease in activity during autumn, prior to denning, and a gradual increase in movements during the spring after leaving the den. These trends are shown by the number of days an individual bear was radio-located relative to the number of different positions mapped for that bear during each month (Table 1). Excluding the winter period of inactivity (late December through March), movement was detected at some time during all 24-hour monitoring periods except 1 occurring in late November and 2 in mid-December.

Monthly track counts and scat collections were compiled by season for the study period. Movement decreased prior to winter inactivity and gradually increased during spring, peaking during the breeding season in June and July (Fig. 2). The combination of limited activity and increased use of bait piles during autumn facilitated collection of scats. In spring and summer, bears ranged more widely and preferred the abundant natural foods; therefore, scats were not concentrated around bait piles—especially during the breeding season.

Table 1. Monthly activity of radio-equipped bears from 1974 to 1976 as indicated by dividing the number of days they had changed locations by the total daily locations determined each month and expressed as a percentage.

Bear no.	Sex	Age (years)	Month								
			Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June
8	M	8	100	100	100	0	13	30	100	100	100
7	F	3	68[a]	83	75	80	0	4[c]	35	87	92
45	F	6	-	-	26	10[c]	0	16	66	-	-
33	F	22	94	44	10	7[b]	0	12[c]	70	100	-
19	F	6	-	75	14	0	80	46	-	-	-
49	M	2	-	-	-	92	-	-	-	-	-
31	M	3	-	-	-	100	100	-	-	-	-

[a] Bear was wounded by a hunter and remained in one location from 17 October to 24 October 1974.

[b] Movement resulted from excessive rainfall.

[c] Movement resulted from human disturbance.

North Carolina has a split hunting season for bears. In 1974-75 and 1975-76, the seasons were mid-October through mid-November and mid-December through 1 January. The 1976-77 seasons were 1-20 November and 13 December-1 January. Bladen County had a known kill of 44 bears (27 males, 16 females, and 1 unknown) for this 3-year period. The percentage of adults, particularly females, in the total harvest decreased from October through December. These data suggest a trend toward decreased activity, especially among adult females, during autumn. The common hunting practice is to search for bear sign along dirt roads and around bait piles and then select the largest track on which to release dogs. This procedure may result in a disproportionately high harvest of adults during early autumn. Adults and subadults probably exhibited similar movement patterns during the early season, but subadults, particularly males, apparently remained more active and were more vulnerable to harvest late in the hunting season.

DISCUSSION

Adaptation of the black bear to a diversity of habitats throughout the United States and Canada is due partially to its ability to become dormant during winter, a period of harsh weather and minimal food supply. In the northern reaches of the bear's range, its annual activity cycle consists of preparing for winter dormancy, denning for periods up to 6 months (Erickson 1965, Hatler 1967, Jonkel and Cowan 1971), and recuperating from dormancy. Moving southward, the period of dormancy decreases usually to less than 3 months as winter weather becomes more moderate and the duration of available food increases. Duffy (1971) suggested that native bears in Louisiana remained active during winter, whereas those transplanted from Minnesota denned for extended periods.

Most studies concerning factors that elicit denning have been conducted in regions with severe winters. Winter weather conditions, particularly snowfall, were reported to have induced denning of bears in Ontario (Northcott and Elsey 1971) and Montana (Jonkel and Cowan 1971). Decreased food availability and physical condition are also important factors (Erickson 1965, Carpenter 1973). Lindzey and Meslow (1976) studied black bears during the dormant period in southwestern Washington, an area of mild winters. They concluded that the proximal stimulus for bears to enter dens was provided by the cumulative effects of low temperatures and above-average precipitation but that good physical condition was an ultimate prerequisite to denning. Carpenter (1973) reported that bears low in stored body fat often remained active throughout the winter.

Bears in our study area were not subjected to extreme weather conditions prior to denning. Although food availability decreased markedly as autumn progressed, most bears in our area apparently were able to build adequate fat reserves before entering dens. There was evidence, however, that subadult males may not den at all. This failure to den may have been related to low fat reserves in this age-class, as subadults harvested in late autumn generally had less fat than older bears.

Adult females and subadult bears of both sexes usually den earlier than adult males (Erickson et al. 1964, Lindzey and Meslow 1976). Jonkel and Cowan (1971) found adult males emerging from dens before subadults, but Lindzey and Meslow (1976) reported that adult males and 2-year-olds of both sexes emerged at approximately the same time, followed by adult females. In our study, females denned earlier and remained inactive later than males.

Black bears use a variety of den sites throughout their range (e.g., Erickson et al. 1964:100). Females and yearlings have been found to select sites offering better protection from weather than do adult males (Cahalane 1947, Erickson et al. 1964). Protected sites may not always be selected, however, as several authorities reported finding females with cubs in open nests, or depressions in thickets, or under the boughs of coniferous trees when the ground was covered with snow (Morse 1937, Smith 1946, Cahalane 1947). As mentioned, 4 bears radio-monitored during our study selected den sites in Carolina bays. These densely vegetated bays appeared to provide adequate protection, except after extended periods of rainfall. The bear that selected a hollow tree was the only one known to den outside a bay. Suitable trees for denning were scarce on the study area as most of the large trees we examined were hollow to the ground and contained swamp water during winter. Eight such trees (7 bald cypress, 1 blackgum) bore signs of having been climbed by bears, an indication that they were examined and found to be unsuitable for denning.

Attempts to observe bears in bay den sites resulted in bears leaving before visual contact was made. The experiences of Poelker and Hartwell (1973:74) and Lindzey and Meslow (1976:411) in southwestern Washington indicated that bears, except most females with newborn cubs, left their dens as humans approached. However, accounts of bears observed in dens are common in the literature (Morse 1937, Schoonmaker 1938, Matson 1954, Duffy 1971, Jonkel and Cowan 1971).

Fecal plugs such as the one found during our study have been reported commonly (Morse 1937, Smith 1946, Matson 1954, Svihla and Bowman 1954), but a quantitative analysis of the contents has not been previously reported. Smith (1946) described the accumulated residue in the lower colon as a heterogeneous collection of material picked up at random, after the suspension of active feeding in fall, together with a residue of secretions. Conversely, it appears that bear No. 7, a 3-year-old female, "selected" the leaves of greenbrier and fetterbush that comprised 99.9 percent volume of the fecal plug we found in March 1975. Greenbriar leaves were not considered a major food item, especially during winter, but were most prevalent in scats collected in May; leaves of fetterbush did not occur in any of the 732 scats collected during our study (unpublished data).

All of our radiotelemetric, track count, scat collection, and harvest data indicated that activities decreased progressively in autumn as bears prepared for winter dormancy, and gradually increased in spring after bears emerged from dens. These trends have been reported in a number of other studies (Jonkel and Cowan 1971, Hardy 1974, Amstrup and Beecham 1976, Lindzey and Meslow 1976).

MANAGEMENT RECOMMENDATIONS

Black bears in the North Carolina Coastal Plain require a diversity of habitat types. One of the most important habitat components is that which provides the necessary protection during winter dormancy, a particulary critical period when females are rearing cubs. Large, relatively impenetrable Carolina bays on our study area served this purpose; however, we feel that bears would have used tree activities almost exclusively, if available, because of the added protection from weather, high water, man, and hunting dogs. Most of the large trees were removed by extensive logging in the past. Now, vast acreages of bay habitat are being converted to farmland. If black bears are to be maintained in viable numbers and hunted as game animals in eastern North Carolina, their existing habitat must be preserved.

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SPECIES PLANNING: AN APPROACH TO BLACK BEAR MANAGEMENT AND RESEARCH IN MAINE

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Abstract: The Maine Department of Inland Fisheries and Wildlife began the active phase of comprehensive species planning in 1974 and implemented the resultant plan for black bears (*Ursus americanus*) in 1975. The black bear's past, present, and projected future status were evaluated in terms of interrelationships among population, density, distribution, habitat, use-demand, and use-opportunity. Alternate goals and objectives were formulated for presentation to wildlife professionals, administrative personnel, and selected segments of the public. The goal set for the black bear was to maintain 1970-74 levels of abundance, distribution, and use. The objective was to provide for an annual harvest of about 800-1,000 bears by 30,000 hunters statewide, with maximum allowable harvest differing according to management units. Experience thus far indicates that comprehensive species planning has greatly benefited black bear management in Maine and can be highly recommended for other areas.

This paper provides a brief background of the status of black bears in Maine and describes the comprehensive species-planning process as it involved bear management and research. Special acknowledgment and thanks go to C. Banasiak, J. Kienzler, J. Hermes, G. Lavigne, and A. Clauson for their work on the bear project.

There has not been a nationally disseminated report on bears in Maine since 1955. What has happened during the last 2 decades will serve as an introduction to the planning process. Black bears were once common throughout New England, but since the late 1700s, they have generally decreased in numbers and distribution (Cardoza 1976). At present, Maine is one of the major strongholds of black bears in the East, with about 59,000 km^2 (72 percent) of the state's land area still occupied. From 1770 to 1957, there was no closed season, no limit, and a bounty on black bears in Maine. From 1957 to 1965, there was no limit and no closed season. From 1966 to 1968, there was a season from June through December but no limit. During 1969-74, there was a 6- to 7-month season with a limit of 1 bear per hunter per year. The seasons of 1975 and 1976 ran from 1 May through 30 November. Legal hunting methods are very liberal; trapping with foot snares or conventional traps, baiting, using dogs to track and chase, and shooting bears incidental to other types of hunting are all legal. The average annual recorded bear kill from 1946 to 1959 was 1,569. From 1970 to 1976, the average registered bear kill was 930, ranging from 1,071 in 1973 to 744 in 1974. Other than keeping track of the legal kill through a mandatory registration system, there was virtually no research done on black bears in Maine from 1954 to 1974.

COMPREHENSIVE SPECIES PLANNING

The Maine Department of Inland Fisheries and Wildlife embarked on comprehensive species planning in 1968, although active planning did not begin until 1974. The effort involved all fish and wildlife species in the state and was guided and administered by the Planning Division of the Department. The program was funded by Pittman-Robertson monies.

A comprehensive planning effort requires much time and money. Ongoing projects were temporarily cut back or halted. The advantages of, and reasons for, implementing research and management policy through a comprehensive planning approach were given by Kennedy (1976), Richards (1976), and Woodgerd (1976). For the Maine program, the justifications were (1) to delineate in one document a species' past, present, and future status with regard to habitat, abundance, distribution, use, and importance; (2) to engineer a management goal and objective that would have input and support from wildlife professionals, administrative personnel, and the public (including nonsportsmen and antihunters); (3) to provide a strategy and a specific program especially designed to achieve a selected goal and objective; (4) to establish a system and a source for giving input into external (non-Department) plans, programs, projects, and other activities that might have an impact on a species; and (5) to maintain continuity in management and research. In short, the purpose was to develop a plan to avoid "management by whim or crisis."

Maine's species plan for the black bear required 18 months to develop. The first step was the assembling of all the available historical data and information regarding black bears in Maine. Most of the history came from old periodicals, journals, and Department records. Next, life history information that was pertinent to management was collected from past research (Spencer 1955), current data from Maine (Hugie

1974), and applicable findings from black bear research conducted outside Maine. A lack of data on any aspect of the species did not stop the planning process. In fact, implementation of programs to obtain basic life history data became an important part of the final plan.

Next, the present status with a specific base year for population, density, distribution, habitat, use-demands, use-opportunities, and the relationships between and among those parameters were summarized from existing data and criteria. Maine harvest data, density estimates from studies outside Maine, and the sex- and age-specific data on hand were used to make rough estimates of the population. The estimates ranged from 7,000 to 10,000 animals. A distribution map of occupied range was made, based upon registration data and questionnaires. Demand was measured in terms of harvest during 1970-74. Use-opportunity was expressed in terms of square kilometers available to the public for consumptive and nonconsumptive demands. Available information suggested that the annual harvest should be no more than 15 percent of the minimum population or 1,050 bears.

The same parameters were then evaluated in terms of the future. Trends in human population growth and shifts in land-use practices were projected for the next 15 years at 1970-73 rates. Habitat, use-opportunity, and supply were projected to decrease but demand was projected to increase. Thus, an unsatisfied demand for consumptive use of bears was estimated to occur as early as 1985.

With the past, the present, and the future in mind, several alternative goals and objectives were written by the plan author. Goals were broad — descriptions of what the distribution, abundance, and use of the bear resource should be in 1990. Objectives were more specific regarding levels of use, areas of distribution, and levels of abundance.

The next step was perhaps the most crucial of the entire process. alternative goals and objectives were presented to biologists within the Department, Department administrators, a political advisory council, a selected steering committee, the university community, several non-Department biologists, and other interested individuals. The steering committee was selected to provide balance among geographical and interest groups. If I were to go through the process again, I would seek out as many interested vocal minorities as possible for their input into the selection of goals and objectives. I firmly believe that success of a management program demands broad base support that can only be attained through honest and open communication during the stage of public involvement. In my judgment, the so-called "controlled sanction approach" common to many state, federal, and provincial agencies with regard to soliciting and using public input is not effective. The importance of widely based public involvement increase when managing a controversial species like the black bear.

The goal agreed upon by these groups was to maintain black bear abundance, distribution, and use at 1970-74 levels. The objective was to provide for an annual harvest of approximately 800-1,000 bears by 30,000 hunters statewide, with a maximum harvest for each management unit of no more than 15 percent of each unit's minimum estimated population.

Once the goal and objective were chosen, it was obvious that specific problems would hinder attainment of the objective. Major problems were an absence of reliable data on population size, hunting pressure, rates of exploitation, habitat requirements, illegal kill, and distribution status in areas of low bear density. Also, legislative and administrative guidelines and authority were needed for controlling use in specific geographical areas. These problems were defined and a strategy for resolving them was developed. The strategy section of the black bear plan included a series of comments that states what was to be done, in what order, and why. Not all of the aspects of the strategy were designed to be implemented at once. Rather, the strategy defined a series of accomplishments leading toward the attainment of the goal and objective. The strategy gave special consideration to public awareness, public involvement, and legislative programs.

Although the strategy section described what was to be done to reach the goal and objective, specific jobs and programs were needed to prepare for actual implementation of the management plan.

More programs and jobs were proposed for funding than the Department's financial resources could support. Therefore, a comparison of all the species plans and their respective strategies and jobs gave administrative personnel and the biological staff an opportunity to select for immediate funding those jobs with highest priority. Approximately two-thirds of the new jobs proposed were funded.

CONCLUSION

The actual implementation of proposed black bear jobs was initiated in 1975. Comprehensive species planning has not solved all of our bear management problems but it has been extremely helpful. The species planning and management process now includes a continual updating procedure as new data become available. Some of the benefits of the process have been the setting of specific objectives, the formulation of clearly defined plans of actions, assured direction and continuity of purpose and effort, and, above all, the provision of a vehicle for continuous refinement of bear management in Maine. I believe that the effort was very worthwhile despite the expense, man-hours, and temporary inconvenience to existing programs that the process entailed. Once the status and importance of bears to the state and to the Department had been made clear, comparison of expenditures was easier. The budget and manpower for bear management rose from $2,000 per year with 1 part-time person to over $40,000 per year and 2½ man-years of effort after the planning stage. Comprehensive planning has facilitated a giant step forward in bear management and research in Maine. I highly recommend similar efforts wherever black bear management and research objectives are unclear or strategies ill-defined. The results and findings of Maine's black bear management and research programs are found in the Pittman-Robertson reports for W-67-R-2 (Hugie 1974, 1976, 1977; Kienzler 1975). A detailed outline of the process may be obtained from the Maine Department of Inland Fisheries and Wildlife, Planning Division, 284 State Street, Augusta 04333.

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DYNAMICS OF HOME RANGE AND MOVEMENTS OF ADULT BLACK BEARS IN NORTHEASTERN PENNSYLVANIA[1]

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Abstract: Home range and movement patterns of 17 radiocollared adult black bears (*Ursus americanus*) were determined from approximately 2,000 radio-locations obtained between January 1973 and December 1976 in northeastern Pennsylvania. Total home range size averaged 173 km^2 for males and 41 km^2 for females. Females traveling with offspring used larger areas than solitary females. Seasonal variations in home range and movement patterns were extensive. Maximum home range size and maximum daily movements of adult males and breeding females occurred during the June and July breeding season, whereas home range size and movements of females with cubs increased from spring through summer, peaking in September. Monthly home range size and distance between daily sequential locations were directly related ($R^2 \varphi 0.74$), indicating that as bears increase their home range size they also become more mobile. Home ranges for both sexes appeared to be geographically stable both on an annual and seasonal basis.

Published home range estimates for black bears refer primarily to the total areas the bears used while they were observed, with little consideration for the length of time or season they were observed or how the animals used the areas dynamically (Erickson and Petrides 1964, Sauer et al. 1969, Jonkel and Cowan 1971, Rieffenberger 1973, Matula 1976, Amstrup and Beecham 1976). This study examined the relationship of home range and movement patterns of adult black bears to sex and season, and related the results to the ecology and management of the black bear in northeastern Pennsylvania.

Field work was conducted throughout most of Pike, southeastern Lackawanna, southern Wayne, and northern Monroe counties in northeastern Pennsylvania. A vegetative chatacteristic of the study area that appears important to this productive bear population is the occurrence of swamps — with interspersions of spruce (*Picea rubra*), rhododendron (*Rhododendron maximum*), and blueberries (*Vaccinium* spp.) — throughout the mixed hardwood forests.

The study area has no major industrial development; however, numerous lakes, large tracks of state game lands and state forest lands, and private hunting and fishing clubs provide the base for a large recreational economy. The recent completion of Interstate Highway 84, connecting this area with New Jersey, Connecticut, and New York City, has greatly stimulated extensive housing developments. These large developments, used primarily for recreational purposes, retirement, or permanent homesites, have resulted in marked changes in available bear habitat. Physiography, geography, climate, vegetation, land use, human population, and the economy of the study area have been described by Eveland (1973) and Kordek (1973).

We gratefully acknowledge funding, field assistance, and cooperation provided by the Pennsylvania Game Commission V. Alt, L. Biesecker, F. Stettler, L. Stettler, and T. Eveland provided valuable field assistance in capturing and instrumenting bears and recording data.

METHODS

Captured bears were instrumented with radiocollars manufactured by AVM Instrument Company, Champaign, Illinois, and EMF Systems Inc., State College, Pennsylvania. Detailed descriptions of capture and telemetry techniques were presented by Alt et al. (1976) and Matula (1976).

Locations of each animal, as determined by radio signal or direct observation, were recorded on U.S. Geological Survey 7½-minute quadrangles and coded as X and Y coordinates of the Universal Transverse Mercator grid system (Kordek 1973). The coded locations were recorded on computer cards, and home range estimates were calculated by a computer program, according to methods described by Jennrich and Turner (1969). The covariance matrix (95 percent confidence region) estimate was used to compare home range data because it does not assume circular home range, it provides a confidence region, and it is statistically unbiased. Repeated locations at den sites were

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excluded because they would have given undue weighting to these positions.

RESULTS AND DISCUSSION

Seventeen adult black bears (5 males and 12 females), radio-instrumented during this study, provided usable home range data. Home range and movement activities are based on roughly 2,000 radio-locations taken between January 1973 and December 1976.

Home Range as Related to Sex of the Bear

The average total home range was 173 km² for males and 72 km² for females. Examination of the distribution of individual home range estimates revealed that 2 females and 1 male occupied areas much larger than those occupied by other bears of the same sex (Fig. 1A). Closer examination showed that both adult females made long excursions while traveling with their cubs during September and October. Similar findings have also been reported for black bears in Minnesota (Rogers 1977). Burt (1943) stated that occasional forays outside the ordinarily occupied areas should not be interpreted as expansion of the home range. A reanalysis of home range, excluding excursions by these 2 females, reduced their respective home ranges from 295 km² to 27 km² and from 206 km² to 50 km² and also reduced the average home range for all females from 76 km² to 41 km² (range, 14-84 km²) (Fig. 1B). These reduced estimates are comparable to home range estimates for the other females and, we believe, they are also more representative of the actual area utilized. In contrast, the movements of the male bear appeared to occur homogeneously throughout his home range, with no irregular excursions. The larger home range estimate for the male may reflect such factors as bear populaion density, social status of individual bears, or some other ecological or behavioral factors (Jewell 1966, Maza et al. 1973). Thus, average home range size for males remained at 173 km² (range, 72-413 km²).

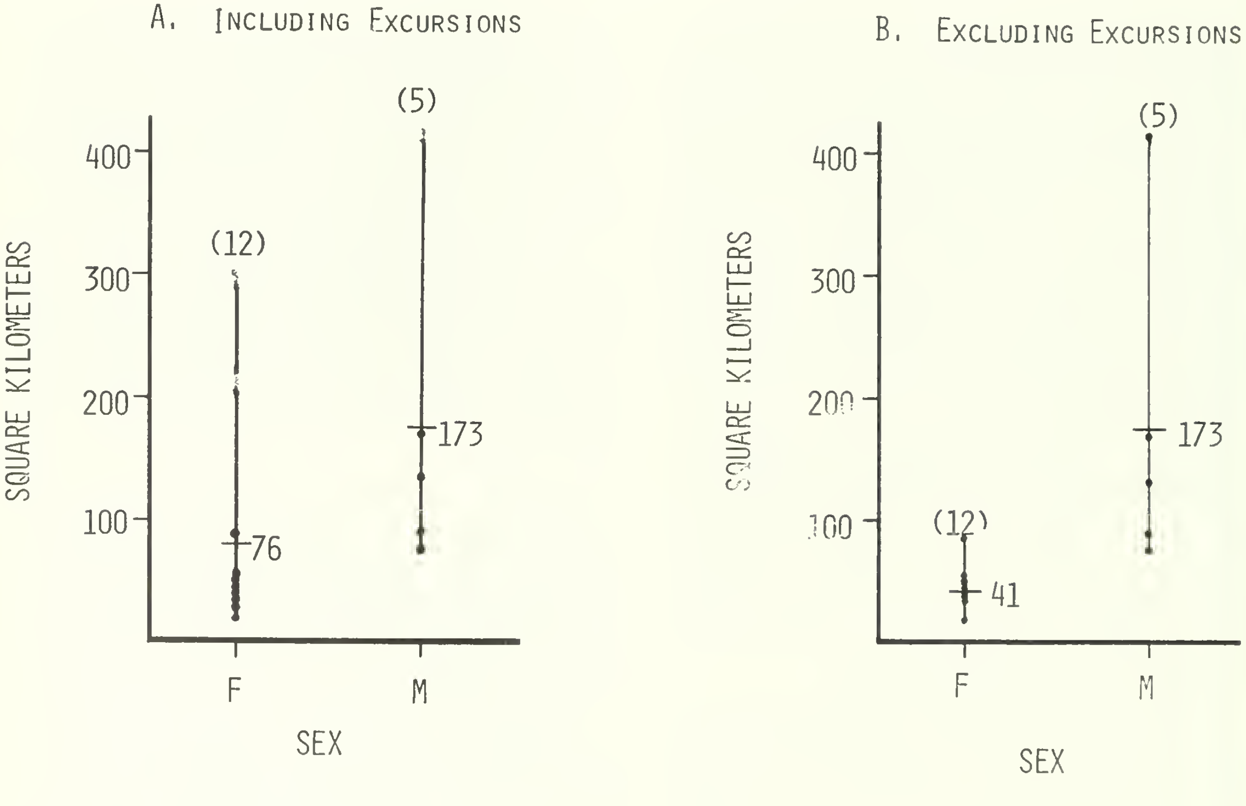

Fig. 1. Home ranges of adult male and female black bears in northeastern Pennsylvania, 1973-76.

Another parameter occasionally used for home range comparisons is the greatest linear distance across the home range. In this study, adult males averages 18.0 km (range, 12.3-25.1 km) whereas adult females averaged only 8.3 km (range, 5.1-12.2 km) when excursions were excluded. Consideration of both area and greatest linear distance across home range indictes that adult male black bears, in general, occupied much larger areas than adult females, which is comparable to findings reported for other states (Erickson and Petrides 1964, Sauer et al. 1969, Jonkel and Cowan 1971, Rieffenberger 1973, Amstrup and Beecham 1976).

Home Range Differences Within the Female Population

Adult female bears in Pennsylvania appear to have a biennial reproductive cycle. They give birth to cubs in their winter dens during January, remain with their offspring for approximately 18 months, breed during June or July (after separating from their yearlings), then remain solitary for about 6 months until cubs are born and the cycle begins again. Females unsuccessful at breeding every other year, or that lose their cubs before the next breeding season, are assumed to repeat the solitary phase of the cycle. Therefore, part of the female population each year is solitary while another part is traveling with offspring.

During this study, 5 adult female bears radiotracked while solitary and also when traveling with offspring, maintained larger home ranges while accompanied by offspring (Fig. 2). If reproductive synchrony (high and low cub-producing years) exists, as suggested by Lindzey et al. (1976), the greater spatial requirements of females with offspring may cause increased competition for available space in densely populated breeding areas during high cub years.

Closer examination of only the females traveling with offspring revealed that during the spring of any given year there are those accompanied by small cubs (less than 4.5 kg) and those traveling with yearlings. Radiotracking confirmed that movements of females traveling with small cubs may be restricted because of the lack of mobility of their offspring.

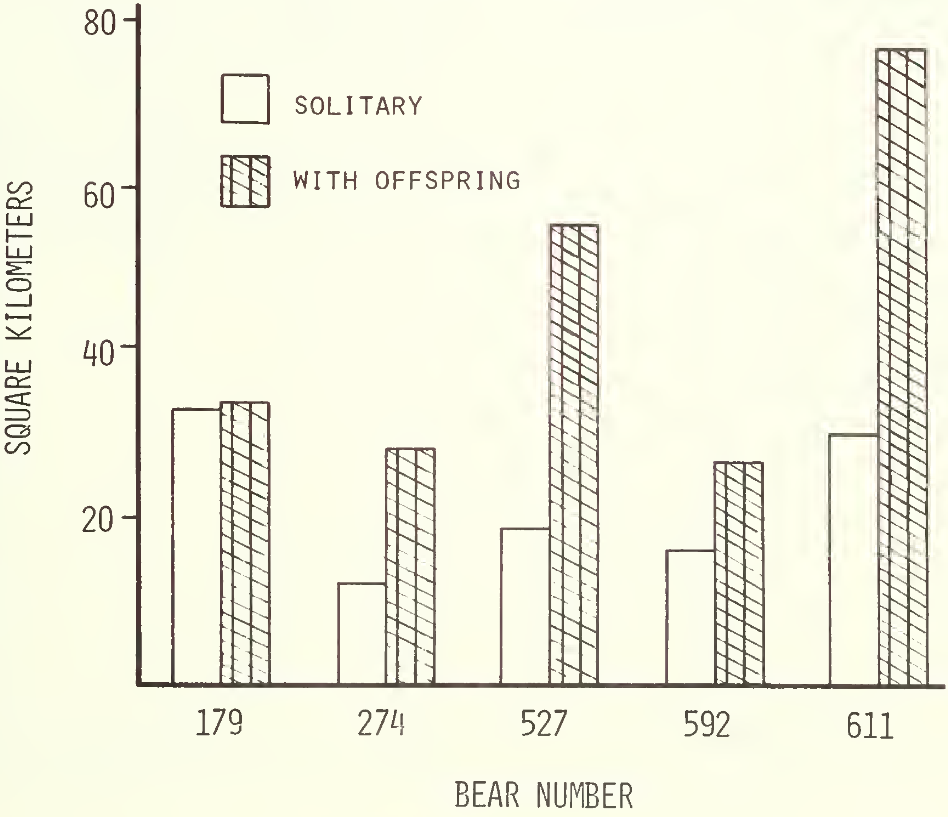

Fig. 2. Home ranges of individual adult female black bears in northeastern Pennsylvania, 1973-76.

Seasonal Variation in Home Range and in Movements

Adult bears were classified into 3 groups: (1) males, (2) breeding females (solitary or with yearlings), and (3) females with cubs. Monthly home range estimates for each group were pooled and averaged, as were average distances between sequential locations taken 1 day apart, to characterize seasonal trends (Figs. 3, 4).

Monthly home range size and movements of all 3 classes of bears demonstrated substantial seasonal variation (Figs. 3, 4), and 2 basic trends were apparent: (1) Adult males and breeding females (the breeding segments of the population) were synchronized to the extent that both segments occupied the greatest area and were most mobile during the June and July breeding season. (2) Females with cubs increased home range size and mobility from spring through summer and reached a peak in the fall as the cubs matured. The greater mobility and home range size of adult males and breeding females during the breeding season may increase the chances of reproduction, particularly when the density of the bear population is low.

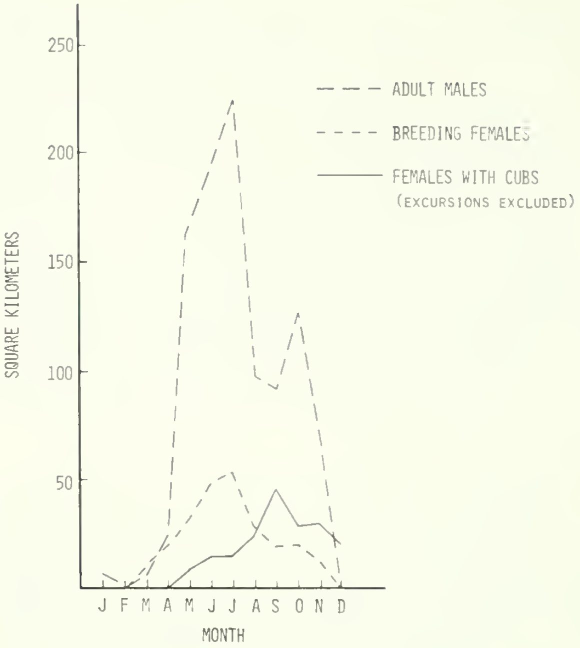

Fig. 3. Seasonal variation in home range size of adult black bears in northeastern Pennsylvania, 1973-76.

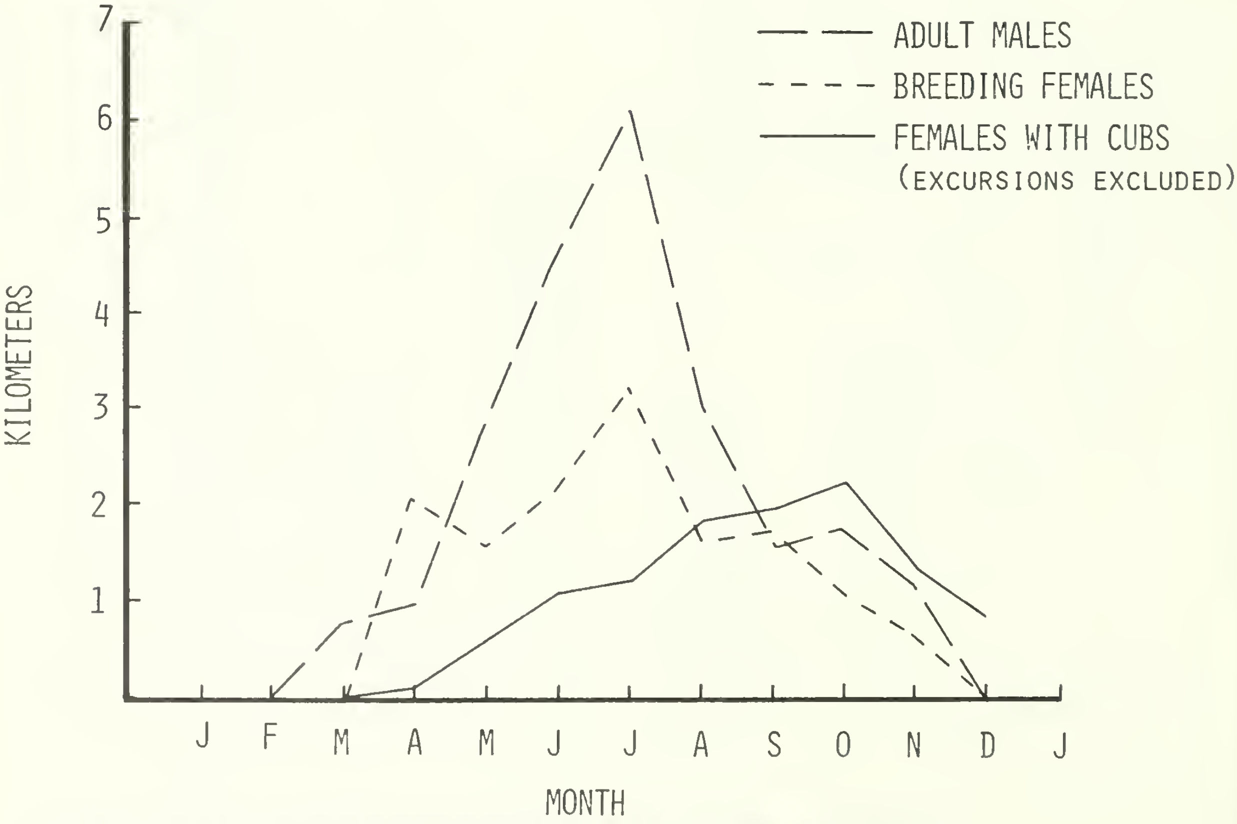

Fig. 4. Distance moved by adult black bears between sequential locations 1 day apart in northeastern Pennsylvania, 1973-76.

The average distance between daily sequential locations for each month and the monthly home range size were directly related ($R^2=0.74$). In other words, as bears used larger areas they also traveled greater distances per day. This strategy should help bears locate foods and mates and perhaps enables them to defend a larger area more effectively.

Percentage of Annual Home Range Used Per Month

Annual home ranges were evaluated for 9 bears: 4 adult males, 3 breeding females, and 2 females with cubs. Bears were radiotracked a minimum of 6 active months during any given year before estimates of their annual home ranges were made. These estimates remained quite stable from year to year, based on data for 5 bears that were radiotracked 2 or more consecutive years. Monthly home range estimates were pooled, averaged, and expressed as percentages of the annual home ranges (Fig. 5). During the breeding season (June and July), breeding bears (adult males and breeding females) utilized areas larger than their annual home ranges, as determined by the method of Jennrich and Turner (1969), but used areas smaller than their annual home ranges during all other months. In contrast, females with cubs used areas smaller than their annual home ranges from January through August but used areas greater than their annual home ranges from September through December.

Geographic Stability of Home Range

Although home range size and mobility of adult bears vary considerably throughout the year, geographic stability of home ranges on an annual basis seems to be maintained. The activity centers (Hayne 1949) of annual home ranges were calculated and the distance between them for consecutive years determined. The average distance between annual home range activity centers was 1.59 km (range, 1.24-1.92 km, $N=2$) for adult males and 0.99 km (range, 0.90-1.78 km, $N=5$) for adult females. These shifts were relatively small when compared with home ranges that averaged 18.0 km across for males and 8.3 km for females.

A similar analysis undertaken to determine the distance between monthly activity centers and the activity centers of annual home ranges indicated that the average distance for males was 2.02 km (range, 0.30-5.48

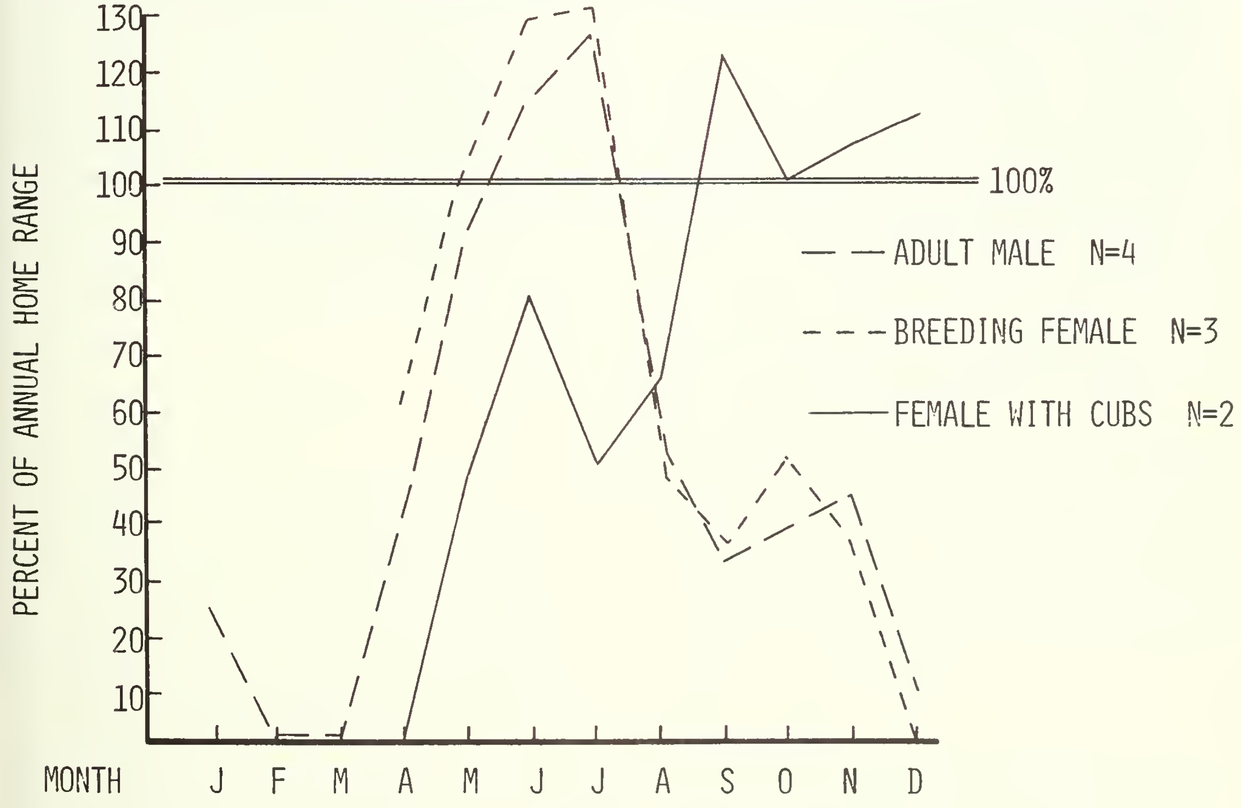

Fig. 5. Percentage of annual home range used per month by adult black bears in northeastern Pennsylvania, 1973-76.

km, $N=31$) and the average for females was 0.93 km (range, 0.11-2.28 km, $N=41$). These averages suggest only slight shifting of seasonal home ranges within the annual home ranges. Both annual and seasonal home ranges appear geographically stable in northeastern Pennsylvania.

CONCLUSIONS

Male black bears, in general, maintained home ranges about 4 times larger than those occupied by females. Females traveling with offspring tended to use larger areas than females that were solitary. Seasonal variation in home range size and in mobility of black bears was substantial. When home ranges increased in size, bears tended to travel greater distances per day. Geographic stability of home ranges appears to be maintained despite the seasonal changes in home range size and in the mobility of bears.

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BLACK BEAR/HUMAN CONFLICTS IN THE GREAT SMOKY MOUNTAINS NATIONAL PARK

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Abstract: An evaluation was made of 1,028 reports of black bear (*Ursus americanus*)/human incidents involving personal injuries, property damage, and bear control actions in Great Smoky Mountains National Park, 1964-76. Respective totals for personal injuries and incidents of property damage were 107 (range, 1-23 per year) and 715 (range, 9-116 per year). Captures and relocations for the period numbered 332, and 18 bears were destroyed. Seventy-six percent of the nuisance bears were males. Improper food storage, violations of park regulations, and high levels of visitor use at certain campsites, shelters and along a few main roads and trails are factors contributing to bear/human conflicts.

Conflicts between black bears and humans have steadily increased in Great Smoky Mountains National Park since its establishment in 1932. Black bears were not common when the park was first established, but populations increased under the protection provided by the park (LaFollette 1974). Likewise, visitor use of the park increased tremendously from 1953 to 1973, averaging nearly 7 percent increase per year (National Park Service 1976). The purpose of this paper is to review black bear/human conflicts in Great Smoky Mountains National Park between 1964 and 1976.

REPORT COLLECTION

Great Smoky Mountains National Park maintained reports of human injuries, property damage incidents, and all bear control actions. We evaluated 1,028 of these reports for the 1964-76 period. Data for 1965 were not available.

Visitor use of backcountry sites was estimated by the number of legal permits issued for each site. Sizes of backcountry sites were taken from a survey conducted in 1975-76 by the staff of Uplands Field Research Laboratory.

BEAR/HUMAN CONFLICTS

Personal Injuries

The number of personal injuries due to black bears ranged from 1 to 23 per year between 1964 and 1976. Personal injuries were more common in years when other bear conflicts increased (Fig. 1). Seventy-six (71 percent) of 107 personal injuries for that period occurred along Newfound Gap Road and Clingman Dome Road. These roads receive the heaviest traffic in the park.

Violations of National Park Service regulations often occur along the roads and are a contributing factor to personal injuries. In 32 instances the person(s) were feeding the bear and in 3 instances the person was petting the bear. Other injuries were incidental to bear concentration and involved visitors photographing bears or picnicking.

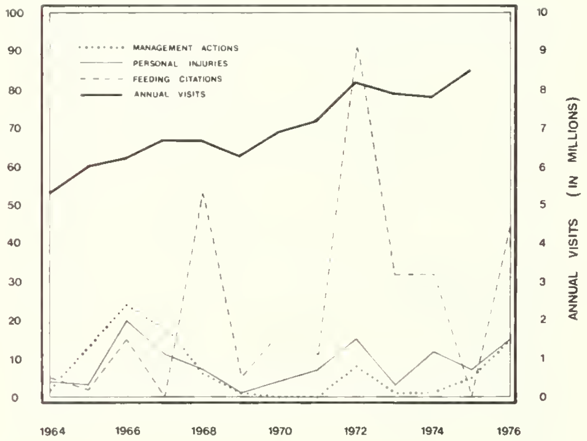

Fig. 1. Annual fluctuations in total damage incidents by black bears contrasted with annual fluctuations in visitor use, Great Smoky Mountains National Park, 1964-76.

Few personal injuries, only 7, occurred in the park's backcountry, all at the most heavily used sites. Thirty-one injuries occurred at frontcountry sites and 4 along heavily used day-hiking trails.

Apparently, the defensive behavior of sows with young increased the likelihood of an injury, as Herrero (1970) and Cole (1972) noted for grizzly bears (*U. arctos*). In order to test this pattern, we compared the number of productive sows involved in personal injuries, 18 (17 percent) the productive sows involved in all other nuisance problems, 37 (6 percent), and found the association significant ($X_2 = 34.96 > 3.84$, $P < 0.05$).

Damage Incidents

Incidents of property damage attributable to black bears totaled 715 in the period 1964-76. The number of incidents in any particular year ranged from 9 to 116 ($\overline{X}$ = 59, SD = 40.2). These fluctuations may represent different reporting emphasis as much as any actual change in incident rates.

Food storage was a contributing factor in many incidents (Table 1). Food was stored in a fashion other than that recommended by park literature and required by park regulations in 214 (30 percent) of the incidents. Misconceptions were common about what constitutes proper food storage. For example, food was often stored in the passenger section of a car or in a separate tent or trailer under the misconception that food was protected there. Even though food and backpacks were suspended from trees in the backcountry, bears often obtained the food by climbing the trees, breaking the limbs, or chewing through tie ropes.

Table 1. Property damage incidents related to food storage, Great Smoky Mountains National Park, 1964-76.

Category	Number	Percent
Food/cooler left out	114	16
Food in passenger section of vehicle	51	7
Food in tent	37	5
Food in tent-trailer	35	5
Backpack unguarded	20	3
Illegal campsite	12	2
Unknown	201	28
Food stored properly	245	34
Total	715	100

Frontcountry damage incidents were in the majority until 1973. Since 1973, the majority of damage incidents have occurred in the backcountry (Fig. 2). The proportion of total damage incidents was chosen as an indicator of the extent of damage because reporting emphasis was inconsistent between years but tended to be consistent within a year. The increase in backcountry use in the park has far exceeded the increase in total visitor use. For example, between 1963 and 1975, total visitor use increased 62 percent and frontcountry camping increased only 23 percent, whereas backcountry camping increased 250 percent, from 30,088 to 105,220 visitor-nights (National Park Service 1976).

Fig. 2. Trends in proporation of damage incidents occurring in the backcountry and increases in backcountry overnight use, Great Smoky Mountains National Park, 1964-76.

Backpacking in the Great Smoky Mountins is concentrated along certain sites and trails. In 1973, 54 percent of nights on the trail were spent in shelters along the Appalachian Trail, which total only 18 percent of the designated backcountry sites (National Park Service 1976). It was hypothesized that bear damage incidents in the backcountry were related to heavy visitor use. To test this hypothesis, the presence or absence of bear incidents for 1975 and 1976 were compared with visitor-nights for the preceding year, 1974 (Table 2), since visitor data for 1975 and 1976 were unavailable. A chi-square test of independence indicated that occurrence of black bear damage incidents was associated with the number of visitor-nights at a site ($X^2 = 22.89 > 5.99, P < 0.05$).

Table 2. Occurrence of black bear incidents in 1975 and 1976 at backcountry sites with high, moderate, and low levels of visitor use (numbers of visitor-nights) in 1974, Great Smoky Mountains National Park.

	Backcountry sites			
	High use (>1,000)	Moderate use (400-1,000)	Low use (<400)	Total
Sites with reported bear incidents	15 (65%)	8 (35%)	0	23 (100%)
Sites without reported bear incidents	18 (21%)	28 (32%)	41 (47%)	87 (100%)

Black bear incidents are apparently related to the area of ground trampled at backcountry campsites. Although few (13 percent) of the very small sites (less than 100 m^2 of vegetation damage) had incidents and many (42 percent) of the very large sites (greater than 20,000 m^2) had incidents, the pattern broke down in the case of the moderate-sized sites. Sites of 5,000-20,000 m^2 had about the same percentage of incidents (23 percent) as sites of 1,000-5,000 m^2 (24 percent). Some of the smaller sites that had bear incidents have recently been moved to new locations and the bears have apparently moved with the sites — or the small sites belong to cluster areas of legal or illegal sites with bear problems.

Many black bear incidents occurred in 4 major clusters of backcountry sites in the park. These problem areas typically involved 3-5 heavily used sites located close together. All 4 areas included Appalachian Trail shelters and nearby sites just off the main ridgeline of the park. Heavy use at many of these sites near shelters was caused by limited visitor capacity at the shelters and the rerouting of surplus campers to the nearest sites.

Interviews with backcountry visitors in 1976, followed by checks on bear incidents reported in park files, indicated that official reports were many times less than the actual number of bear incidents. Low reporting rates for the backcountry were due to (1) lack of manpower to adequately contact visitors in the backcountry, (2) lack of emphasis upon reporting incidents, (3) visitors leaving the park at a number of points that are unmanned by rangers, and (4) absence of notices encouraging visitors to report incidents.

Management Actions on Bears

A total of 332 captures and relocations of black bears were made for the period 1964-76, and 18 bears were disposed of. Research personnel from the University of Tennessee made 41 captures for the purpose of park management. Large numbers of relocations and disposals consistently occurred in Cades Cove (130 actions, 40 percent), and the Newfound Gap-Clingmans Dome Roads (63 actions, 19 percent). Some problem areas were corrected by permanent closure of sites or by installation of bearproof garbage cans.

A total of 27 bears were captured and relocated 37 times during 1975 and 1976. Transplant success was 86 percent for bears transferred 16-30 km and only 9 percent for bears transferred 3-15 km. The difference is significant ($X^2 = 6.59 > 3.84, P < 0.05$). Beeman and Pelton (1976) analyzed relocations in the park for 1967-74 and also found a strong inverse relationship between distance to relocation site and probability of returning.

Sex ratio of nuisance bears handled was 76 percent males and 24 percent females, which differs significantly ($X^2 = 12.72 > 10.81, P < 0.001$) from the ratio of free-ranging bears in the park population, which is 52 percent males and 48 percent females (Beeman 1975). Yearling and cub ratios were identical in the nuisance and free-ranging populations.

DISCUSSION

Information and warnings concerning black bears may be lacking both in quantity and effectiveness. Violations of National Park Service regulations were a major contributing factor in personal injuries, as were violations and misconceptions of proper food storage in damage incidents. Pelton et al. (1976) also found that many visitors receiving property damage from bears were guilty of rule violations.

Occurrence of black bear incidents at backcountry sites was associated with high numbers of visitor-nights. A disproportionately high number of visitors use backcountry sites along the Appalachian Trail and adjacent drainage heads, the same areas with clusters of bear problem sites. The highest densities of black bears (1 bear per 0.42-0.54 km^2) in the park apparently occur along these same mountain crest areas (Marcum 1974), further increasing the likelihood of bear/human conflicts. The Appalachian trail, with attendant trail shelters, is a major backpacking attraction in Great Smoky Mountains National Park. A challenge to park management will be to redistribute or to minimize the bear/human conflicts resulting from ever-expanding visitor use along this trail.

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SEASONAL FOODS AND FEEDING ECOLOGY OF BLACK BEARS IN THE SMOKY MOUNTAINS

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Abstract: Between June 1969 and January 1972, 75 stomachs and 1,025 scats from black bears (*Ursus americanus*) were collected from the Great Smoky Mountains National Park and vicinity for food content analysis. Grasses and the other herbaceous leaves and stems, squawroot (*Conopholis americana*), huckleberries (*Gaylussacia* spp.), black cherry (*Prunus serotina*), acorns from oaks (*Quercus* spp.), blackberries (*Rubus* spp.), and blueberries (*Vaccinium* spp.) composed 81 percent of the diet by volume. Eleven percent of the food consumed was animal matter, principally Coleoptera and Hymenoptera. Artificial food constituted 6 percent of the diet. The most critical season with regard to food availability appears to be late fall because mast (nuts) is the only preferred natural food source available and mast failures occur frequently. There is additional evidence that nutrition, productivity, movement, and bear/person incidents are also influenced by feeding ecology of the species.

Black bears must fulfill nutritional needs for the entire year in 6-8 months. Furthermore, much of the bear's growth and weight gain takes place in late summer and fall, when it must obtain enough food for normal body maintenance, storage of body fat for the winter, and production and maintenance of cubs by females. Knowledge of the kinds of foods, their quantity, quality, and utilization are important to biologists and managers for determining management procedures.

Food habits of black bears in the Southeast are not well documented. This research was undertaken to determine the seasonal diets of black bears in the Great Smoky Mountains of Tennessee and North Carolina and to relate food habits to some possible nutritional, ecological, and management implications.

We acknowledge the National Park Service (NPS) and the North Carolina Wildlife Resources Commission for their cooperation and L. J. Korschgen, Missouri Department of Conservation, for aid in identifying seeds. This study was supported by funds made available through McIntire-Stennis Project No. 12, Department of Forestry, Wildlife and Fisheries and Agricultural Experiment Station, The University of Tennessee, Knoxville, and the Great Smoky Mountains Natural History Association.

STUDY AREA

The study area included the Great Smoky Mountains National Park (GSMNP) in Tennessee and North Carolina and 6 wildlife management areas in the southern Appalachian Mountains of North Carolina. This area is part of the Blue Ridge Province (Fenneman 1938:172), with steep slopes and narrow valley bottoms ranging from 221 m to 2,025 m.

Over 1,300 species of flowering plants have been identified in the southern Appalachians (Stupka 1964:10). These mountains comprise a complex of several vegetative cover types, conforming in a general way to varying altitudinal limits in drainage basins (Kendeigh 1942), with Fraser fir (*Abies fraseri*) and red spruce (*Picea rubens*) on the highest ridges and hickory (*Carya* spp.) and oak on the lower ridges. Trees in the lower parts of these drainages are chiefly cove hardwoods, with northern hardwoods predominating in upper portions of the valleys and on slopes. There are at least 6 distinct forest associations covering over 95 percent of the study area (Great Smoky Mountains National Park 1969:5-10): spruce-fir, cove hardwood, hemlock (*Tsuga canadensis*), northern hardwood, closed oak, and open oak. Common fruit producers are 10 species of oak, 7 species of hickory, 2 species of cherries (*Prunus* spp.), and 6 species of grape (*Vitis* spp.) (Stupka 1964:37-38, 47-51, 84-85, 105-106). The remaining part of the study area is covered by grassy balds. Many of these balds are being invaded by serviceberry (*Amelanchier* spp.), blackberry, and blueberry.

Much of the study area is in second-growth timber less than 50 years old. The variety of understory plants included 2 species of huckleberry, 15 of blackberry, and 12 of blueberry (Stupka 1964:78-81, 124-128).

Precipitation varies and is generally distributed evenly among the seasons, averaging 140 cm per year at lower elevations to 229 cm at higher elevations. Temperature ranges in the lower elevations from a mean of 4 C in January to 23 C in August (extremes, −21 C and 32 C). With each 1,000-m increase in elevation, the temperature decreases approximately 4 C. The ranges of precipitation and temperature combined with the variety of topographic exposures produce a diversity of microhabitats.

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METHODS

A total of 1,025 scats and 75 stomachs were collected between June 1969 and January 1972. Hatler (1967) appraised scat analysis as a technique to determine food habits of bears. He found that fresh green plant material appeared nearly the same in both volume and form after passing through the digestive tract of a bear as it did in the stomach. He also noted that animal matter may undergo substantial quantitative changes but that identity is seldom lost, due to the presence of some material resistant to digestion (exoskeleton, hair, claws, bones). Hatler concluded that a good collection of scats can serve justifiably as a base for nearly any food-habits study of bears.

In the GSMNP, foot trails and abandoned logging roads were selected to include various forest associations and ranges of altitude. Ten trails covering approximately 228 km were walked at 2-week intervals for collecting bear scats. Each trail was walked 14 times a year for a total of 9,600 km over the 3-year period.

Areas surrounding 10 shelter cabins and 1 garbage pit in the GSMNP were searched for scats at 2-week intervals. Scats were also collected from campgrounds and picnic areas if they appeared to be recently deposited. In the late fall, scats were more difficult to find because of the leaf cover.

All but 5 stomachs were collected from hunters during the open season (October-January) on wildlife management areas in North Carolina. Stomachs from bears in the GSMNP were obtained from 2 road kills, a poached bear, a bear killed accidentally by a drug overdose, and a nuisance bear dispatched by the NPS.

Scat and stomach samples were frozen or placed in alcohol for preservation prior to identification of food items. The frozen samples were soaked in water to make the contents pliable and we then washed through a series of sieves (mesh openings of 2mm, 1mm, and 0.25 mm), using the technique described by Tisch (1961:23-25).

Material for macroscopic examination was spread to a depth of about 6 mm. Berries, seeds, and insects often could be identified without the aid of magnification. Further examination of material with a binocular microscope continued until all food items were identified.

Volume of each item in scat or stomach contents was estimated by the methods of Clark (1957) and Tisch (1961:24). Each food item was expressed by frequency of occurrence and assigned an index value based on percentage volume of the food item: 0, trace; 1, 1-25 percent; 2, 25-50 percent; 3, 50-75 percent; and 4, 75-100 percent. From the ocular estimates, a volume index percent was calculated using the following formula:

Volume index percent =

$$\frac{\text{Index value for an individual food item}}{\text{Sum of index values for all food items}} \times 100.$$

These percentages were computed for each time period (spring, summer, early fall, late fall) and the entire year. The frequency index alone can be misleading in delineating the amount of a food item actually consumed. A better evaluation of the importance of a food item can be presented if both frequency of occurrence and volume index percentage are used.

RESULTS

In the Great Smoky Mountains, black bears used the seasonally abundant foods. These foods appeared tc group naturally into 4 time periods: spring (emergence from limited winter activity through 30 June), summer (1 July through 30 August), early fall (1 September through 15 October), and late fall (16 October to approximately the first snow).

Foods of plant origin composed 81 percent by volume and foods by animal origin amounted to 11 percent by volume of the total diet of the bears (Table 1, Fig. 1). Artificial foods and debris composed the remaining 6 and 2 percent, respectively. Analysis of the samples indicated that bears consumed at least 58 different foods of plant origin, insects from 5 orders, snails (Gastropods), centipedes (Symphyla), crayfish (Crustacea), and 8 kinds of mammals. Seasonal changes in their diet are illustrated in Fig. 2.

Specific plant foods are shown in Table 1. After emergence, the bears' spring diet was 90 percent grasses and other herbaceous stems and leaves. Squawroot, a parasite that grows abundantly on the roots of trees (especially oaks), composed 10 percent of the spring diet.

During summer, intake changed to fruits and seeds (Fig. 2). Fruits of squawroot (15 percent), blackberry (12 percent), blueberry (12 percent), huckleberry (11 percent), and black cherry (10 percent) accounted for most of the diet.

The early fall diet included a variety of fruits, black cherries (23 percent) being the single most important food. The fruits of huckleberry (5 percent), blackberry (2 percent), and blueberry (3 percent) were still constituents of the diet because of the long period of availability caused largely by altitudinal variation. At

Table 1. Food items identified in 1,025 scats and 75 stomachs of black bears in the Great Smoky Mountains by percentages of frequency and volume index, 1969-72.

Food item	Spring (145 scats, 1 stomach)		Summer (457 scats, 2 stomachs)		Early fall (326 scats, 28 stomachs)		Late fall (97 scats, 44 stomachs)		Entire year	
	Freq.	Volume index	Freq.	Volume index	Freq.	Volume index	Freq.	Volume index	Freq.	Volume index[a]
Plant origin										
Prunus serotina			7	8	29	23	13	12	18	11
Conopholis americana	13	10	15	15	1	2	T		11	9
Quercus spp.	T	T	T	T	14	14	30	30	10	9
Rubus spp.	T	T	14	12	10	2	2	T	11	8
Vaccinium spp.	1	T	13	12	4	3	T	T	10	6
Gaylussacia spp.			12	11	6	5	T	T	9	6
Gramineae	47	28	2	3	4	3	2	2	8	6
Carya spp.			T	T	6	6	9	9	3	3
Vitis spp.					4	4	10	10	3	3
Ranunculus spp.	3	1	4	3	1	T	2	T	4	2
Fagus grandifolia					6	6	6	6	3	2
Malus spp.	T		T	T	T	T	3	3	2	1
Prunus pennsylvanica			1	2	3	3			2	2
Amelanchier spp.	T	T	1	1	T	T			1	1
Amaranthus blitoides	6	2	T	T			T		1	1
Unidentified herbs	83	43	2	3	4	3	2	2	8	6
Animal origin										
Coleoptera	10	2	12	5	17	5	15	6	29	5
Hymenoptera										
Vespidae	T	T	5	3	6	5	8	8	8	3
Formicidae	3	2	3	2	2	1			8	3
Artificial food	8	4	9	8	6	6	3	2	7	6
Debris (wood, rocks, etc.)	5	1	2	2	3	1	7	2	6	2

[a] Trace quantities of 31 other plant species made up an additional 5 percent of the Volume Index.

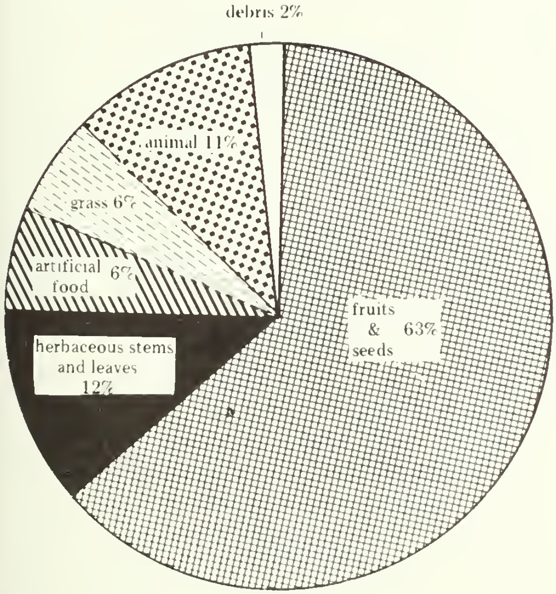

Fig. 1. Food items eaten by black bears (by percentage volume) from spring emergence to winter inactivity (entire year) in the Great Smoky Mountains National Park and vicinity, 1969-72.

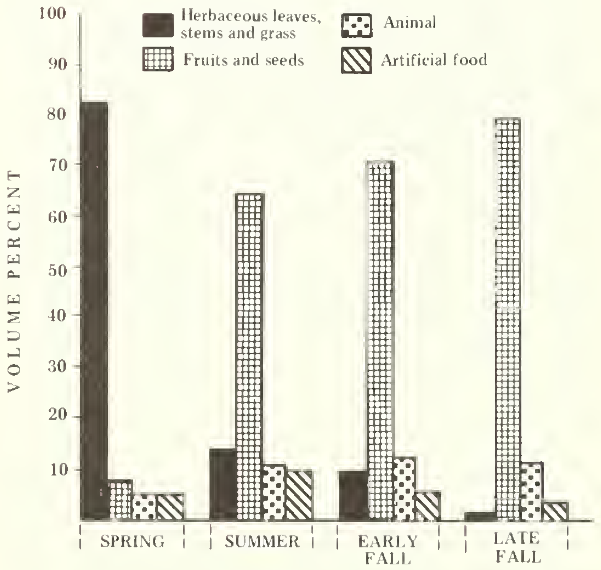

Fig. 2. Seasonal food items of black bears (by percentage volume) in the Great Smoky Mountains National Park and vicinity, 1969-72.

lower elevations, nuts were beginning to mature, with acorns (14 percent), hickory nuts (6 percent), and beechnuts (*Fagus grandifolia*, 6 percent) forming a substantial part of the diet.

In late fall, important foods were mast of oak (30 percent), hickory (9 percent), and beech (6 percent). Fruits of black cherry (12 percent) and grape (10 percent), and to a lesser degree apple (*Malus* spp., 3 percent) were also eaten.

Animal foods were in relatively low volume (11 percent) (Table 1); yellow jackets, wasps, and hornets (Vespidae, 3 percent), and ants (Formicidae, 1 percent) composed more than one-third of the animal food. When these insects were eaten, they usually composed a substantial percentage of the scat or stomach contents. Larvae and eggs were only occasionally identified with adult insects; however volume of the larvae and eggs was probably underestimated in scat samples because of their digestibility.

Beetles (29 percent) were the most frequently eaten animal food but composed only 5 percent of the diet by volume. This high frequency of occurrence and relatively low volume may be explained in 1 or more of the following ways: (1) Most species of beetle were not colonial insects and probably were eaten as isolated individuals. (2) Beetles may be a highly preferred and/or available food item. (3) Because of their large, thick cuticle, beetles were easily identified in scat and stomach remains.

The 8 kinds of mammals identified in the samples were eaten frequently. Many of the samples with mammal items also contained Diptera larvae and scavenger beetles, suggesting that the mammals consumed might have been carrion.

Consumption of artificial foods gradually increased during late spring to 4 percent, peaked in summer (8 percent), gradually decreased in early fall (6 percent), and was at its lowest level in late fall (2 percent) (Table 1). This type of food was available at campgrounds, picnic areas, backcountry shelters, roadsides, and 1 garbage dump.

DISCUSSION

Food Availability

The present food habits study suggests that black bears of the Great Smoky Mountains are largely herbivorous and exhibit distinct seasonal cycles in food consumption. During spring, bears lose weight (Beeman 1975:159). Poelker and Hartwell (1973:116) and others have referred to this period from spring emergence to the ripening of more nutritious and abundant summer foods as the "negative foraging period." Droppings observed during this period exhibit a very loose consistency. We assume that the large amounts of grasses and other herbaceous material in the diet (90 percent) contribute to this phenomenon and wonder whether the loose consistency in turn contributes to a period of conditioning of the gastrointestinal tract after a long period of quiescence. The cause-effect relationship in the above speculation is unclear.

Bears began feeding on fruit as soon as the more plentiful fruits matured. Since there are a variety of fruit-bearing plants and numerous microclimates in the Great Smoky Mountains, fruits are generally plentiful and a reliable food source from year to year. Therefore, availability of food is probably not a limiting factor for bears in summer and early fall. In fact, the plentiful foods of summer may contribute to the small home range sizes during this period (Beeman 1975).

Black cherries are available only through October; grapes and the nuts of oaks, hickories, and beech are staple foods for the remainder of the year. Baker (1950:192-193) summarized the production of nut crops of oaks, hickories, and beech as follows: oak acorns — crop failures frequent, good crops produced every 2-3 years; hickory nuts — some produced annually, good crops every 2-3 years; beechnuts — crop failures frequent, 3-5 years between good crops. Mast failures are not uncommon in the Smoky Mountains. Two have been reported in the last 6 years by the Tennessee Wildlife Resources Agency (R. H. Conley, personal communication). Bears add most of their body fat in late summer and fall (August to November); this fat is their only source of energy during winter dormancy. Therefore, scarcity of foods during August to November causes many bears to leave the confines of the park in search of food and hence they are subjected to a mortality rate higher than at other times of the year.

During fall, bears were observed climbing fruit-producing trees to feed. Adult males and females as well as cubs were noted in trees and were observed pulling in limbs with their paws and using their mouths to pick cherries, acrons, beechnuts, and hickory nuts. In addition, limbs as large as 10 cm in diameter were torn and/or chewed off and dropped to the ground. This "pruning" by bears allowed them to consume mast that otherwise would have been unavailable. Although some damage to these trees was noted, it was probably insignificant when compared with damage caused by high winds and ice storms.

The climbing and feeding behavior of bears in trees may have 2 important ramifications. Insects, particularly the larvae of the nut weevil (*Curculio* spp.), account for the greatest damage to acorns in the Southeast (Strickland 1972:22). Strickland (1972) found that over 40 percent of the white oak (*Q. alba*) and 31 percent of the northern red oak (*Q. rubra*) acorns that were well formed were damaged by insects. Korstian (1927:36) suggested that acorns subject to insect infestations during summer and early fall are also susceptible to more rapid decay than unifested ones. Climbing oak trees allows bears to obtain acorns before infestations lower the acorns' nutritional value.

Arboreal feeding by bears may also give them an advantage over most (with the exception of sciurids) other mammals dependent on mast in the fall. The wild turkey (*Meleagris gallopavo*), white-tailed deer (*Odocoileus virginianus*), gray squirrel (*Sciurus carolinensis*), and European wild hog (*Sus scrofa*) all depend on mast and likely compete with black bears, especially in years of mast scarcity.

Tisch (1961:43), Poelker and Hartwell (1973:111), and others have shown that black bears subsist mainly as vegetarians. There are 60 species of mammals in the GSMNP (Linzey and Linzey 1971:87-89), including localized high densities of white-tailed deer (Fox and Pelton 1973) and European wild hog (Great Smoky Mountains National Park 1969). During our study, wild hogs in traps were attacked by bears. Bacon (1973:91) demonstrated that meat is a highly preferred food of black bears and, since these palatable foods are present but not preyed upon, implications are that bears are opportunistic and eat only what is readily available.

Nutrition

This study estimates the relative percentages of food items included in the diet of the black bear but does not include the nutritional values of these foods in relations to their use. The nutritional requirements of an animal vary with age and season (Beck and Beck 1955); growing cubs and females bearing young require more energy than is needed for normal body maintenance.

The nutritional quality of foods in this study indicated that the diet is high in carbohydrates and low in protein. According to Wainio and Forbes (1941:631), the skin and pulp from black cherry, blackberry, blueberry, and grape are all less than 1.3 percent protein (wet basis); the protein content of seeds was excluded since they did not appear to be digested. The protein content of grasses varies among species but is generally between 5 and 15 percent (dry weight). The acorns of white oak and northern red oak are 3-4 percent protein (wet basis).

Insects, although estimated as a minor food item in quantity, may provide a critical source of protein for bears. For example, beetles contain 41 percent protein, wet basis (Beck and Beck 1955), and ants contain 55 percent, dry basis (Southwood 1973:7). Mammals also contribute another source of protein. However, the amount of protein a bear can utilize during digestion is unknown.

Artificial food consumed by bears was correlated with visitor use of the park and represents another possible source of protein for black bears. From our tagging and population studies, we estimated that in most years 90-95 percent of the bears seldom, if ever, visited an area where artificial food was available. We therefore concluded that artificial food may comprise a substantial percentage of the diet of a few bears but is not eaten by the majority of the population. Also, the NPS has been replacing most of the regular garbage cans with bearproof cans. This measure has probably reduced, although not eliminated, the amount of artificial food available to bears.

Jonkel and Cowan (1971:49) found a direct correlation between black bear productivity and huckleberry production in Montana. The reproductive capacity of bears in the Smoky Mountains seems to be affected by nutritional deficiencies probably caused by poor mast crops in the fall, although only direct evidence is available from our study. In 1973, the number of different litters observed ($N = 13$) was the lowest of the 4-year study (Beeman 1975:164). This decrease in productivity appears to correlate with the poor mast year of the previous fall (1972). However, this correlation is not conclusive evidence because other causes may also be involved.

Movement

In 1968, a complete failure of the acorn crop from all oak species was recorded whereas hickories and beech produced some mast at low elevations (R. H. Conley, personal communication). Twenty-five bears (a 4-fold increase over the annual average harvest) were reported killed from Tennessee counties adjacent to the northern perimeter of the park. Bears killed in these peripheral areas were originally from the park because the open counties do not support resident bear populations. The next year (1969), when the production of mast was rated fair in oaks, poor in hickories, and excellent in beech, only 6 legal kills were reported from the same Tennessee counties. The next year of poor mast production occured in 1972 (R. H. Conley, personal communication). There was no bear season in the Tennessee counties in 1972; however, 40 bears (a 7-fold increase over a 7-year average) were handled by the Tennessee Wildlife Resources Agency during late fall in Tennessee counties adjacent to GSMNP. A high percentage of these bears were young males in very poor condition. This occurrence indicates that bears sometimes move into areas outside their normal home ranges in search of food during years of mast scarcity and are killed both legally and illegally.

During the summers of 1968 and 1972, prior to poor mast crops, there was a total of 252 bear/person incidents in the GSMNP. Bear/person incidents included bears damaging pickup and trailer campers, ice coolers, and tents. During the years that immediately followed those years of poor mast production, a total of only 32 incidents were reported. Since male bears are involved in 87 percent of bear/person incidents in the Park (Beeman and Pelton 1976) and home ranges and movements of males are much greater than those of females (Beeman 1975), a high proportion of males are obviously involved in fall foraging activities on the periphery of and outside the park. The males are thus more vulnerable to various mortality factors: this differential vulnerability may partly explain the difference in average ages between the sexes in the relatively protected population in the park — males, 4.1 years; females, 6.4 years (Pelton 1976).

The periodic egress of bears (predominantly males) from the park during fall foraging activities as well as removal of male panhandlers in summer by the NPS may contribute to maintenance of the population at relatively high densities (Marcum 1974:59) if the hypothesized regulatory effect of adult male bears in the population is valid (Kemp 1976). However, severe and/or frequent mast scarcities are likely to have a detrimental effect on the population and to play a role in population regulation. Data presently being analyzed covering the past 5 years indicate that the population in the park is relatively stable.

These data emphasize the importance of the park as a dispersal point of bears to surrounding areas and illustrate how the availability of fall mast effects this dispersal, provides surplus animals for hunting, and may play an important role in regulating the population.

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DEN SELECTION BY BLACK BEARS IN THE GREAT SMOKY MOUNTAINS NATIONAL PARK

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Abstract: Dens of black bears (*Ursus americanus*) were located in the Great Smoky Mountains National Park using radiotelemetry. Bears preferred cavities located high in large trees; 7 dens were 6-17 m aboveground. Dens were associated with northern hardwood and cove hardwood forest types. All but 2 of the 12 dens located were at elevations above 1,000 m. The average dbh of 7 den trees was 97.1 cm. Inside dimensions of 7 tree dens averaged 218.4 × 59.6 × 62.0 cm. Tree dens are of definite survival value to bears, particularly females and cubs. Such dens offer protection from precipitation, cold temperatures, and human activities. Perpetuation of tree dens outside protected areas such as national parks is unlikely under current forest management practices.

Black bears are not hibernators in the classic sense, but they do enter a state of inactivity during winter months that is referred to by Hock (1961) as ''carnivore lethargy.'' During winter dormancy, bears neither eat, drink, urinate, nor defecate (Folk et al. 1972). Parturition occurs during winter. Selection of winter dens that provide substantial protection from harsh weather and from harassment by man or by other animals has significant value for females with young. Den sites of black bears exhibit a high degree of variability, ranging from shallow depressions in forested areas (Smith 1946, Leopold 1959, Erickson et al. 1964, Part III) to man-made structures such as drainage culverts (Barnes and Bray 1967) or cabin subspace (Jonkel and Cowan 1971). Use of tree cavities as dens was reported for black bears by Switzenberg (1955), Jonkel and Cowan (1971), and Lindzey and Meslow (1976), and for Asiatic black bears (*Selenarctos thibetanus*) by Bromlei (1973). Only Lindzey and Meslow, and Switzenberg, reported bears denning in tree cavities above ground level. This paper presents preliminary findings regarding the selection of den sites by black bears in the Great Smoky Mountains National Park.

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STUDY AREA

The Great Smoky Mountains National Park is a 2,072-km^2 mountainous area on the eastern Tennessee - western North Carolina border. The area has been under the protection of the National Park Service since 1934. The park is characterized by steep narrow valleys, with elevations ranging from 230 to 2,025 m. Precipitation ranges from 130 cm at lower elevations to over 200 cm at higher elevations. Vegetation is diverse, in part reflecting the wide variety of microclimates created by the relief of the area (Whittaker 1956). Six broad forest types are recognized: cove hardwood, hemlock, northern hardwood, closed oak, open oak and pine stands, and spruce-fir (Shanks 1954).

METHODS

Black bears were trapped in the Great Smoky Mountains National Park during the summers of 1972, 1973, and 1974, and equipped with radiocollars. Their activities were monitored until movement and activity ceased in late fall and early winter. Specific den sites were located by homing on the radio signal. Dens were checked periodically to determine approximate dates of emergence. When dens were vacated in spring, the physical characteristics of the dens and vicinity were recorded.

RESULTS

Twelve dens were located; occupants included 6 adult females (> 3.5 years), 3 subadult males (2.5-3.5 years), and 1 subadult female. Two dens were located in the same winter for each of 2 of the adult females.

The mean elevation of den sites was 1,194 m, with all but 2 of the dens located above 1,000 m. Den elevations were related to the inaccessibility of these elevational areas during pre-park logging; most logging in more accessible areas eliminated large trees. Dens were associated with northern hardwood and cove hardwood forest types. Five of 12 den trees were located on slopes with a southern exposure. Bears entered dens

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between 5 December and 21 December. Dates of spring emergence were less accurately determined but appeared to occur during late March.

All dens were associated in some way with large, mature trees. Seven dens were located high in trees, with their entrances at heights of 6.1-17.4 m ($\bar{x}$ = 13.3) above the ground. Two dens were inside the bases of trees, with their entrances located high above the ground; 2 were in cavities beneath the root networks of large trees or stumps; and 1 was at the sheltered base of a red maple (*Acer rubrum*). Of the 7 tree cavities for which we have specific data, 3 were in eastern hemlocks (*Tsuga canadensis*), 2 in red maples, and 2 in northern red oaks (*Quercus rubra*). The average dbh (diameter at breast height) of 7 of the trees with den cavities was 97.1 cm (range, 84.0-122.3 cm). Entrances of tree cavities averaged 37.7x55.4 cm, and inside dimensions of cavities averaged 218.4x59.6x62.0 cm (height x width x length).

The entrances of dens of all 6 adult females were located high in trees (2 cavities were at ground level). Dens of the 2 subadult males were the only ground dens occupied throughout the period of winter dormancy.

DISCUSSION

Data from the present study substantiate earlier reports that pregnant females and juveniles may be more selective in their choice of den sites than adult males (Cahalane 1947, Erickson et al. 1964). Lindzey and Meslow (1976) found that adult female black bears enter dens earlier than other members of the population. They are followed by the subadults of both sexes; adult males were the last segment of the population to den. Earlier denning by adult females probably enabled them to select more protected sites than other segments of the population. The smaller size of females allows them to utilize dens with entrances too small for many adult male bears and thus reinforces the selective advantage of small body size. Dimensions of interior cavities are enlarged by the scraping actitivites of bears on cavity walls; the punky wood is then used as bedding material. Our observations of black bears in the wild and of those held in enclosure indicate that adults spend more time in trees than was previously assumed, particularly while feeding on serviceberries (*Amelanchier* spp.), wild cherries (*Prunus serotina*), and acorns (*Quercus* spp.). The ability of bears initially to locate tree dens is likely enhanced by their arboreal activities.

By taking advantage of tree cavities aboveground, black bears avoid 3 major environmental factors that affect the rate of heat loss or energy consumption in winter: cold air drainage along the surface of the mountain slopes (above ground cavities), cold winds above ground level (insulation provided by trees), and moisture (dry interior of cavity). In the better protected and insulated tree dens, females likely expend less stored energy for body maintenance and thus conserve this energy for fetal development and lactation. In addition, tree dens high aboveground (entrances and/or cavities) afford a high degree of protection to bears from harassment by man and by other animals. Bears are easily and routinely routed from ground-level dens, but in only 1 instance did a bear leave a tree den in our numerous visits to these sites. Tree dens made it possible for bears to spend the winter in 1 location and thus avoid any hazards that might be precipitated by their movements.

A significant fact emerging from this study is the apparent importance of large, mature trees in providing den sites for black bears in the Great Smoky Mountains National Park. Bromlei (1973: 94-102), discussing the closely related Asiatic black bear, reported that hollow trees are preferred denning locations, and that it is considered abnormal for this species to den elsewhere. He further reported that hollow trees suitable for winter sleep are limited in number in most Russian forests and are almost completely lacking in secondary pyrogenic forests. The present study provides strong evidence of the extensive use and importance of hollow trees for the North American black bear.

Black bears in the park exhibit a strong affinity for relatively small home ranges in spring and summer. After dramatic departures in the fall (up to 25 km), most bears return to their former home ranges to den (Pelton, unpublished data). To what degree the propensity of bears to den on spring-summer range is due to familiarity with prime den sites there, or to other factors, is unclear at present. Also unclear is the incidence of year-to-year reuse of tree dens by the same or different bears. We hypothesize that the frequency of reuse may be high due to the relative scarcity of tree dens compared with other potential den sites.

There appears to be a high rate of natural attrition among trees suitable for black bear denning. Of the 7 trees providing cavities high off the ground in the Smokies, 3 have broken off at the den cavity or have blown down since 1973. One of the ground dens has been rendered useless by the further falling of the tree that formed the den. We feel that lightning and wind play an important role in both den formation and destruction. Large trees are move vulnerable to wind damage and are also weakened at the locations of cavities. A survey of 68 random sites in our study area revealed an incidence of wind and lightning damage of 20.6 percent and 8.8 percent, respectively. The population dynamics of so-called cull or overmature trees is essentially unresearched. Cavity formation, longevity, and destruction as well as factors affecting cavity size and use are fertile areas for further research.

Forest management practices outside the confines of protected areas like the park have eliminated potential den trees either by cutting cull trees during forest stand improvement or by cutting trees before they reach the minimum size necessary for large cavities to form. Known den trees in the Great Smoky Mountains National park were located in areas unaffected by logging before creation of the park in 1934. However, outside the park much of the remaining black bear habitat in the southern Appalachians is on national forest lands where intensive forest management has resulted in elimination of den trees and potential den trees. Most remaining den trees are in areas previously inaccessible to logging; even on these sites timber stand improvement has eliminated some cull trees. The advent of new techniques for harvesting trees on previously inaccessible terrain (e.g., balloon, helicopter, or cable logging) will hasten the further elimination of den trees on national forest lands. Unless current forest management policies are revised, some form of wilderness designation may be the only feasible alternative to ensure the perpetuation of black bear tree dens.

Although black bears are quite versatile in selection of dens, available tree cavities appear to be extensively used and provide the most suitable sites for black bears in the southern Appalachians. We feel that more attention should be given to preserving prime den sites as an important component of black bear management. These sites may be particularly important in maintaining viable black bear populations in marginal habitat.

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CURIOSITY IN THE AMERICAN BLACK BEAR

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Abstract: American black bears (*Ursus americanus*) were tested to quantify their response to novel objects placed in their environment. The results indicate that the level of orientation may be greater in the black bear than in other North American carnivores. The exploration of objects by the black bear is characterized by a high degree of contact with the objects. This contact consists primarily of manipulating the objects with the forepaws and chewing the objects. The intense curiosity of the black bear should be recognized and considered in the management of this species and in the evaluation of bear/human conflicts.

Understand the behavior of an animal and its relationship to its environment is an important consideration in management of areas where humans and bears come into frequent contact, but it is often overlooked as a topic of research. The relationship of game species to their environment is usually studied in terms of populations and trends without considering behavior of individual animals. In practice, however, management of large, solitary animals such as the black bear in a preserve situation is often on an individual level, which requires an understanding of their behavior.

To obtain useful information about behavior, research must be designed to gather data systematically through direct observation. Information about behavior is too often obtained anecdotally, without actual observation of the animals. Observation is difficult but necessary to obtain clear information about what the animals are doing. Data from captive animals can be very important in explaining behavior observed in the field and in directing the field researcher toward behavior that may otherwise be overlooked.

Also, the behavior types being studied need to be defined so that their importance is not lost in semantics. With this need in mind, curiosity is operationally defined as an animal's orientation and/or contact with novel objects in its environment. Behavior that falls under this definition includes play, exploration, approach/avoidance, and orientation. Theoretical components of behavior will not be considered here. This paper deals with what the animal is likely to do in given situations. In other words, how curious is the black bear?

The study of curiosity in mammals began early. Scientists such as Darwin (1878), Morgan (1890), and Romanes (1969) clearly established the existence of intense curiosity in mammalian species, particularly in the primates. Unfortunately, this early interest in curiosity was not continued, and not until the late 1940s did curiosity again become a topic of behavioral study. These studies, however, tended to discuss the observed behaviors theoretically, and descriptions and quantitative data on behaviors considered as curiosity were lacking.

The curiosity of the bear had primarily been related by anecdotal and narrative information. Everyone has a good story but no quantitative data. Several authors have noted that the bear exhibits a great deal of curiosity about humans and man-made objects. Leyhausen (1948) and Burghardt and Burghardt (1972) described young black bears manipulating unfamiliar objects and food with both mouth and forepaws. Krott and Krott (1963) described the first outing of 2 bottle-raised brown bears (*Ursus arctos*); both young animals immediately explored by digging, eating, or chewing on almost all objects available to them in a garden.

Older bears also seem to exhibit a good deal of curiosity. Skinner (1952) speaks of bears investigating campsites in Yellowstone National Park without attempting to obtain food. Bears in campgrounds and backcountry campsites are a problem in Great Smoky Mountains National Park. Food may be a factor, but Beeman (1971) reported that even campground bears consume only about 15 percent nonnative foods, which does not support the assumption that bears rely on garbage as a food staple. In addition, nonfood-related objects, such as trail signs, polyethylene aerial survey markers, mast traps, and weather stations, have all been damaged by bears.

Describing and quantifying curiosity in the black bear could help to evaluate and possibly predict outcomes of bear/human, bear/environment, and bear/management interactions. This study is an introduction to the description of curiosity in the black bear. The research was conducted near Tremont Environmental Center in the Great Smoky Mountains National Park in 1972-73. An extensive study by Glickman and Sroges (1966) of displayed curiosity in more than 100 species of zoo animals was used as a model. Glickman and Sroges intended to quantify the response of animals to novel objects placed in their environment. The procedure was simple; but it provided, for the first time, a method whereby species could be compared, and not only quantitative but qualitative information could be collected.

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METHODS

The subjects were 2 female sibling black bears. These animals were hand-raised together from 3 months of age in a large seminatural enclosure. The enclosure was partitioned in half so the bears could be placed on either side or separated. Both animals normally had full access to both sides of the enclosure.

The bears' ages at the 3 test dates were approximately 16 months, 20 months, and 26 months. Their enclosure and care are described in detail by Bacon (1973).

During the test, the bears were separated. Pairs of novel objects were placed in each bear's side of the enclosure. Four sets of objects were used:

(1) Two pine blocks, 1 measuring 5.0 = 10.2 = 61.0 cm and the other 2.5 = 30.5 cm.
(2) Two steel chains, 1 #20 welded chain measuring 61.0 cm and 1 smaller chain measuring 30.5 cm.
(3) Two maple dowels, 1 measuring 2.2 = 91.4 cm and the other 1.6 = 30.5 cm.
(4) Two water hoses, 1 measuring 2.5 = 61.0 cm and the other 1.3 = 30.5 cm.

The blocks, dowels, and hoses were used only once. The chains were reused but were washed between presentations to eliminate olfactory cues.

Each set of objects was placed in each animal's home cage, 1 set at a time. The objects remained 6 minutes and were then removed. The next set of objects was placed in the cage after a time lapse of 10 minutes. Objects were always presented to the bear in this order: blocks, chains, dowels, hoses.

Responses to the objects were recorded during the 6-minute period. Notation was made during each of the 72 5-second intervals as to whether the bear was orienting to or in contact with the presented objects. An orientation score (0) was given when the bear paid attention to but did not touch the objects. A contact score (C) was given when the bear was in contact with the objects. If contact occurred without noticeable orientation toward the objects, no score was given.

Three different tests were run, using this procedure. An account of the bear's behavior during the first test was recorded by hand. Behavior during the second and third tests was recorded with super-8 movie film.

RESULTS AND DISCUSSION

Quantitative Results

Quantitative results of this study indicate a very high level of curiosity. The scores of each animal for the novel objects presented in the 3 tests are given in Table 1. It is unfortunate that only visual orientation and actual contact are scored with this technique. Odor responses are ignored, and these repsonses may be important in bears that have well-developed chemosensory systems.

Chains aroused the highest degree of curiosity in the bears, followed in descending order by dowels, hoses, and blocks. The attention given to the objects is best appreciated by comparing the percentage of time spent

Table 1. Time spent oriented to and in contact with novel objects introduced for 6-minute periods (72 consecutive 5-second intervals) to 2 captive American black bears, at 3 age levels. All scores are given in number of 5-second intervals the subject oriented to or was in contact with the novel objects.

	16 months old			20 months old			26 months old		
	Orientation	Contact	Total response	Orientation	Contact	Total response	Orientation	Contact	Total response
Subject 1									
Blocks	1	18	19	3	0	3	1	70	71
Chains	2	70	72	0	70	70	1	66	67
Dowels	1	65	66	0	72	72	1	67	68
Tubing	0	35	35	0	72	72	1	71	72
Subject 2									
Blocks	6	10	16	0	72	72	0	69	69
Chains	2	70	72	0	72	72	2	68	70
Dowels	0	67	67	0	72	72	1	48	49
Tubing	2	31	33	0	64	64	1	70	71

with them. The bears attended to the objects an average of 82 percent of the time the objects were in their enclosures.

A comparison of the responses to the 4 set of objects among the bears, other carnivores, and primates is given in Table 2. The greater response of the bears to the chains, compared with the responses of other carnivores, may result from the bears' greater ability to use the forepaws to grasp and manipulate objects.

Table 2. Average of the time spent oriented to and in contact with novel objects for 2 captive American black bears, compared with averages for other carnivores and for primates. All scores are given in number of 5-second intervals of a possible 72 intervals per session that the animals spent oriented to or in contact with novel objects.

	Black bears	Carnivores[a]	Primates[a]
Blocks	41.67	38.49	33.79
Chains	70.50	19.07	24.43
Dowels	65.67	29.58	28.39
Tubing	57.83	39.98	26.21

[a] Glickman and Sroges (1966).

The effect of captivity on the responses was not assessed. However, Davis and Dugan (1975) conducted a similar study with the same 2 bears and 4 zoo animals — a black bear, 2 Malayan sun bears (*Helarctos malayanus*), and an assumed hybrid between the grizzly (*Ursus arctos*) and a black bear. Their results indicated that the more sterile the environment, the higher was the responsiveness to the novel objects. Within their sample, age, sex, and species differences were not as apparent as housing differences. The 2 black bears of this study housed in a seminatural enclosure were less responsive than the zoo animals.

Although Glickman and Sroges (1966) found older zoo animals tended to be less responsive, their results with bears were inconclusive.

A comparison of the mean of total responses among the carnivores is shown in Table 3. The bears exhibited a greater level of curiosity toward the novel objects than the other carnivores tested. Even though these data were collected from captive animals and the number of subjects was small, the intensity of the bears' response still has important implications. Black bears may be more likely to approach and come in contact with novel objects in their environment than other animals. Problems with black bears have not typically been viewed in terms of curiosity. However, it seems that bears may exhibit an intrinsic behavior to approach and manipulate new objects in their home ranges.

Table 3. Mean total of responses of carnivores to novel objects introduced into their environment. All scores are given in number of 5-second intervals of a possible 72 intervals per session that the animals spent oriented to or in contact with novel objects.

Carnivores	Mean score
Superfamily: Feloidea[a]	29.65
Family: Felidae[a]	32.10
Genus: *Panthera*[a]	45.06
Genus: *Felis*[a]	17.94
Superfamily: Canoidea[a]	34.35
Family: Canidae[a]	31.00
Family: Procyonidae[a]	36.91
Family: Mustelidae[a]	32.86
Family: Ursidae	58.92

[a] Glickman and Sroges (1966)

Behaviors Toward Novel Objects

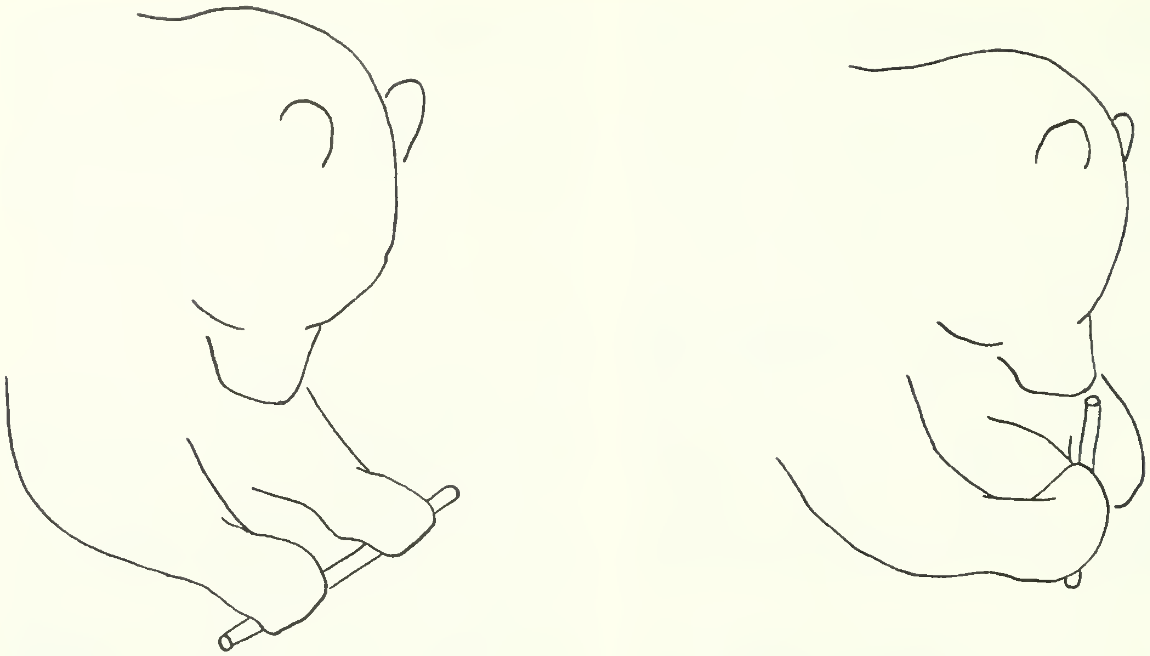
The bears initially reacted to all test objects in a similar manner. When the object was introduced, the animals would approach, smell the object, manipulate it with their forepaws, and then begin to chew on it.

The use of the forepaws was very pronounced. The bears seldom were in contact with the objects unless they were using their forepaws to grasp, hold down, or turn the objects. Both animals were adept at lifting and turning over the objects. The animals could partially grasp the objects by bending the claws of the front foot downward, almost touching the front pad of the foot. Lifting and turning over an object was accomplished by grasping the farther side of the object and pulling upward and back toward the body. Although the pads of the front paws of the bears could be turned so that they were perpendicular to the ground, flipping of objects by a rotation of the foreleg was not observed. Also, the bears never lifted an object with the pads of the front foot turned upward. All lifting was a raking motion with the claws turned downward and back. The bears were observed using one forepaw to lift the chains, dowels, and tubing from the ground. The chain was grasped between the claws and the foot pad, as described. The dowels and tubing were lifted in the same manner as the chain or by pushing the object between the toes and lifting the forepaw upward.

The objects were often held between the forepaws for chewing. The blocks, dowels, and hoses were held in 1 of 4 positions, illustrated in Fig. 1.

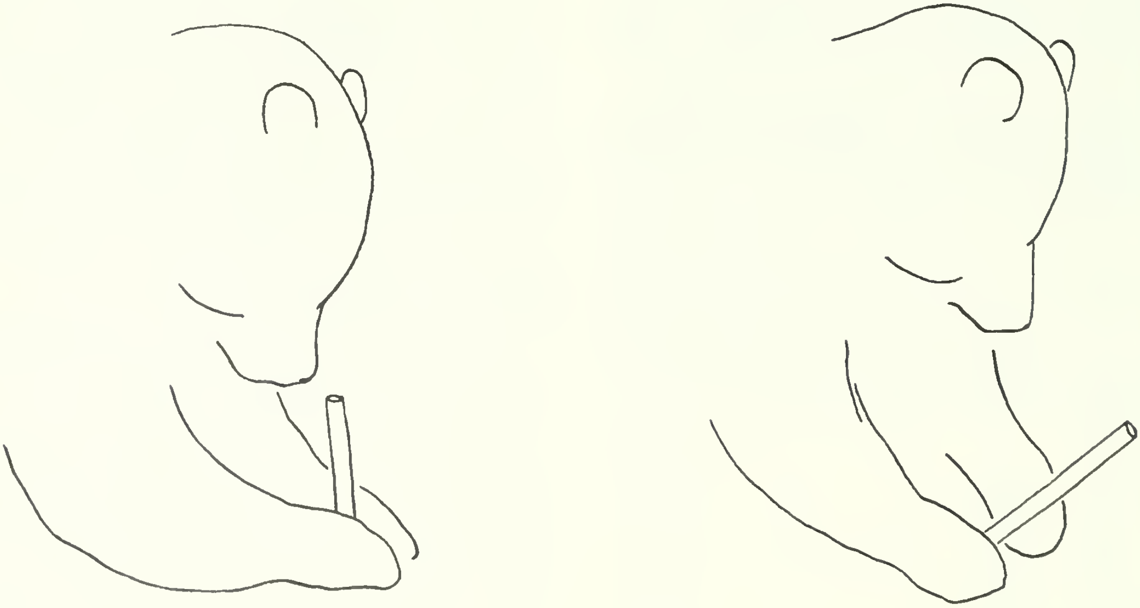
Exploration of the blocks, dowels, and hoses generally occurred with the bears lying on their stomachs. Exploration of the chain included playing with it, which was often the case with other objects. During play, the bears would assume a variety of body positions. Both bears would sit upright, with legs forward, and pull the objects to their stomachs, rolling and wrestling with them.

Clawing at the objects was observed but did not occur frequently. The blocks and tubing were pawed



FLAT ON GROUND

ONE PAW AGAINST THE OTHER



BETWEEN PAWS

DOWNWARD PRESSURE WITH ONE PAW

Fig. 1. Use of the forepaws by black bears to hold objects.

initially but were then turned, held, and chewed. Both bears oriented to the opening at each end of the hoses. They would place a claw in the hole and pull, as if trying to pry something out.

Exploration also invariably involved chewing. The methods of holding illustrated in Fig. 1 were used to secure the objects in order to chew, lick, and smell them. The bears would use a pair of canines or molars to splinter the wood. After it was splintered, the bears would use the incisors to grasp the objects lightly and pull pieces from them. The canines were used to grasp the tubing in attempts to pull portions away. Both bears intermittently smelled the objects between bouts of chewing.

The response to the chains was the most interesting. After initially smelling and chewing a chain, both animals would rake and lift it and let it fall several times. Then the bears would begin to play with the chain. They would assume a variety of body positions and were very active. The forepaws were used to hold, lift, and swing the chain. One bear would lie on her back and hold the chain above her face with one forepaw. She would then pass the chain from paw to paw, placing 1 or 2 claws in the links and allowing an end of the chain to dangle and brush her face.

Curiosity is one of many behaviors that should be assessed for ideal management of this family of animals. Behavioral data are being recognized as an important management tool, and delineation of predictable behavior is important in evaluation, control, and prevention of bear/human conflicts. The recognition of a high degree of intrinsic curiosity in the black bear may aid managers in conflict situations. The bear is not motivated solely by a search for food in its approach to the human environment. The conscientious removal of food without regard to the bears' innate curiosity may not eliminate potential conflict.

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PRELIMINARY ANALYSIS OF FEMALE REPRODUCTIVE TRACTS FROM PENNSYLVANIA BLACK BEARS[1]

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Abstract: Reproductive tracts were collected from 87 female black bears (*Ursus americanus*) killed by hunters in northeastern and north-central Pennsylvania during November 1974 and 1975. Pregnant animals carried an average of 2.75 corpora lutea. Corpora lutea were significantly larger in tracts that had implantations than in tracts during the delay stage. The sources of ova were found to be equally divided between ovaries. Twelve blastocysts and 22 implanted embroys were examined. Variation in development stage among these samples indicated that implantation occurred late in November or early in December. An average of 2.88 placental scars were observed in animals bearing scars. Potential recruitment from first breeding (2.39 animals) was significantly less than from second or later breedings (3.23 animals). Minimum breeding age for female bears was 2.5 years, at which time 38 percent of the animals bred. The majority of females bred by the time they were 3.5 years old. A very low incidence of nonbreeding females was found.

Pennsylvania maintains one of the largest populations of black bears in the northeastern United States, but in recent years increasing concern for the status of the population has created a need for improved management information.

We extend our appreciation to J. Giles, J. Lambiase, and W. Shope for aid in examination of reproductive tracts and in age determination; to Pennsylvania Game Commission personnel, graduate students, and successful hunters for their efforts in collecting the tracts; and to R. Anthony, J. Lambiase, and G. Storm for their helpful suggestions for improving the manuscript.

METHODS

Reproductive tracts and first premolar teeth were collected from 87 female bears harvested in northeastern and north-central Pennsylvania on 24 November 1974 ($N = 35$) and 25 November 1975 ($N = 52$). Most tracts were fixed in 10 percent formalin within several hours of death, although some were received frozen. All tracts were stored in 10 percent formalin until examined. Uterine cornus length was measured to the nearest mm from the point of bifurcation to the bursa-cornus junction. Outside diameter and inside circumference at the midpoint of each uterine horn were measured to the nearest mm. Horns were then opened to locate and count blastocysts, embryos, or placental scars. To simplify recording of blastocyst and implantation sites, cornu were divided into four regions. Region 1 was the quarter of each uterine horn nearest to the ovary, regions 2 and 3 were the next nearest quarters, and region 4 was the quarter of each uterine horn closest to the bifurcation.

Ovaries were excised, cleaned of extraneous material, blotted dry, and weighed to the nearest 0.01 g. Each ovary was then divided along its long axis to count and measure any corpora lutea present.

The bears were assigned to age-classes by counting cemental annuli in prepared tooth sections (Willey 1074). Age distribution of the 87 animals is shown in Table 1.

Table 1. Age distribution and reproductive condition of 87 female bears harvested in Pennsylvania, 1974 and 1975.

Age	Sample size	Number pregnant	Number with placental scars	Number with no evidence of breeding
Cub	2	0	0	2
1.8	21	0	0	21
2.8	10	5	0	5
3.8	16	9	5	2
4.8	9	1	8	0
5.8	7	0	7	0
6.8	3	0	2	1
7.8	8	3	4	1[a]
8.8	5	2	3	0
9.8	3	1	2	0
11.8	1	0	1	0
13.8	1	0	1	0
20.8	1	0	0	1[b]
Total	87	21	33	33

[a] Less than half of tract available for examination.
[b] Cyst on antimemetrial side of one horn.

RESULTS

Size of reproductive tracts, as reflected by cornus measurements and ovarian weights, increased with age and with pregnancy. Heaviest ovaries were those bearing corpora lutea, with each corpus adding about 0.50-1.25 g to ovarian weight (Table 2, 3). The largest of the 44 corpora lutea examined measured 18 × 12 ×

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[1] Paper No. 210 of the Pennsylvania Cooperative Wildlife Research Unit; The Pennsylvania State University, Pennsylvania Game Commission, U.S. Fish and Wildlife Service, and the Wildlife Management Institute, cooperating.

Table 2. Cornus sizes of Pennsylvania bears, 1974 and 1975. SD = Standard Deviation.

Age	Length (mm)		Inside circumference (mm)		Outside diameter (mm)	
	Mean	SD	Mean	SD	Mean	SD
10 months	64.2	12.0	4.5	0.7	2.6	0.5
1 year, 10 months	82.8	16.9	7.1	1.4	3.3	0.6
2 years, 10 months Never bred	97.8	37.2	11.2	4.8	5.0	1.8
2 years, 10 months Pregnant	111.4	23.6	14.3	1.8	6.4	1.0
3 years, 10 months Bred previous year	117.8	14.2	11.4	3.0	5.2	0.6
3 years, 10 months Pregnant	140.8	15.0	15.6	2.3	7.0	0.9
≥4 years, 10 months Bred previous year	115.1	21.9	11.7	1.9	5.5	0.9
≥4 years, 10 months Pregnant	164.5	28.1	16.0	3.5	7.8	1.6

Table 3. Ovarian weights (g) by number of corpora lutea from Pennsylvania bears, 1974 and 1975. SD = Standard Deviation.

Age	Number of corpora lutea							
	0		1		2		3	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1 year, 10 months	1.24	0.49	-	-	-	-	-	-0-
2 years, 10 months Never bred	1.30	0.31	-	-	-	-	-	-
2 years, 10 months Pregnant	-	-	1.17	0.27	-	-	-	-
3 years, 10 months Bred previous year	1.95	0.62	-	-	-	-	-	-0-
3 years, 10 months Pregnant	-	-	1.92	0.63	2.47	0.81	3.70	-
≥4 years, 10 months Bred previous year	2.35	0.71	-	-	-	-	-	-0-
≥4 years, 10 months Pregnant	-	-	2.19	0.87	3.39	0.71	4.45	0.87

14 mm and was from a tract in which implantation had occurred. Mean maximum diameter of corpora lutea was 9.8 mm ($N = 24$) in tracts that had not implanted and 12.3 mm ($N = 20$) in implanted tracts, the difference being significant ($P < 0.01$). Corpora lutea counts for 15 animals from which complete tracts were obtained yielded an average of 2.75 luteal bodies per animal.

Thirteen of the 15 bears mentioned above carried more than 1 corpus each. Erickson and Nellor (1964.29, 32) stated that "Multiple ovulations seem for the most part to be confined to one ovary, indicating that in most cases one ovary is more active than the other during the breeding season. . . . " Our observations, however, indicate that there is insufficient evidence for rejecting the hypothesis that both ovaries contribute equally to the total conceptus complement (Table 4).

Table 4. Distribution of corpora lutea in ovaries from 13 Pennsylvania bears having 2 or more corpora. For hypothesis of equal distribution between ovaries, chi-square = 3.44, $P > 0.25$.

Number of corpora lutea	Distribution between ovaries	Number of bears	
		Expected	Observed
2	0, 2	3.00	1
	1, 1	3.00	5
3	1, 2	2.25	2
	0, 3	0.75	1
4	0, 4	0.50	0
	1, 3	2.00	2
	2, 2	1.50	2

Twelve of 29 potentially recoverable blastocysts (based on corpora lutea counts) were located. Two were found in region 1 (the quarter of the cornus nearest the ovary), 6 in region 2, 3 in region 3, and 1 in region 4. All blastocysts were free-floating within the lumen or were unattached within the rugose folds of the uterus. The inner cell mass and trophoblast were evident in well-preserved specimens. All blastocysts were enclosed in a zona pellucida as described by Wimsatt (1963).

Twenty-two implantations occurred in 8 animals. Variation of multiple embryo development within animals was negligible, but variation among animals ranged from stages of recent implantation to well-developed embryos with limb buds and recognizable somites.

Implantation sites determined by placental scars and current implantations were equally divided among the three regions of the cornu closest to the bifurcation. Only 1 or 88 (1.1 percent) occurred in the region closest to the ovary. Scars were readily observed on the inner surface of the cornus but could not be seen by external examination of the tract. Changes in, and proliferation of, the endometrium of pregnant animals effectively obscured placental scars. These scars reappeared after parturition in at least some animals. In 2 tracts, scars could be categorized as faded or bright. Sixty-nine recent placental scars were counted on 29 complete tracts bearing scars, an average of 2.88 scars per tract.

Potential recruitment from first breeding averaged 2.39 animals ($N = 23$, Sd = .066) as derived from a sample formed by combining counts of corpora lutea from 2- and 3-year-old animals with recent scar counts from 3- and 4-year-old animals. Potential recruitment from second and later breedings averaged 3.23 animals ($N = 22$, SD = 0.75). This estimate was determined from a sample formed by combining corpora lutea counts from animals older than 3 years with placental scar counts from animals older than 4 years. Second and later breedings had a significantly greater potential for recruitment than did first breedings ($P < 0.01$).

Using the same technique to estimate the proportion of females breeding, we found that 38 percent of the females entered the breeding population at 2.5 years of age (Table 5). Our sample indicates that 88 percent of all females were bred by the time they reached 3.5 years of age.

Table 5. Proportion of sample of female bears in Pennsylvania showing evidence of breeding by age-class 1974-75.

Age	Number breeding/total	Percent
2.8	10/26	38
3.8	17/25	68
4.8	8/16	50
5.8	2/10	20
6.8	4/11	36
7.8	6/13	46
8.8	4/8	50
⩾2.8	51/109	47

DISCUSSION

Variability in conceptus development observed among bears harvested during the third week of November is sufficient evidence for placing time of implantation in Pennsylvania between mid-November and early December. Because of rapid growth immediately after implantation (Daniel 1974), we would expect embryos larger than those observed if implantation occurred much earlier. Had implantation occurred much later, it is doubtful that any well-developed embryos would have been found.

High potential recruitment in Pennsylvania bears appears due to high ovulation rates, low intrauterine mortality, a low incidence of nonbreeders, and early sexual maturity. Corpora lutea and placental scar counts are considerably higher than those reported in Virginia (Stickley 1957), Michigan (Erickson and Nellow 1964), North Carolina (Collins 1974), and Montana (Jonkel and Cowan 1971). Our observations indicate that all females older than 2.5 years have the potential to produce approximately 2.5 cubs every other year.

Although reports of successful breeding by 2.5-year-old female bears are not unprecendented (Stickley 1957, Ammons 1974, Collins 1974), it was believed to occur only rarely (Collins 1974). The estimated 38 percent of Pennsylvania females breeding at 2.5 years of age significantly increases the reproductive potential of the population. The high reproductive potential may be explained, in part, by the large quantity and variety of foods provided in Pennsylvania's oak and transition forests.

Since only 1 of the bears examined was of known age, failure to determine accurately the age of the animals could be a source of bias in this study. Nevertheless, comparisons of our age assignments with those of other workers showed essential agreement in 36 of 38 tooth sections. The recorded increase in cornus size and in ovarian weight with increasing assigned ages provides added confidence in our age determinations. Although error might also occur through overestimation of the implantation rate through counting both old and recent placental scars and considering them one pregnancy, the probability of this occurrence appears minimal because of the obvious difference in brightness between old and new scars. Old scars also fade more rapidly than new ones when exposed to formalin, further lessening the chances of confusing old and new scars (Erickson and Nellor 1964).

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FOSTERING BLACK BEAR CUBS IN THE WILD

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Abstract: Three black bear (*Ursus americanus*) cubs were abandoned, at approximately 2 weeks of age, on 4 February 1976, in New York State's Catskill region. The dens of 4 radio-telemetered adult female bears were located by the Department of Environmental Conservation during research on the black bear population in the Catskills. Two of the abandoned cubs were placed in the only maternity den existing among the 4 radio-telemetered female bears. The 6-week-old foster cubs were accepted by the adult female bear. The foster mother left the den in mid-April accompanied by 3 cubs. The family group was observed twice from radiotracking aircraft during the spring and summer of 1976.

Since 1970, the Department of Environmental Conservation has intensively investigated the population of black bears inhabiting the Catskill region of New York State. The research was prompted by a decline in the number of legally harvested bears during the preceding 20 years. A mark-and-recapture program and examination of all hunter-killed bears were the principal initial aspects of the study. Chief among the preliminary findings was the existence of 2 subpopulations (McCaffrey et al. 1976): a northern component distinct from a smaller southern component contiguous with a bear population in Pennsylvania.

Research continued in an effort to obtain additional information necessary for completion of a long-range management plan (Clarke 1976a). Attention was focused on the northern subpopulation (approximately 150 bears, summer 1976) occupying an area of about 2,250 km^2. The northern range includes a major portion of the Catskill Forest Preserve (948 km^2), an area of extensive unbroken northern hardwood forest with red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*) at high elevations, dominated by the Catskill Mountain landform (Stout 1958).

Radiotelemetry was used in the northern Catskills to acquire data on bear habitat preferences, home ranges, and reproductive success. Five adult bears (4 females, 1 male) possessed active radiocollars during the winter of 1975-76. Plans to locate and inspect the dens of the 5 radio-telemetered bears were altered by a midwinter incident. On 4 February 1976, an adult female bear was displaced from her den by a dog whose owner was hunting varying hares (*Lepus americanus*). The adult female abandoned the 3 cubs she had with her in an exposed den, a shallow depression partially shielded by a pole-sized windfall (Clarke 1976b). The den was situated at an elevation of approximately 731 m on the upper southwest slope of High Point Mountain in Olive Township, Ulster County. The cubs were removed from the den on the day of abandonment. Our observations during the next 2 weeks failed to produce evidence that the adult female had returned to the den. A decision was made to attempt fostering the cubs with 1 or more of the radio-telemetered adult females if they were found to possess cubs.

We wish to thank H. E. Doig, Director of the Division of Fish and Wildlife, and S. L. Free, Chief of the Bureau of Wildlife, for their support in the early decision to attempt fostering the cubs. Further acknowledgment is given to N. Clarke, N. O'Pezio, and A. Hackford, who assisted in care of the cubs; also to M. Kent for initial cub care. This work has been part of Catskill black bear research conducted under Federal Aid in Fish and Wildlife Restoration Project W-89-R, Job X-7.

METHODS

Effort to locate and inspect the dens occupied by the 4 radio-telemetered female bears was accelerated upon commitment to attempt fostering the cubs. Severely restricted den openings prohibited our entry to determine the presence of cubs with the 4 adult female bears. Consequently we used a portable cassette tape recorder and a remote omnidirectional microphone for recording sounds within the dens. We hoped to discern the presence of cubs and judge their numbers by analysis of recorded vocalizations. Only 1 maternity den was found among the 4 dens examined.

The abandoned cubs, 1 female and 2 males, weighed 0.81 kg, 0.84 kg, and 0.89 kg, respectively, on 7 February, 2 days after the Big Game Project received them (Fig. 1). We estimated their age to be 2 weeks on the basis of close similarity to cubs aged by Poelker and Hartwell (1973). The cubs were immediately placed on a ration, presented for *ad libitum* consumption 4 times daily, of 1 chicken egg yolk and 15 ml honey mixed with 390 ml of Esbilac (a Borden Company enriched milk substitute).

On 27 February, the cubs were prepared for the fostering attempt. We decided not to place ear tags on the cubs because such marks might make the cubs appear

Fig. 1. Abandoned black bear cub at about 2 weeks of age, Catskill region, New York, 1976.

alien to the foster mother. A number was tattooed on the inner surface of each cub's upper lip; distinctive digits 2, 3, and 4 were given to the female and 2 males, respectively. The lip tattoos were considered permanent marks that would permit the bears to be identified if they were captured again or were taken by hunters.

We attempted to freeze-brand each cub for possible distant recognition upon emergence from the den. A livestock freeze-branding iron was used to place a mark on 1 of 3 readily observable sites: left shoulder, right thigh, or left thigh. The branding iron was equilibrated in a mixture of dry ice and denatured alcohol. The hair at each site was clipped close to the skin surface with surgical scissors. Branding iron application time for each cub was 12-15 seconds.

The cubs were transported to the den site on 4 March. We planned to attempt the fostering during a period of cold weather, anticipating an increased probability that the foster mother would be dormant. The den was situated on a south-facing slope in an area of hardwoods and extensive rock outcrops, at an elevation of about 975 m, approximately 3 km from the nearest road. Accumulated snow had been reduced to about 15 cm under forest cover. Sites lacking overhead cover had intermittent patches of exposed ground at upper elevations, grading to extensive areas free of snow at lower elevations. The den was a ground cavity between 2 layers of rock outcrop, with the entrance facing downhill. The interior of the den was approximately 1 m wide, 2 m deep, and 0.5 m high.

We carried the cubs to the den in a vented styrofoam container. We fed them their scheduled morning ration later than usual, within 30 minutes of reaching the den, hoping to induce a quiescent state for their placement with the foster mother. The cubs were handled in their soiled cotton towel bedding, which had not been changed for several days, to eliminate direct human contact and thus to avoid leaving human scent on the cubs. We devised a tool for placing the cubs into the den, realizing that it would be impossible to approach the den from downhill without the risk of being seen by the denned female. The cubs had to be placed in the den from a position on top of the rock outcrop extending over the den entrance. The tool was constructed out of a metal pipe, a plastic pail, scraps of wood, bolts, and cord. Its function was to lower the cubs in the pail, mounted on the pole, to the den entrance and spill the cubs into the den through a pivoting action of the pail. We set up a time-lapse Kodak Analyst super 8 mm camera to monitor the den site and document spring emergence of the bears. A timer activated the camera from dawn to dusk exposing 1 frame of film about every 50 seconds.

RESULTS.

Analysis of the cub vocalizations recorded at the 1 maternity den suggested the presence of only 1 cub. We decided to attempt fostering only 2 of the cubs, the female and the larger of the 2 males, rather than risk overtaxing the adult female's lactation capability if she really had more than 1 cub.

An average body weight gain of 1.44 kg was achieved by the 3 cubs over the 26 days preceding fostering on 4 March (Table 1). Male cub number 3 was shipped via commercial aircraft to the West Virginia Department of Natural Resources at Elkins, where facilities existed for extended care of the bear, with possible contribution of management information. During the 46 days proceeding shipment on 24 March, the cub gained 3.00 kg in body weight.

Table 1. Body weights (kg) of abandoned black bear cubs, Catskill region, New York, 1976.

Sex	Tattoo number	7 February (2 weeks old)	3 March (6 weeks old)	23 March (9 weeks old)
Female	2	0.81	2.47	-
Male	3	0.84	2.17	3.84
Male	4	0.89	2.21	-

A predictable initial response was achieved with the freeze-branding. The skin had a white appearance upon withdrawal of the branding iron, followed by a slight reddening and swelling over the ensuing 24 hours. A small scab formed and flaked off with the regrowth of hair at each brand site during the 6-day period after branding. We observed no white hair at the brand sites before the cubs were fostered, at 6 days postbranding, or when the remaining cub was shipped to West Virginia at 26 days postbranding. Reports received from personnel of the West Virginia Department of Natural Resources indicated that white hair never appeared at the branding site on cub number 3.

We attempted the fostering when the cubs were approximately 6 weeks of age. Although we fed the 2 cubs about 30 minutes before placing them in the den, they vocalized loudly when picked up and taken from the warm styrofoam container. We quickly put the cubs into the pail and lowered them to the den entrance. They crawled into the den, aided by the momentum of their exit from the cub-placing tool. Before introducing the cubs we had looked into the den, using a mirror attached to a pole; the adult female was asleep, facing the den entrance. After introducing the cubs, the adult female, apparently still asleep, was observed in a different position with her back toward the den entrance. The foster cubs had apparently crawled to the adult female and had begun nursing, judging by the suckling sounds emanating from the den during the hour we waited nearby. The only other sounds we heard were subdued cub vocalizations previously associated with nursing. We heard no sound suggesting distress.

The time-lapse camera recorded the emergence of the adult female from the den on 7 April. She was photographed over the next 2 days spending considerable time moving around immediately outside the den. Cubs were photographed outside the den for the first time on 14 April. The adult female and cubs were last photographed on 16 April. The family unit apparently left the den for the final time before dawn on 17 April. Despite observing individual cubs engaged in such activity as climbing small trees immediately outside the den, we were not able to distinguish more than 2 cubs at any 1 time in the film.

On 2 occasions during the spring and summer of 1976, the adult female and 3 cubs were observed from our radiotracking aircraft. During this period, the adult female's home range covered about 50.7 km^2 and included the area of the preceding winter's den. The adult female had selected her winter den site for 1976-77 by 6 December, approximately 2.5 km from her previous den. We observed the adult female with an undetermined number of yearlings in the den during that winter. We planned to immobilize the adult female and the yearlings during late winter in an effort to collect physical data, change the adult female's radiocollar, and examine the yearlings for lip tattoos to ascertain the ultimate degree of fostering success.

DISCUSSION

This case of cub abandonment may be viewed as the documented loss of 3 individuals from the Catskill bear population to a cause of mortality other than legal hunting. Previously reported estimates that legal hunting represents 90 percent of all Catskill bear mortality (McCaffrey et al. 1976) still appear valid. Death is the expected consequence of abandoning young preweaned cubs in winter dens. In this case we counteracted, in part, the imminent population loss, at least initially, of the cubs by placing 2 of them with a nursing foster mother in a den in the wild, to our knowledge the first reported such attempt involving the black bear.

Human developmental encroachments upon black bear habitat may present serious problems for the integrity of relatively small populations of black bears and their ranges. Increasing human activities in winter in some areas may adversely affect reproductive success of black bears. Adult female black bears selecting exposed surface dens appear to be most vulnerable to disturbance. In the Catskills we have observed most dens to be ground cavities, which apparently afford the occupants maximum protection from intrusion.

Fostering young abandoned or orphaned black bear cubs with wild adult female black bears appears to be a feasible technique. Its management application is obviously limited; wildlife managers must have knowledge of the locations of occupied black bear maternity dens. During black bear investigations employing radiotelemetry, there is an opportunity, although usually short-term, to apply this technique if precipitating circumstances arise.

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CHEMICAL AVERSION CONDITIONING OF POLAR AND BLACK BEARS

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Abstract: Emetine hydrochloride (EHCl), alpha-naphthyl-thiourea (ANTU), and lithium chloride (LiCl) were tested as aversion-conditioning chemicals on black bears (*Ursus americanus* Pallas) and on polar bears (*U. maritimus* Phipps) from 1975 to 1977. Captive black bears were fed varying doses of EHCl and LiCl to establish effective dose levels of these chemicals. Four cow kills, treated with LiCl and ANTU, showed an apparent 50 percent increase over controls in the times taken by free-ranging black bears to consume the carcasses. ANTU, EHCl, and LiCl reduced the consumption of Gainesburger baits by free-ranging polar and black bears. Approximate effective dosages of each chemical (orally administered and based on body weight) are 25 mg/kg for ANTU, 100-350 mg/kg for LiCl, and 2.0-4.0 mg/kg for EHCl.

Polar and black bears sometimes constitute serious pest animals where they come into contact with man and his activities. Berghofer (1964) outlines several techniques for dealing with nuisance bears. Gilbert and Roy (1977) discuss damage caused by black bears to beeyards at Peace River, Alberta. Jonkel (1975) summarizes several encounters between polar bears and men in the Canadian Arctic, citing 3 previously unreported attacks. Stirling (1975) details a fatality involving an employee on an Imperial Oil offshore drilling rig located on the Beaufort Sea in the Mackenzie Delta. The employee was attacked by a subadult that appeared to be in a semi-starved condition.

The objectives of this study were to (1) define problems associated with field applications of aversion-conditioning chemical agents; (2) evaluate 2 previously untried potential aversive-conditioning chemicals; and (3) assess the abilities of EHCl, ANTU, and LiCl to reduce problem situations involving polar and black bears by inducing a conditioned response to a bait stimulus.

Ingestion of a sickness- or nausea-inducing chemical agent along with a bait food will reduce consumption of that bait type upon subsequent exposure (Rozin and Kalat 1971, Seligman and Hager 1972). This procedure is currently viewed as a viable technique for reducing predator attacks on sheep (Gustavson 1974, 1976), raptor attacks on lambs (Brett et al. 1976), bear damage to beeyards (Gilbert and Roy 1977), and various other pest situations involving visitation to a site and consumption of food or livestock (Gustavson 1976). Gustavson believes that coyotes (*Canis latrans*) can be taught to avoid sheep through an association developed with LiCl-treated mutton strip baits. Gilbert and Roy (1977) were able to reduce black bear damage to beeyards by placing LiCl baits (6-g capsules) around the yards and erecting charged electric fences near the sites.

Shumake et al. (unpublished), in experiments with 4 captive coyotes, were able to reduce consumption of specific mice (albino vs. normal) through a single peritoneal injection of LiCl. They found, however, that the transfer of an aversion from dead baits to live prey was not always successful. This finding is in agreement with Gustavson and Garcia's (1974) observations and is the basis of a criticism of the technique by Shumake et al. (unpublished).

LiCl has been the subject of aversion-conditioning experiments on various species of predatory and nonpredatory animals. Nachman (1970), Krames et al. (1973), and O'Boyle et al. (1973) have studied the effects of this chemical on rats and mice. Its mode of action has not been clarified. The substance is very hygroscopic and dosage levels determined by Gustavson (1974) were in the range of 100-500 mg/kg. It is inexpensive, safe to handle, and of low toxicity to humans.

EHCl was selected for tests because it is employed in human pharmacology as an emetic for use in cases of orally injected poisons. Its side effects in humans include nausea, extended periods of vomiting, headaches, and other discomforts relating to the gastrointestinal tract. It is normally given intravenously; however, it is active in humans when administered orally but has greater variation in effect and duration (Goodman and Gilman 1975). Human dosages are approximately 1 mg/kg intravenously and 15 ml of syrup orally. It is considerably more expensive than LiCl but the lower specific dose offsets this disadvantage.

ANTU is a species-specific Norway rat (*Rattus norvegicus*) poison that has shown strong emetic properties in dogs (Richter 1945) and some rodents (Passof et al. 1974). Richter (1945) noted that it produced vomiting and retching in dogs subjected to rat-lethal doses in the laboratory. He found the LD_{50} for dogs to be less than 100 mg/kg. He believed that the nausea and vomiting resulting from oral ingestion protected the animal from continued intake of the chemical.

DuBois et al. (1946) studied this drug further and determined an LD_{50} of 50 mg/kg for domestic dogs. He also noted the development of a degree of tolerance to the drug when sublethal doses were continued.

Shumake et al. (unpublished) state specific problems that they believe might interfere with the success of LiCl or other chemical agents in aversion-conditioning techniques. Their main criticism is that a predator eating a sublethal dose of an aversive agent will not eat that food on subsequent exposure but that only a fraction of the affected animals will transfer this aversion to live prey. The remainder, although avoiding other treated baits, are unlikely to be successfully conditioned from killing a live prey animal. Shumake et al. (unpublished) were able to demonstrate this effect with their test coyotes.

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METHODS AND MATERIALS

Captive Black Bears

Two male black bears, each weighing 100 kg and located at the Olympic Game Farm, were subjected to control and experimental baits using LiCl and EHCl. The bears were kept separate during feeding, and were maintained on the feeding regime specified on Table 1. An attractant bait was used to conceal the implanted chemical. Homogenized honey was used in LiCl experiments; raw beef was used in EHCl experiments. In each series of tests, both animals were offered untreated bait food, followed by test doses of the chemical agent under study. In the case of LiCl, a test of the effects of NaCl on bait acceptance was also carried out due to the very salty taste and high dosage levels of LiCl. After tests with aversive agents, both animals were then placed on a feeding regime that restricted their normal intake of food on specified days in order to establish the effects of hunger on the acceptance of offered baits. Untreated (no aversive chemical) baits were offered for 10 days after LiCl ingestion and for 7 days after EHCl ingestion. The acceptance or rejection of offered baits was recorded.

For the purposes of this study, rejection of an offered bait was defined as any reaction ranging from hesitation in approaching baits to complete rejection of baits upon visual or olfactory investigation.

Free-Ranging Black Bears: Open Range Country

Four bear kills of domestic cows in the interior of British Columbia were used as treated baits in order to evaluate the effects of aversive chemical agents on free-ranging black bears. Three fresh kills were observed during the experimental period; 1 kill occurred just before this experiment, and I was able to make observations on this carcass during the study. The experiments tested for differences in the time used to consume a freshly killed cow carcass (measured in days) between control and treated kills. Two of the cows were treated with chemicals, 1 with LiCl and the other with ANTU. One yearling was handled but not treated with chemicals. The fourth animal was used as an unhandled control. Each chemical was placed in shoulder incisions under the hide or was sprinkled over the exposed and partially eaten viscera of each cow. Handling of each carcass involved several procedures to minimize the effects of human odor. All experimental and control carcasses handled were approached on horseback, and disposable poly gloves and a new scalpel blade were used to make each shoulder cut. Inspection of carcasses was always carried out on horseback, except once when the carcass had been almost completely consumed.

Approximately 25 g of LiCl was placed in each of 4 incisions in 1 experimental cow. The other cow was treated with approximately 2.0 mg of ANTU in each of 4 incisions. Carcasses were evaluated twice daily, once early in the morning and once in the late evening. All carcasses were initially observed from a distance to determine whether any predator was present.

Free-Ranging Black Bears: Dumps

The responses of free-ranging black bears to control and experimental baits in British Columbia dumps was evaluated at Golden, Parsons, Bush River Camp (Columbia River valley), the Rogers Pass Park dump, and at Mission (lower mainland). Gainesburger dog food patties were placed at bait stations at each of the 4 dumps. For the first 5 days, these baits were left untreated (no aversive agents) but were soaked in sardine oil. The number of baits consumed was noted. During the next 2 days, baits treated with LiCl, EHCl, or ANTU were set out.

Treatment of baits consisted of placing the aversive chemical between 2 or more patties, as needed, to conceal the chemical. The patties were then tied together with soft string and were soaked in sardine oil. Dosages were based on a bear weight of 100 kg. After this treatment and a 1-day wait, chemically untreated dog food patties were placed at the bait stations, and the number of baits consumed were noted for 5 successive days. At the Mission dump site, bait stations were observed on alternate days for an additional 10-day interval. Observations were made in the area around each bait station in order to estimate the occurrence of other scavengers.

Free-Ranging Polar Bears: Dumps

The responses of wild polar bears to control and experimental baits were evaluated at and near the dump at Churchill, Manitoba. Baits were prepared as for black bears, and dosages of LiCl, ANTU, and EHCl were based on a bear weight of 250 kg. A dosage of 100 mg/kg of LiCl was used for polar bears, instead of the 200 mg/kg dosage used for polar bears, to reduce the total volume of LiCl which had to be concealed in the bait. Baits were covered in brown paper to reduce removal by ravens (*Corvus corax*) and arctic foxes (*Alopex lagopus*). In addition, baits were observed continuously during 2 occasions at the Churchhill area dump in order to note observable reactions by bears after ingestion of baits and to note bait removal by other scavengers. As with free-ranging black bears, the consumption of baits was noted during control and experimental periods.

RESULTS

Tables 1 to 5 summarize the responses of polar and black bears to treated and untreated baits. Effective dosages for each agent, as determined from these tests, were 25 mg/kg for ANTU, 100-300 mg/kg for LiCl, and 2-4 mg/kg for EHCl.

Table 1 summarizes the initial determinations of LiCl dose levels and the behavioral responses of 2 captive black bears. The NaCl controls were readily accepted, perhaps reflecting the pre-experiment starvation of each test bear for 3 days. Two dosage levels of LiCl administered were 300 and 500 mg/kg. Both of these dosages represented considerable amounts of salt, requiring careful mixing of agent and bait to reduce concentrated lumps of LiCl. Both bears accepted the LiCl-treated baits with hesitation, but all of the baits were consumed. Subsequent untreated honey baits, offered each day for the next 10 days, appeared to elicit a conditioned aversive response, and, in cases of acceptance, considerable hesitation was shown. The feeding regime, involving periods of starvation, may have prompted the bears to try the honey. Some indications of discomfort followed ingestion of the treated baits. Both bears moved away from the bait containers and lay down. Two hours after treatment, some diarrhea was observed in the bear subjected to 500 mg/kg LiCl. The bear that received 300 mg/kg exhibited a hunching behavior that had not previously been seen by the animal attendant, and which probably reflected some level of gastrointestinal distress.

Table 1. Effects of LiCl-treated honey baits on 2 male captive black bears, each weighing 100 kg. A = accepted and ate bait; R = rejected bait. Time to visually apparent onset of discomfort (e.g., hunched walking, diarrhea) after treatment: Bear 1, 9 min; Bear 2, 11 min (my observations only). Bears were fed on "Bear Bread" manufactured at the Olympic Game Farm.

Bait and dosage	Delay before investigating or ingesting bait (min)	Bear 1	Bear 2
Untreated honey	0	A, rapidly	A, rapidly
Honey + NaCl (300 mg/kg = 30 g)	0.2	A, rapidly	A, rapidly
Honey + LiCl (300 mg/kg = 30 g)	0.5	A, hesitantly	Not tested
Honey + LiCl (500 mg/kg = 50 g)	0.5	Not tested	A, hesitantly
Untreated honey: Day 1 feed	-	R	R
2 feed	-	R (hunching)	R
3 feed	-	R	R
4 feed	-	R	R
5 starve	-	R	R
6 starve	-	R	R
7 starve	No data[a]	R	A, hesitantly
8 feed	-	R	R
9 feed	No data[a]	A, hesitantly	A, hesitantly
10 feed		R	A, hesitantly

[a] Game Farm staff did not take these data but observed bears' reaction during acceptance.

Table 2 summarizes observations of the effects of EHCl on 2 captive black bears. Raw beef proved to be a suitable bait for these animals, as they readily accepted untreated material. The small dose levels of EHCl allowed easy concealment of the agent in each bait, which apparently prevented detection of the chemical by the bears. Treated baits were rapidly accepted. Starvation appeared to prompt bear 1 to try untreated beef again but did not prompt bear 2 to try the untreated baits. Visually apparent indications of discomfort (the bears lay down) occurred later than with LiCl. No hunching was observed.

Table 3 outlines the apparent effects of LiCl and ANTU on free-ranging black bears. Percentage increases in the time taken for a bear to consume a carcass were based on 1 unhandled control, 1 handled control, and additional data obtained from the rancher. His data had been collected according to my specifications for a period of approximately 3 months prior to the tests. Carcass areas treated with chemical agent were consumed first, as the preparation allowed easy access by predators. LiCl placed in open incisions absorbed water and blood, but the large quantity of LiCl used was sufficient in most instances to dry out the surrounding tissue, leaving quantities of the salt unaffected by water. The aversive effects of this chemical apparently remained unaffected by dilution with water or other fluids. Gelatin capsules were not used to package LiCl because their capacity was too small for the amounts used in this experiment. ANTU was considerably easier to package. It is not soluble in water and therefore should remain in place longer on baits and carcasses. Ingestion of ANTU would require ingestion of an entire capsule, as opposed to LiCl sprinkled freely on the carcass. The ANTU-treated carcass showed a greater increase in the time required for the carcass to be consumed than the LiCl-treated carcass. The handled control showed no increase over known times required for consumption. It was assumed that secondary scavengers, as well as the bear that killed each cow, were feeding on the carcasses and that these scavengers would also ingest the chemicals present in the flesh of the bait cows.

Table 3. Effects of LiCl and ANTU on the consumption of cattle carcasses by black bears. The average for the complete consumption of a full-grown cow by a black bear and scavengers is approximately 5 days (data on range kills from the rancher and from the Predator Committee of the Cattlemen's Association).

Cow, dosage, and chemical	Days to consume	Percent increase over 5-day average
Kill 1 (prior to experiment): Cow	5	0
Kill 2: Cow		
4 25 g LiCl, shoulder incisions 10 g LiCl sprinkled on viscera	9	44
Kill 3: Cow		
4 2.0 mg ANTU, shoulder incisions	11	55
Kill 4: Yearling		
Handled only	5 (adjusted[a])	0

[a] Assume 2 yearlings, mean weight = 140 kg; mean weight of 1 adult = 280 kg. Mean increase for kills 2 and 3 = 49.5 percent.

Table 4 presents observations on the responses of wild black bears to LiCl, ANTU, and EHCl in Gainesburger baits. Consumption of baits placed at bait stations is misleading, because consumption over 100 percent does not indicate what might have been consumed if more Gainesburgers were present. Increased consumption before the experimental chemicals were used would have led to a greater apparent reduction in consumption after exposure to these chemicals. LiCl showed less variation in effect (52.5 percent ± 14.85) than ANTU (37.5 percent ± 23.33). I could not establish variations with EHCl because only 1 bait station

Table 2. Effects of EHCl-treated raw meat baits on 2 male captive black bears, each weighing 100 kg. A = accepted and ate bait (immediately after investigation); R = rejected bait. Time to visually apparent onset of nausea after treatment: Bear 1, 15-18 min; Bear 2, 12-15 min.

Bait and dosage	Delay before investigating or ingesting bait (min)	Bear 1	Bear 2
Untreated meat	0	A, rapidly	A, rapidly
ECHl + meat (2.5 mg/kg = 250 mg)	0	A, rapidly	Not tested
ECHl + meat (4.0 mg/kg = 400 mg)	0	Not tested	A, rapidly
Untreated meat: Day 1 feed	-	R	R
2 feed	-	R	R
3 starve	-	R	R
4 starve	No data[a]	A, hesitantly	R
5 feed	-	R	R
6 feed	No data[a]	A, rapidly	R
7 feed	No data[a]	A, hesitantly	A, hesitantly

[a] Game Farm staff did not take data on delay times but observed bears' reactions during acceptance.

Table 4. Effects of LiCl-, ANTU-, and EHCl-treated baits on bait consumption by black bears at British Columbia garbage dumps. Average weights of bears was assumed to be approximately 100 kg for purposes of dosage calculation. LiCl (200 mg/kg) = 0.20 g; ANTU (25 mg/kg) = 2.5 g; ECHI (3.0 mg/kg) = 300 mg.

Location and chemical	Number of bait stations	Number of baits per station	Mean percent consumption		
			Untreated (5 days)	Treated (2 days)	Untreated (5 days)
Golden (LiCl)	5	2	85	80	42
Parsons (ANTU)	6	2	96	92	21
Bush River Camp (LiCl)	4	2	100	88	63
Rogers Pass (ECHl)	4	2	69	56	44
Mission (ANTU)	6	2	100	100	54
					(15 days)
LiCl mean percent consumption			92.5 ± 10.6		52.5 ± 14.9
LiCl mean percent reduction in consumption				43.2	
ANTU mean percent consumption			98.0 ± 2.8		37.5 ± 23.3
ANTU mean percent reduction in consumption				61.7	
EHCl percent reduction in consumption				36.2	

was set up. EHCl showed the least reduction in percentage of Gainesburger baits consumed by free-ranging black bears.

Table 5 presents data on the responses of free-ranging polar bears to Gainesburger dog food baits treated with LiCl, ANTU, and EHCl. No arctic fox sign was seen around the Churchill bait stations. The brown paper appeared to prevent the ubiquitous ravens from seeing the baits, as none of these birds was ever observed feeding on them. The baits became frozen soon after they were placed at each station, which may also have prevented consumption of baits by scaven-

Table 5. Effects of LiCl-, ANTU-, and EHCl-treated baits on the rate of bait consumption by polar bears at Churchill, Manitoba. Average polar bear weight was assumed to be approximately 250 kg for purposes of dosage calculation. LiCl (100 mg/kg) = 0.25 g; ANTU (25 mg/kg)= 6.3 g; EHCl (3.0 mg/kg) = 750 mg.

Location and chemical (per bait amount)	Number of bait stations	Number of baits per station	Mean percent consumption		
			Untreated (5 days)	Treated (2 days)	Untreated (5 days)
Site 1, dump[a] (LiCl - 25 g)	6	6	100	78	20
Site 2, dump (LiCl - 25 g)	5	6	90	75	30
Site 4, incinerator[b] (LiCl - 25 g)	4	6	85	65	25
Site 7, incinerator[a] (EHCl - 5 g)	6	2	75	80	60
Site 5, rocket range (EHCl - 5 g)	5	2	100	100	45
Site 6, rocket range (EHCl - 5 g)	5	2	100	98	35
Site 7, incinerator[a] (ANTU - 6 g)	6	2	85	90	40
Site 8, dump (ANTU - 6 g)	4	2	100	95	35
Site 9, dump (ANTU - 6 g)	5	2	75	60	22
LiCl mean percent consumption			91.7 ± 7.6		25.0 ± 5.0
LiCl mean percent reduction in consumption				72.7	
EHCl mean percent consumption			91.7 ± 14.4		46.7 ± 12.6
EHCl mean percent reduction in consumption				49.1	
ANTU mean percent consumption			86.7 ± 12.6		32.4 ± 9.3
ANTU mean percent reduction in consumption				62.6	

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[a] Hunching observed.

[b] Vomiting observed.

gers. As with the previous experiment with wild black bears, LiCl exhibited the least posttreatment variability (25.0 percent ± 5.0), and EHCl showed greater variability and greater effect (46.7 percent ± 12.6). ANTU was less variable and less effective (32.3 percent ± 9.3) than EHCl. At the lower temperatures experienced at Churchill, no problems were experienced with the hygroscopic nature of LiCl.

DISCUSSION

Studies with 2 captive black bears indicated that effective doses of LiCl and EHCl were administered. These experiments did not indicate what the minimum effective dose might be, but field use of such agents would probably involve overdoses to insure effectiveness with bears of unknown weight. The emetic properties of LiCl, ANTU, and EHCl would tend to protect an animal from ingesting a lethal dose of any of these agents.

The large dose of LiCl required for effectiveness presents a problem in administration of a proper dose. Bears seem to require 20-50 g of this salty-tasting chemical, and if they are not sufficiently hungry, bait avoidance without achievement of an aversive response could result from initial tasting of the chemical. The captive animals subjected to LiCl were starved prior to the experiments, a condition not necessarily occurring in natural situations. Knowledge of the presence of a chemical in a bait, by taste, sight, or odor, could itself train a nuisance bear, whereas undetected chemicals would induce aversions only to the bait. Thus, LiCl may be a repelling stimulus in itself.

ANTU appeared effective as a conditioning chemical on wild black and polar bears. Experiments involving carcasses serve only as indicators of the efficacy of this chemical, as the low number of tests precludes any definitive statement on its potential. These data, however, when considered in conjunction with results of dump experiments, suggest that ANTU is a useful conditioning chemical. ANTU may present other problems, however, as it is possible for an animal to ingest a lethal dose. Care would have to be exercised in the dosage level placed in baits. Effective dosages appeared to be approximately 25 mg/kg; the established LD_{50} for dogs is about 50 mg/kg (Dubois et al. 1946).

EHCl produced results at 4 mg/kg in tests on 2 captive black bears. Tests at 2.5 mg/kg were less conclusive, and the bear subjected to this level was observed accepting untreated beef. Dump tests with EHCl suggested that this chemical could produce an aversive response to Gainesburger baits upon subsequent exposure. In these tests, EHCl did not generate the same percentage reductions as either LiCl or ANTU. EHCl may be considerably safer than ANTU because it is a strong, quick-acting emetic, thus preventing absorption of a lethal dose.

The successful transfer of an aversive response from a bait to a live prey may not occur after 1 exposure to a treated bait. This technique would probably lead initially to a strong aversion towards bait alone. The transfer of this aversion to live prey may occur in some animals (Gustavson 1974), but others may continue to kill live prey. However, I question the ability of an animal to then consume the killed prey, and it is this resulting futility that has the potential to produce the desired transfer of the aversive response from bait to live prey. The inability of the predator to consume its victim will be energetically inefficient and should lead to cessation of the preliminary killing sequences. This theory counters the arguments of Shumake et al. (unpublished) against bait-prey association.

Dump inhabitants need not form complex associations between baits and prey. A baiting program using many of the typical foods found in dumps should lead to strong aversions to each treated food. Of greater value would be the development of a *location-avoidance* response. Continued noxious or uncomfortable experiences at the bait site should lead to a reduction in visitations to that site. Gilbert and Roy (1977) apparently observed this response in black bears at beeyards, and I feel that this site avoidance was at least partially responsible for the reductions in bait consumption at Churchhill. Although I did not expect this result and therefore did not quantify it, bear numbers seemed to be reduced after treated baits were consumed. Location avoidance may well be a viable technique for reducing the numbers of bears inhabiting dump or camp areas.

The administration of LiCl under field conditions required some care. Carcass tissues treated with this substance were directly affected by the hygroscopic nature of this chemical. Alteration of the tissues surrounding the chemical may have affected their palatability or some other factor relating to their acceptability to the predator. The large dose required for polar bears made packaging difficult. ANTU and EHCl were much easier to handle under identical circumstances, and, for this reason alone, may be of greater use under field conditions.

All the chemicals tested produced a reduction in consumption of the baits or carcasses used. These chemicals will eventually be used to reduce, rather than eliminate, damage by nuisance bears. They are relatively safe compared with poisons and should prove useful in situations where animals must be controlled but need not be destroyed. It is recommended that an experimental program be developed using large numbers of bait stations or carcasses. Such a program would allow a definitive statement to be made about the viability of the technique for bear management.

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SOME ASPECTS OF BLACK BEAR ECOLOGY IN THE ARIZONA CHAPARRAL

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Abstract: A study of the black bear (*Ursus americanus*) on a 100-km^2 study area in the chaparral vegetation type of Arizona was initiated in 1973. During the subsequent 3.5-year period, 44 individual bears were captured and minimum density of 1 bear per 2 km^2 was estimated. Twenty-eight bears were radio-instrumented and more than 1,100 locations were recorded. The radio-locations indicated that subadult males have a home range averaging 42 km^2, adult males 29 km^2, adult females 18 km^2, and subadult females 13 km^2. There is considerable overlap of home ranges among adult males. A lesser degree of overlap was observed for adult females. Twenty-four dens were located. Most den sites were at elevations between 1,300 and 1,500 m. Some bears den by 1 November, the majority by 15 November. Emergence from dens begins about 15 March and all bears, except females with cubs, leave their dens by 15 April. Females with cubs remain at den sites approximately 30 days longer.

Until recently, Arizona black bears were of little interest to either hunters or wildlife biologists. The majority of bears taken in the state were shot incidental to the hunting of other big game. Few sportsmen hunted specifically for bears. Campers and picnickers also encountered bears on occasion, and livestock operators suffered varying degrees of livestock loss each year from bears.

As Arizona's population has increased, campers, picnickers, and summer home residents have increasingly encountered bears. Also, more hunters began to pursue the black bear as an interesting and unique trophy in itself, rather than something to be shot incidental to other hunting. The increased interest and awareness led to a statutory change in classification for the bear in 1968, when the state legislature changed the status of bears from small game to big game. This change led to an increased emphasis on bear management in Arizona and pointed up the need for more information. This study is an attempt to fill some of the gaps in our knowledge of the ecology of black bears in Arizona.

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STUDY AREA

This study was conducted in the vicinity of Four Peaks in the southern portion of the Mazatzal Mountains in central Arizona on an area of approximately 100 km^2 (Fig. 1). Only one major road traverses the area, but an extensive trail network allows access by horseback and foot. The elevation within the area ranges from 1,200 to 2,300 m. Topography is rocky and steep with many slopes exceeding 50 percent.

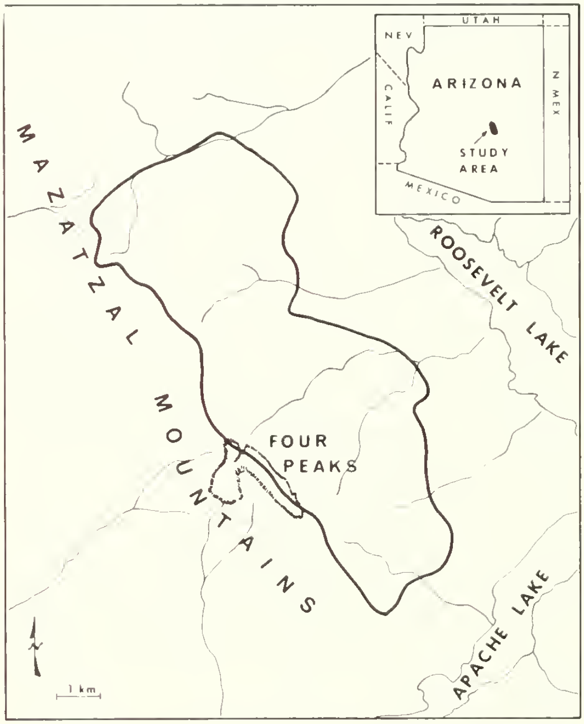

Fig. 1. Study area in the Mazatzal Mountains of Arizona.

Annual precipitation averages about 63 cm. Summer rains (July-September) are usually in the form of thunderstorms. Winter precipitation (December-March) normally comes from major weather fronts of 1-3 days duration. Snow falls occasionally but seldom remains on the ground for more than a week. Midwinter dry periods are not uncommon. Average temperatures range from −5 C during midwinter to over 38 C in summer. Daytime temperatures of 10-15 C are not uncommon during the winter months.

The primary vegetative community on the study area is Interior Chaparral (upper Sonoran life zone) (Brown and Lowe 1974). This type intergrades with the Arizona Upland Desert Scrub (lower Sonoran zone) at the lower elevations (approximately 1,200 m) and with some species such as ponderosa pine (*Pinus ponderosa* Laws.) and Gambel oak (*Quercus gambelii* Nutt.) of the Montane Coniferous Forest (transition zone) at the highest portions of the study area.

The chaparral is a complex association of shrubs and low trees which, when well developed, create a cover so dense as to be nearly impenetrable. Variations in soils, elevations, and exposure produce differences in species composition and dominance. One or 2 species often dominate the type locally to give it a specific character, but some 50 species of plants having chaparral characteristics have been classified in the area. Manzanita (*Arctostaphylos* spp.), ceanothus (*Ceanothus* spp.), mountain mahogany (*Cercocarpus* spp.), garrya (*Garrya* spp.), and turbinella oak (*Q. turbinella* Greene) are dominante and comprise a crown density of 50-90 percent. Trees such as Arizona cypress (*Cupressus glabra* Sudw.), pinyon pine (*Pinus edulis* Engelm.), Emory oak (*Q. emoryi* Torr.), and sugar sumac (*Rhus ovata* S. Wats.) make up 5-15 percent of the cover. Major drainages contain riparian communities composed of Arizona sycamore (*Platanus wrightii* S. Wats.) and Fremont cottonwood (*Populus fremontii* S. Wats.).

Fruits produced by such chaparral species as serviceberry (*Amelanchier bakeri* Greene), manzanita, chokecherry (*Prunus serotina* Ehrh.), pigeonberry (*Rhamnus californica* Esch.), and the various species of oaks — as well as the prickly pear (*Opuntia* spp.) in the adjoining desert scrub type — provide an abundant food supply for bears.

The primary economic land use of the chaparral type in Arizona is cattle grazing. Allotment size and grazing intensities are established by the Forest Service. A portion of the study area is on the Three Bar Wildlife Area, where no livestock grazing has been permitted since the mid-1940s. Bear hunting is allowed on the entire study area in season (1 September-1 December).

MATERIALS AND METHODS

Bears were captured with foot snares and immobilized with Sernylan (phencyclidine hydrochloride) at a dosage rate of 1.10 mg/kg of body weight.

A first premolar was extracted from each captured bear and age was determined by the cementum layer technique (Stoneberg and Jonkel 1966).

Each bear was tagged with a numbered metal ear tag in each ear, and a numbered plastic ear tag in one ear, for subsequent identification. Radio-transmitter collars were attached to 28 randomly selected bears. Subsequent radiotracking was done from the ground and from aircraft, with over 1,100 radio-locations recorded.

Twenty-two bears were radiotracked to dens. Denning dates were noted and the exact location of each den was established in late December and January. Information on each den and denning site was gathered the following spring after the bears' emergence.

RESULTS AND DISCUSSION

Population Information

From June 1973 to September 1976, 44 individual bears were captured and marked. In addition to the animals captured, 2 cubs and 4 older unmarked bears were known to occupy the study area, for a total of 50 bears on approximately 100 km^2 (1 bear per 2.0 km^2). This total is considered to be a minimum population estimate. Similar densities have been found in Alberta (Kemp 1970), Montana (Jonkel and Cowan 1971), and Washington (Poelker and Hartwell 1973), and lower densities in Michigan (Erickson and Petrides 1964) and New York (McCaffrey et al. 1976).

Of the 22 adult bears captured, 55 percent were males. However, the actual sex ratio might be closer to the theoretical 1:1 because some bias undoubtedly occurred as a result of the selectivity of the capture technique. Males were more likely than females to encounter a trap because of their significantly larger home ranges.

We observed little evidence of mortality during the course of the study. Natural mortality is certain to occur but finding the evidence was extremely difficult in the dense chaparral.

The study area was open to bear hunting each autumn but no bears, marked or unmarked, were known to have been taken during the study. Bear hunting in the dense chaparral was evidently difficult and unproductive. Even hunters with bear hounds had low success rates because of the difficulty in following hounds in the heavy brush. The last known bear killed by a hunter on the study area was taken in 1971. One marked subadult male, however, was taken during the 1976 bear season about 100 km northwest of the study area. This was the only marked bear known to have been harvested since the study began.

On the grazed portion of the study area, bears could be taken legally any time of year by livestock operators, under a depredation clause of the Arizona law. This clause allowed a cattleman to remove, at any time and by any means, any bear killing his livestock. However, since the study began, no depredating bears were reported taken under this law. This fact does not necessarily mean that no bear were taken by ranchers, however, since some ranchers were known to be reluctant to report the taking of bears because of criticism by protectionists. Some bears were killed on the study area by ranchers prior to the study but exact figures were unobtainable. Total mortality attributable to hunting by either sportsmen or ranchers, however, appears to be low at present.

The low harvest level probably accounts for the relatively high proportion (68 percent) of adults (3+ years of age) found in the population. In areas where bear populations have been exploited more heavily by hunters, investigators have reported subadult:adult ratios approaching 50:50 (Erickson and Petrides 1964, Kemp 1970, Jonkel and Cowan 1971). However, in relatively unexploited populations, as many as 70 percent of the animals have been found to be adults (Beecham 1980).

Home Range Sizes

Estimated home range sizes, as computed by the use of a minimum size polygon that calculated the area from the sum of the areas of interior triangles, for 11 adult and 8 subadult bears, are shown in Table 1.

Table 1. Home range data for 19 black bears on the Four Peaks, Arizona, study area, based on radio-locations.

Age-class	Number of bears	Number of radio-locations	Home range size (km²)	
			Mean	Range
Adult male	6	327	29	15-69
Adult female	5	380	18	10-30
Subadult male	5	193	42	19-64
Subadult female	3	147	13	10-19

Sudadult males appeared to have the largest home ranges followed in descending order by adult males, adult females, and subadult females. Although there were marked differences in mean home range sizes between age-classes, there was considerable overlap among individuals.

Home range size for adult black bears has been determined by other investigators (Erickson and Petrides 1964, Jonkel and Cowan 1971, Poelker and Hartwell 1973, Amstrup and Beecham 1976). However, the variety of methods used to determine home range, differences in sample size, and the spread of home range size within any one age-class make direct comparisons difficult. Amstrup and Beecham (1976:345) suggest that the quantity, quality, and distribution of food, as influenced by climate and topography, probably determine minimum home range size. Our data appeared to support this hypothesis. The chaparral with its great diversity of berry- and mast-producing species produced a wide variety of foods available to bears from spring through fall. As a result, bears were able to meet all seasonal food requirements within relatively small areas.

Home Range Overlap

Radio-locations suggested considerable overlap in the home ranges of adult males (Fig. 2), a phenomenon also reported from Idaho by Amstrup and Beecham (1976:346). Overlap was less pronounced in Montana (Jonkel and Cowan 1971:35) and Washington (Poelker and Hartwell 1973:73). Adult females appeared to have more distinct home ranges than males (Fig. 3). Some degree of overlap occurred but on a lesser scale than among adult males.

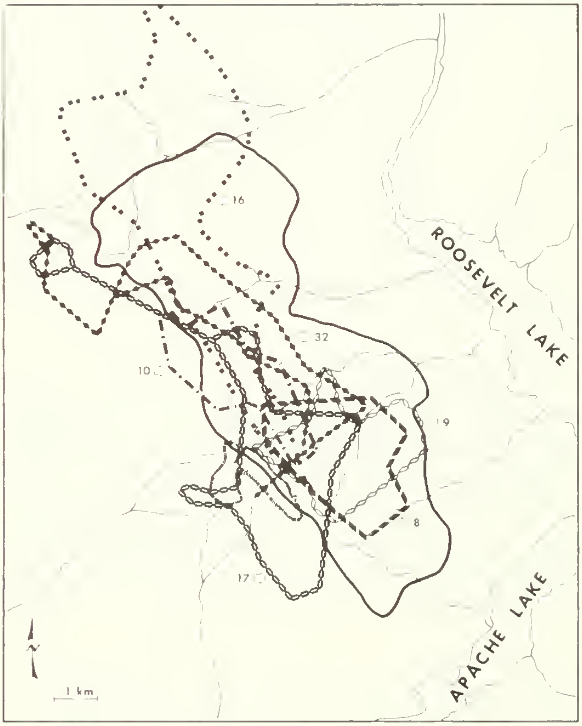

Fig. 2. Home range overlap of 6 adult male black bears on the Four Peaks, Arizona, study area.

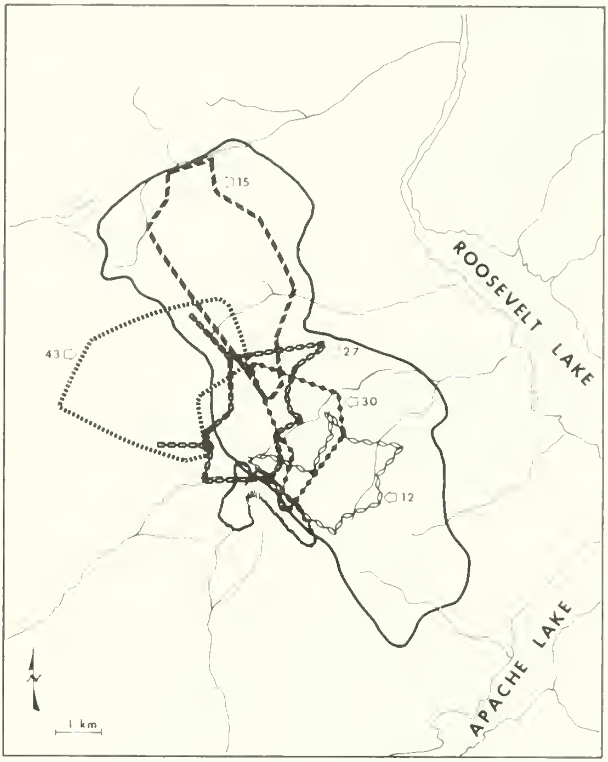

Fig. 3. Home range overlap of 5 adult female black bears on the Four Peaks, Arizona, study area.

Intraspecific tolerance among bears was observed in the course of radiotracking during the study. Two adult males were observed traveling together on 7 different occasions, and adult females were observed together in 2 instances. Although agonistic behavior was not observed, it probably occurred between males because many adult and subadult males carried the wounds and scars of battle.

Denning Behavior

Fifty percent of the 24 dens located were on north-facing slopes, 25 percent on west-facing slopes, 17 percent on south-facing slopes, and 8 percent on east-facing slopes. All dens were dug under large boulders surrounded by dense vegetation. Two instances of bears using multiple dens during 1 winter were also observed. Most den sites were at elevations of 1,300-1,500 m. However, 2 dens were located in the desert scrub type, 1 at approximately 1,200 m and the other at slightly less than 700 m.

Data from this study indicated that bears within this area began to enter dens approximately 1 November, with the majority of females denning before the males. Some bears remained active into early December but the majority of the population was denned by 15 November each year, regardless of presence or absence of snow. In late fall, the ground normally was free of snow, daily temperatures averaged 15 C, and night temperatures −2 C. Den sites at the higher elevations received several light snowfalls (12-15 cm) during the winter, but the snow usually melted within 2 weeks.

In February and early March, bears were frequently observed lying outside their dens during the warm (12-15 C) midday hours. However, these bears did not appear to leave the den sites at such times. By 15 March, most bears began to emerge from their dens on a daily basis, but movements were confined to within 100 m of the dens. Movements from the dens gradully increased in distance, and by 15 April, all bears, except females with cubs, had left their dens. Females with cubs remained at the den sites approximately 30 days longer, not leaving until about 15 May. These denning dates are similar to those determined by other investigators (Baily 1930, Gilbert 1952, Spencer 1955, Erickson 1965, Jonkel and Cowan 1971, Amstrup and Beecham 1976, Lindzey and Meslow 1976).

CONCLUSIONS

The black bear is normally thought of in association with a forest habitat. The Interior Chaparral in Arizona, however, is a scrubland vegetation type composed primarily of shrubs and low trees, interspersed with a few forest species along major drainages and at the higher elevations. It is composed of numerous mast- and fruit-producing species, and when well developed it creates cover so dense as to be nearly impenetrable.

These are the virtues that appear to make the chaparral excellent bear habitat. The diverse fruit- and mast-producing species not only provide an abundant food supply each year but also provide excellent cover. As a result, this type is capable of supporting a bear density of at least 1 per 2.0 km^2 while at the same time making it very difficult for hunters to overexploit the population.

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HOME RANGE ACTIVITIES AND REPRODUCTION OF BLACK BEARS IN WEST-CENTRAL IDAHO[1]

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Abstract: Home range activities of 21 adult, 1 subadult, and 10 yearling black bears (*Ursus americanus*) in west-central Idaho were studied between March 1975 and December 1976. Adult males occupied significantly larger and less stable home ranges and ranged farther between radio-locations than adult females or yearlings. Habitat selection and movements were governed primarily by the distribution, availability, and phenology of key food plants. Home ranges overlapped extensively within and between sex-classes. Females separated from their yearling offspring about 1 June; however, occasional reassociations occurred shortly after the initial breakup. Dispersal appeared to occur primarily in the 2.5-year-old age group. The nondenning period extended from about the second week of April to about the last week of November. Time of entrance into and emergence from dens was highly variable among bears and between years. The minimum breeding age for females was 3.5 years; regular alternate-year breeding was not noted. Breeding began in late May, peaked in June, and extended through late July. Mean litter size was 1.9 cubs with a nearly even sex ratio. The reproductive rate was 0.782.

Studies from Maine (Spencer 1955), Florida (Harlow 1961), Virginia (Stickley 1961), Michigan (Erickson et al. 1964), Montana (Barnes and Bray 1967, Jonkel and Cowan 1971), California (Piekielek and Burton 1975), Washington (Poelker and Hartwell 1973, Lindzey 1976), and Minnesota (Rogers 1976) have shown that black bears exhibit great variation in habitat use, social behavior, population dynamics, and reproduction within and among regions. Because of this variation in black bear biology, data collection from other studies could not be used reliably to formulate a black bear management program in Idaho.

In 1973, the Idaho Department of Fish and Game and the Idaho Cooperative Wildlife Research Unit initiated a cooperative study of black bears to acquire management data. Part of the study, including movements and activities, was reported by Amstrup and Beecham (1976). Home range use, dispersal, and reproduction are reported here.

We extend our appreciation to M. G. Hornocker, Leader, Idaho Cooperative Wildlife Research Unit, and L. E. Oldenburg, Game Research Supervisor, Idaho Department of Fish and Game, for initiating and administrating this study. We also thank D. Rhodenbaugh and M. Luque for their assistance in trapping and handling of bears; E. G. Bizeau, R. A. Mead, W. B. Krohn, and C. H. Nellis for reviewing the manuscript; and W. Dorris and J. Slingerland, pilots. Additional thanks are given to R. A. Mead for his advice and assistance on the reproduction work. We are especially grateful to our wives, Adrienne Reynolds and Denise Beecham, for their moral support and for enduring the hardships created by months of separation during the field work. This study was a contribution of Federal Aid in Wildlife Restoration Project W-160-R.

STUDY AREA

The study area, about 950 km^2, is located in the Middle Fork of the Weiser River and Little Weiser River drainages in west-central Idaho. Elevations range between 975 and 2,470 m and slopes generally exceed 30 percent. The Columbia River basalt formation and the Idaho Batholith granitic formation are the two major geologic formations of the area. The climate is characterized by heavy precipitation in winter and spring, and hot, dry summers. Eighty percent of the mean annual precipitation of 86 cm falls during October through April at the upper elevations. The mean annual temperature is 4 C and ranges from -32 C to 43 C at Council, Idaho, 15 km northwest of the study area.

At the lowest elevations, ponderosa pine (*Pinus ponderosa*) grows in open and scattered stands with a predominantly grass understory. Hawthorn (*Crataegus columbiana, C. douglasii*) and chokecherry (*Prunus virginiana*) occur along intermittent streams and on some north slopes, and big sage (*Artemisia tridentata*) is common on many drier sites. Vegetation tends to become heavier with increasing altitude, and ponderosa pine remains dominant up to 1,525 m elevation. Between 1,525 and 1,700 m, Douglas-fir (*Pseudotsuga menziesii*) becomes the dominant tree species, with huckleberry (*Vaccinium globulare*) and buffaloberry (*Shepherdia canadensis*) as important understory shrubs. In wetter areas and at upper elevations of the

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[1] Contribution of the Idaho Cooperative Wildlife Research Unit, U.S. Fish and Wildlife Service, Idaho Department of Fish and Game, Wildlife Management Institute, and the University of Idaho, College of Forestry, Wildlife and Range Sciences, cooperating.
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Douglas-fir zone, grand fir (*Abies grandis*), subalpine fir (*Abies lasiocarpa*), and lodgepole pine (*Pinus contorta*) dominate the tree canopy. Grass meadows are common in the subalpine fir zone, generally above 1,830 m.

The area is used primarily for commercial timber production and cattle grazing. Recreational use is moderate.

METHODS

Bears were captured with Aldrich foot snares in or adjacent to baited cubby sets. All bears were immobilized for handling with phencyclidine hydrochloride (Sernylan, Bio-ceutic Laboratories, Inc., St. Joseph, Missouri 64502), administered intramuscularly with a jab stick. Thirty-two bears were fitted with radiocollars during 1975 and 1976. About 75 percent of the radio fixes were taken from the ground and 25 percent from a fixed-wing aircraft. Individual bears were located on the average once every 4.5 days. Equipment and tracking procedures were comparable to those described by Seidensticker et al. (1970). All locations of bears were plotted on U.S. Geological Survey topographic maps (scale 1:62,500) gridded into 0.65-km^2 areas. Daily activity patterns were determined by periodically monitoring selected bears at hourly intervals for 24-hour periods. We used the minimum area method to estimate home range size (Mohr 1947). The t-test was used for most statistical comparisons.

Vaginal smears and the appearance of mammary glands and vulvas were used to ascertain reproductive status of females. To provide a rough indicator of male reproductive status (as suggested by R. A. Mead, Department of Biology, University of Idaho), testes were measured (through the scrotal sac) to the nearest millimeter for length and width with size expressed as equivalent diameter (ED) where ED = length + width ÷2. Similar measurements have been used to indicate reproductive condition of polar bears (*Ursus maritimus*) (Erickson 1962). Maximum mean testis size for all males and data from vaginal smears were used to indicate the peak of the breeding season.

Bears were placed in 1 of 4 age-classes: cubs, 0-1 year old; yearlings, 1-2; subadults 2-4 for males and 2-3 for females; and adults, older than 4 for males and older than 3 for females. A first premolar or incisor tooth was extracted from all bears 2 years old or older and age was determined by cementum annuli (Stoneberg and Jonkel 1966).

In 1976, phenological development of 10 key food plants was recorded by using the method of West and Wein (1971).

RESULTS AND DISCUSSION

During 1975 and 1976, 1,517 radio-locations were obtained from 32 black bears (21 adults, 1 subadult, and 10 yearlings). Individual bears were radiotracked for periods ranging from 2 to 24 months.

Movements

Adult Movements. — Adult male bears were the more mobile sex, having significantly greater mean distances between fixes than females for all months of the study with the exception of June and July in 1975 (Table 1).

Table 1. Mean distance, km (number of fixes) between radio-locations for adult black bears, west-central Idaho, 1975-76. *P* is the significance level of *t*-test, tested between sexes within years.

	1975			1976		
	Male	Female	*P*	Male	Female	*P*
May	-	-	-	5.8 (12)	1.8 (36)	<0.001
June	2.4 (18)	2.0 (20)	>0.5	4.8 (39)	1.9 (68)	<0.001
July	2.1 (62)	1.8 (52)	>0.2	4.2 (46)	1.9 (64)	<0.001
Aug.	2.6 (65)	1.5 (49)	<0.001	3.7 (29)	2.1 (42)	<0.01
Sept.	3.5 (69)	1.6 (59)	<0.001	4.2 (20)	1.8 (31)	<0.001
Oct.	2.7 (53)	1.4 (64)	<0.1	2.8 (12)	1.6 (36)	<0.2
Nov.	2.3 (38)	1.2 (32)	<0.05	-	-	-
Mean	2.6 (305)	1.5 (276)	<0.001	4.3 (158)	1.9 (277)	<0.001

Mobility of Adults During the Breeding Season. — The distance between radio fixes within sex-classes was relatively constant among months during both years of our study (Table 1). Thus, greater movements by adults during the breeding season apparently did not occur in west-central Idaho.

Lindzey (1976) reported greatest movements fo adult male black bears during the breeding season Barnes and Bray (1967) reported that adult male blac bears moved from their usual areas to be with female during the breeding season. In agreement with th findings of Amstrup and Beecham (1976), Lindze (1976), and Rogers (1976), our adult male range overlapped the ranges of several adult females; however, unlike the findings of Lindzey (1976), our male did not use their total ranges during the breeding sea son.

Mobility of Females with Cubs. — Cubs in our stud were very energetic and, except for a short period in mediately after emergence from the dens, their pr sence did not restrict the females' movements. Hor ranges were similar in 1975 and 1976 for 3 of 4 females that were accompanied by cubs in 1975 only. The fourth female occupied a larger home range the year she was with cubs. For female U-41, whom we followed from denning to denning in both years (with and without cubs), the mean distance between fixes for 3 seasonal periods was not significantly different between years (Table 2). Thus, our results do not support the conclusions of Barnes and Bray (1967) and Eveland (1973), who used the maximum distance between observations of marked bears to conclude that females with cubs were less mobile and used smaller areas than those without cubs.

Table 2. Mean distance (number of fixes) between radio-locations for a female black bear, U-41, with and without cubs, west-central Idaho. *P* is the significance level of *t*-test.

Period	With cubs	No cubs	*P*
	1975 (km)	1976 (km)	
May-July	2.4 (8)	1.7 (22)	>0.1
Aug.-Sept.	1.5 (19)	2.5 (7)	>0.2
Oct.-Nov.	1.5 (10)	3.5 (3)	>0.2

Home Range Size

Adults. — Adult males occupied significantly larger home ranges than adult females (Table 3). Among animals followed during both years, mean annual range for males was 60 km^2 (SE=$\pm$29 km^2) and mean total range for 2 years was 105$\pm$39 km^2; comparable figures for females were 12$\pm$6 km^2 and 18$\pm$5 km^2, respectively. Stickley (1961), Erickson and Petrides (1964), Jonkel and Cowan (1971), Poelker and Hartwell (1973), Amstrup and Beecham (1976), and Lindzey (1976) reported similar results.

Subadults. — Trapping data from out study indicated the presence of both resident and dispersing subadults. Of 52 bears less than 4 years old, 23 (44 percent) were recaptured in 1 or more years subsequent to their initial capture. Fourteen of the 23 recaptures were known residents, whereas all of 29 (56 percent) captured in only 1 year were considered to be dispersing. Males comprised 56 percent of the resident group and 93 percent of the dispersing group.

One subadult male followed through 1975 used a home range of 16 km^2 (Table 3). This range was about the same size as the mean annual home range for adult females but was significantly smaller than that for adult males. Eveland (1973) reported that subadult males in Pennsylvania traveled farther between observations and presumably occupied the largest home ranges of all sex/age-classes. The difference between Eveland's findings and ours may be due to a difference in the social status of the bears on the 2 areas.

The size of subadult bears' home ranges depends upon whether they are residents or dispersers (seeking to establish a home range). The subadult we followed was known to be a resident because it had adopted the home range of its mother after she was killed (the subadult was a yearling at the time). Perhaps the subadults Eveland reported on were dispersing; if so, this fact would explain their large home range size.

Yearlings. — Yearlings remained with their mothers from the time they emerged from dens until about 1 June. Of 4 family units monitored, 2 were intact on 24 May but were separated by 3 June, 1 was intact on 27 May but was separated by 3 June, and the fourth was intact on 30 May but had separated by 4 June. After family breakup, there were occasional reassociations between the female and 1 or both yearlings and also between the yearlings. In 1 reassociation, the female

Table 3. Mean sizes (range of individual values) of annual and total home ranges of black bears, west-central Idaho, 1975-76.

1976 sex- and age-class	Sample size	Number of months bears were radio-tracked	Annual range		Total area used (km^2)
			1975 (km^2)	1976 (km^2)	
Male					
Adult	4	14 (12-18)	60 (47-73)	61 (32-123)	105 (61-156)
Subadult	6	6 (2-8)	46 (26-84)	18 (14-25)	-
	1	10	16	-	-
Yearling	7	19 (13-24)	-	9 (5-13)	-
Female					
Adult	5	19 (12-24)	13 (5-25)	10 (5-16)	18 (12-26)
	6	9 (3-12)	9 (6-14)	16 (11-27)	-
Yearling	3	20 (17-24)	-	5 (4-7)	-

and yearling were sleeping under a tree during a rainstorm and the yearling was lying atop the female. This observation demonstrated that females do not always show antagonistic behavior toward separated yearlings, as reported by Barnes and Bray (1967). After family breakup, 9 of 10 instrumented yearlings remained in their mothers' home ranges and denned there the following fall. Mean distance between locations of females and yearlings from the time of family breakup until denning became greater as the season progressed (Table 4). The same relationship was recorded for mean distance between locations of siblings, indicating that the family bond became progressively weaker over time. Even though both sexes of yearlings remained within their mothers' home ranges, there was a significant difference ($P<0.05$) between the mean areas used by males and females (Table 3). One yearling moved from the study area. He traveled approximately 20 km south where he used a 5-km² area until denning in November.

Table 4. Mean distance ± SD between radio-locations of female and yearling black bears and between siblings after family breakup, west-central Idaho, 1976. Sample sizes are in parentheses.

Month	Females and yearlings (km)	Siblings (km)
June	2.0 ± 1.7 (41)	2.2 ± 2.1 (23)
July	2.5 ± 1.7 (41)	1.6 ± 1.1 (23)
August	1.7 ± 1.2 (25)	1.8 ± 1.3 (12)
September	4.0 ± 4.0 (24)	5.5 ± 6.8 (12)
October	4.5 ± 4.7 (31)	5.0 ± 7.4 (16)

Our findings agree with those of Jonkel (1962), Barnes and Bray (1967), and Lindzey (1976), who all reported that family breakup generally occurred in early June. Jonkel (1962) and Barnes and Bray (1967) also reported that yearlings remain in the mother's home range.

Home Range Stability

Adult females used about the same home ranges in 1975 and 1976; thus, the mean annual home range size of 13±7 km² for females tracked from 3 to 12 months ($N=6$) did not differ significantly ($P>0.25$) from the mean total home range (18±5 km²) for those tracked from 12 to 24 months ($N=5$) (Table 3). In contrast, 3 of 4 adult males used different annual home ranges in 1975 and 1976; therefore, the mean total range of 105±39 km² for individual bears followed from 12 to 18 months ($N=4$) differed significantly ($P<0.01$) from the mean of 31±26 km² for those tracked from 2 to 8 months ($N=6$).

Black bear home ranges that are relatively stable and habitual from year to year were suggested by Jonkel and Cowan (1971) and Amstrup and Beecham (1976). Our study confirms such a pattern of use for adult females but not for adult males. Sauer et al. (1969) speculated that 1 or 2 seasons may be inadequate to define accurately black bear home ranges. Our findings support their speculation, particularly for adult males.

Fig. 1 illustrates the typical pattern of home range shift that the 3 males displayed. In all cases their centers of activity differed significantly between 1975 anc 1976, and 50-80 percent of their locations in 1976 wer outside the home ranges used in 1975. The intensiv use of areas outside the 1975 range demonstrates th near-completeness of the home range shifts.

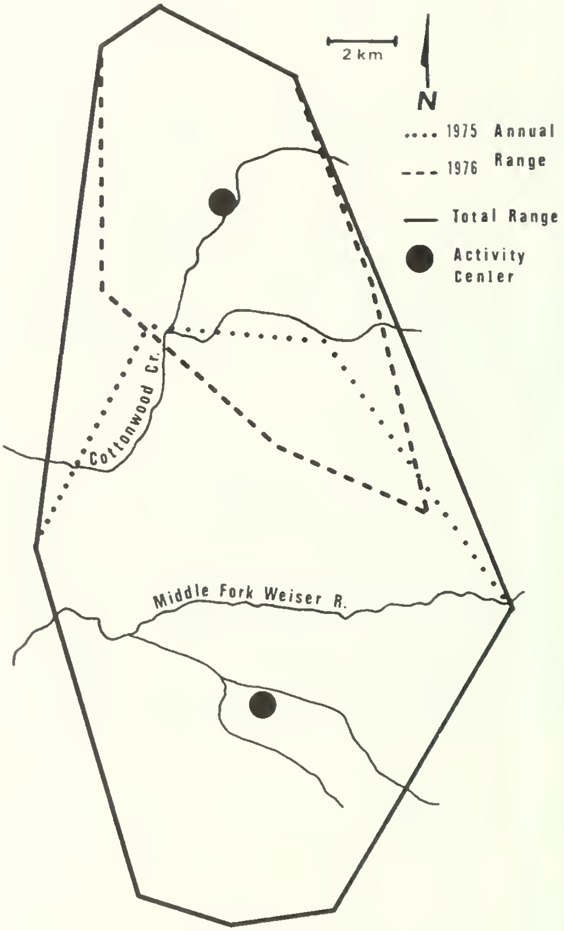

Fig. 1. Home range shift by adult male black bear U-11.

Because estrous females were present in the males ranges in 1975, and food availability did not diffe between the ranges of 1975 and 1976, we feel that the shifting of males was not a response to these factors. Perhaps these shifts are caused by behavioral factors, but further study is needed to make this determination.

Home Range Overlap

The black bears we studied did not appear to be territorial. They did not exclude bears from their ranges and several observations were made of bears feeding close to each other without displaying aggressive behavior. Thus, factors that help to explain high intraspecific tolerance may also help to explain home range overlap.

The extensive home range overlap for adult males and females is depicted in Figs. 2 and 3, respectively. In 1975, the minimum home range overlap ranged from 54 to 100 percent for males and from 34 to 89 percent for females. Home range overlap between sexes was near 100 percent.

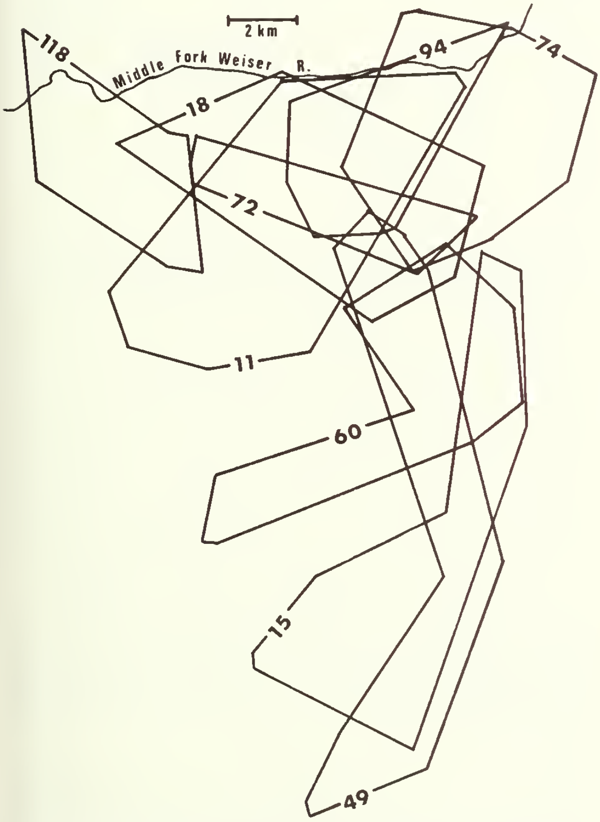

Fig. 2. Home range overlap for 9 adult male black bears. Polygons are the smallest area within which 75 percent of all their radio-locations occurred. Overlap of total ranges was more extensive.

As a result of heavy hunting before 1975, the age structure of this population was weighted heavily toward the younger age-classes. Eighty of 134 (64 percent) of our captured bears were less than 4 years of age. Because young bears tended to be less aggressive than older bears, the high degree of intraspecific tolerance we observed can proably be explained in part by the population's young age structure.

The other factor that may explain the extensive home range overlap and high intraspecific tolerance is the spatial and temporal distribution of food on the study area. Horn (1968) showed that it is not advantageous for animals to defend fixed areas where a patchy and temporally unpredictable food distribution occurs. Weins (1976) agreed with Horn and predicated that spatial or temporal patchiness of resources (e.g., food, breeding space, and nest or shelter sites) governs the pattern of social and space-related behavior of a population. Territoriality may be optimal where resources are plentiful and evenly distributed or accessible and predictable. However, as resource aggregation or unpredictability increases, the territory size required to meet individual needs must become larger. At some point, energy expenditure in defense of territory must place a limit on territory size, boundary defense must slacken, and spatial overlap will ensue. At that point, selection would favor home range as the optimal spacing mechanism.

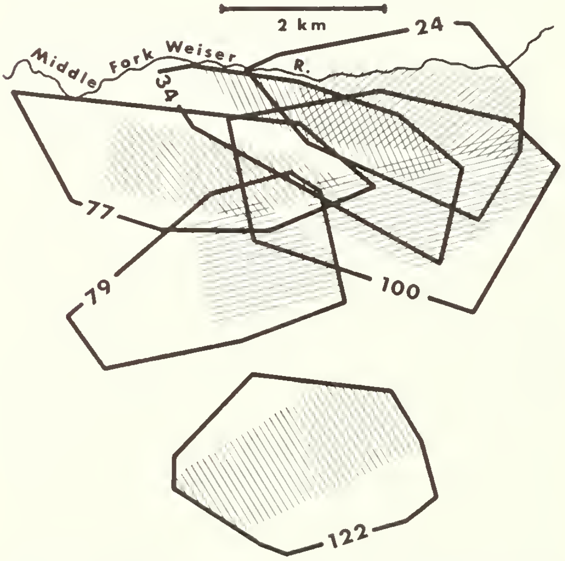

Fig. 3. Home range overlap for 6 adult female black bears. Hatch lines represent the smallest area within which 75 percent of all their radio-locations occurred.

Reported home range overlap within sex-classes of black bears has ranged from slight (Jonkel and Cowan 1971, Poelker and Hartwell 1973) to extensive (Lindzey 1976, this study). Jonkel and Cowan (1971) interpreted limited overlap of ranges as an indication of territoriality. They felt the great diversity of topography, climate, and vegetation on their study area allowed bears to occupy small ranges. This diversity presumably provided uniformly distributed and continuously renewing food resources. In contrast, annual and seasonal variability in food production on our study area resulted in a patchy and unpredictable distribution that contributed to overlapping home ranges.

To see if bears were minimizing contact with members of the same sex by limiting most of their activity to some portion of their range, we delimited the smallest area that would encompass 75 percent of each bear's activities (Figs. 2, 3). The overlap in these areas became minimal for females but remained high for males. Females appeared to minimize contact with other females by concentrating their activities in a portion of their ranges. Lindzey (1976) found similar home range overlap within sex-classes and concluded that a dominance hierarchy produced spatial and temporal separation within the female cohort.

Although we cannot be certain that a dominance hierarchy did not induce the spacing pattern we observed, we speculate that it was caused by avoidance behavior. Females with cubs show a marked avoidance of other bears (Erickson 1965, Barnes and Bray 1967), although exceptions have been reported (Amstrup and Beecham 1976); perhaps avoidance behavior by females is carried over to years when they are without cubs. Since home ranges of females are stable, females should know where they are most likely to encounter neighboring females. They could then largely restrict their movements to that part of their range where contact with neighboring females would be minimal. If all females display such behavior, a pattern of spacing similar to the one we found would occur.

Other studies (Craighead 1971, Jonkel and Cowan 1971, Mundy and Flook 1973, Poelker and Hartwell 1973, Lindzey 1976) have shown that intraspecific tolerance is variable among black and grizzly bears (*Ursus arctos*). Food distribution, age structure, and social relationships are interrelating factors determining intraspecific tolerance.

Annual Home Range Use

The seasonal and daily use of annual home ranges was influenced primarily by food availability and distribution. Spencer (1955), Stickly (1961), Hatler (1966), Jonkel and Cowan (1971), and Amstrup and Beecham (1976) reported that bear home range use was influenced by distribution, quantity, and quality of food resources. Black bear activity on our study area moved up and down the elevation gradient (Table 5) in response to key foods (Fig. 4). Food habits, phenology of food plants, and elevational usage together revealed that from April to mid-July, bears followed the "green-up" as snowmelt progressed upslope, and fed on grasses and forbs that were in early phenological states. By mid-July, snowmelt was complete, grasses and forbs at the lower elevations had begun to cure, and bear acitvity tended to occur at the higher elevations. Huckleberries and buffaloberries began to ripen at middle elevations by mid-July, and by late July bears were concentrating most of their activity at those elevations in response to the ripe berries. In August, huckleberries and buffaloberries began to diminish. By

Table 5. Mean elevation ± SD of black bear radio-locations, west-central Idaho, 1975-76.

Month	1975 (m)	1976 (m)
May	-	1,432 ± 186
June	1,676 ± 169	1,493 ± 182
July	1,706 ± 224	1,584 ± 248
August	1,615 ± 200	1,463 ± 181
September	1,432 ± 247	1,341 ± 163
October	1,432 ± 280	1,371 ± 178

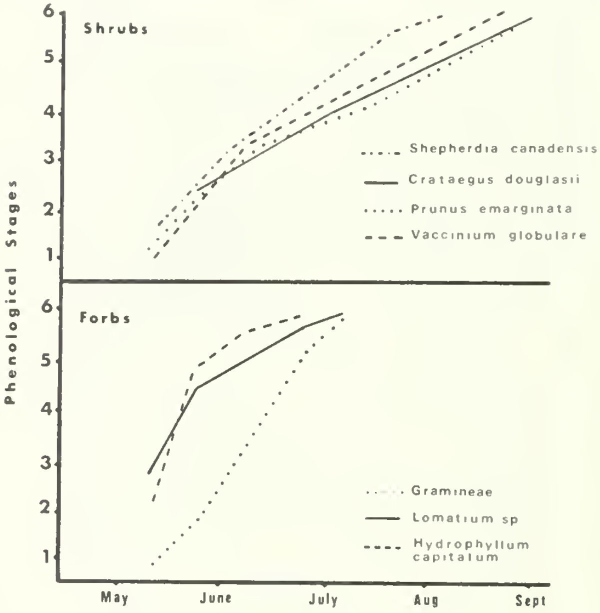

Fig. 4. Phenological changes in 7 key food plants. 1976. Respective phenological stages for shrubs and forbs are: 1 = flower, vegetative growth; 2 = fruit set, flower buds; 3 = fruit swelling, flower; 4 = fruit turning color, fruit set; 5 = fruit ripe, fruit swelling; and 6 = fruit dry or dropping, plant curing (based on method of West and Wein 1971).

mid-August, bears were feeding on newly ripened bittercherries (*Prunus emarginata*), chokecherries, and hawthorn berries at lower elevations (Beecham, unpublished data). Bears remained at these lower elevations and generally concentrated their activity around those foods until denning.

Day-to-day use of home ranges appeared to be primarily influenced by the patchy distribution of food. Bears did not use established trails but tended to move from 1 area of their range to another and then back again, following nearly the same route (Fig. 5).

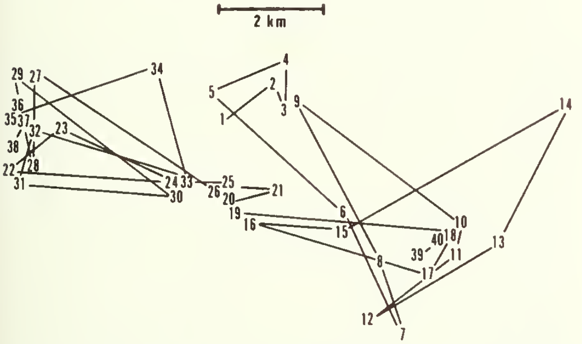

Fig. 5. Movements of subadult male U-72, 1976, which typify home range use of black bears in west-central Idaho. Numbers represent sequential radiolocations. Location clusters correspond to seasonal food distribution.

When animals are rewarded with temporary sites of food concentration, the heterogeneity of resource distribution may be reflected in a pattern of home range use consistent with Herrnstein's principle of reinforcement (Wilson 1975). Herrnstein (1971) found that domestic pigeons (*Columba livia*) learned to peck at disks in direct proportion to the percentage of times each disk reinforced the pigeon with food.

We believe that as bears moved among food patches they probably experienced varying degrees of success in obtaining food. When they reached their home range boundary, or an area where food was scarce, they retraced the route along which they had recently experienced their highest foraging success. We considered this to be an efficient foraging pattern for exploitation of patchily distributed food resources.

Bear activity shifted within home ranges to take advantage of locally abundant food, but there was very little movement to sites of abundant food outside home ranges. In 4 years of radiotracking, 2 instances were recorded where residents (both females) made foraging trips outside their home ranges. These females moved distances of 11 km and 19 km, respectively, from the centers of their home ranges, in fall, traveling from the upper elevations of a drainage where food was scarce to lower elevations where berries were still available. One trip lasted about 3 weeks; the duration of the other was unknown.

Daily Activity Patterns

Black bears have been reported as both nocturnal (Erickson 1965) and diurnal (Amstrup and Beecham 1976). Bears in this study were diurnal throughout their active season. Daily activity peaks occurred at 1000 and 2100 hours. Black bears were inactive most often between 0100 and 0400 hours.

Reproduction

Breeding Season. — The use of vaginal smears to determine stages of the estrous cycle in black bears has not, to our knowledge, been reported in the literature. We feel that our interpretation of the smears was reliable because of their close similarity to smears from other carnivores (Liche and Wodzicki 1939, Hansson 1947, Farris 1950, Asdell 1964). Since we were unable to varify the smears by analyzing the reproductive tracts, there is a possibility of error. However, we feel certain that the vaginal smears were a more reliable criterion for determining the breeding season than the usual technique of rating the vulval swelling.

Cell types and their relative abundance in vaginal smears from 14 females showed 10 bears in estrus in June, 3 in the first half of July, and 1 in the last half of July. Two observations of consort pairs, 1 of which involved copulation, occured in July.

Greatest male reproductive activity as measured by mean monthly testis size occured in June (Fig. 6).

The breeding season began in late May and extended through July, with the peak occurring in June. This breeding season was similar to those reported by Erickson and Nellor (1964), Poelker and Hartwell (1973), and Lindzey (1976).

Breeding Age and Productivity. — Between 1973 and 1977, we determined the age at first successful breeding for 9 females to be 3.5 years ($N=3$), 4.5 years ($N=5$), and 5.5 years ($N=1$). Our data showed that black bears in west-central Idaho had a much lower minimum breeding age than the 5.5- to 6.5-year minimum reported for Montana (Jonkel and Cowan 1971), but not as low as that reported for North Carolina where 80 percent bred first at 3.5 years of age (Collins 1973).

The mean size of 16 litters was 1.9 cubs:1 single and 15 sets of twins. The sex ratio of 27 cubs did not differ significantly from 50:50 ($X^2=0.92$ $P<0.3$).

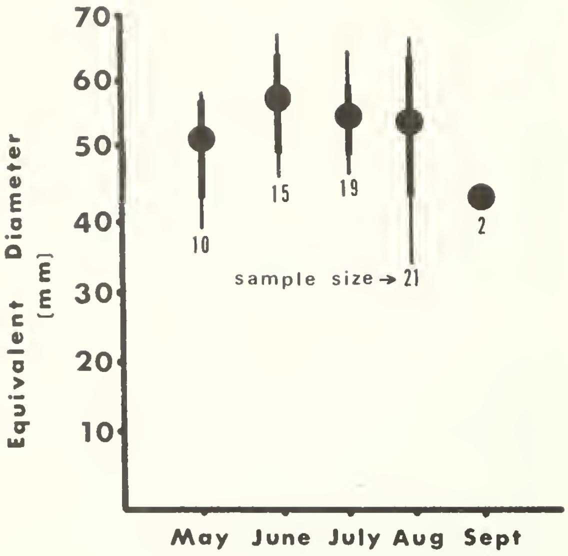

Fig. 6. Size of testes of black bears 3 years of age and older.

• = X̄, ▮ = SD, | = Range.

Mean litter size (1.9), mean litter frequency (31 percent for 3 years), and low minimum breeding age indicated that black bears in west-central Idaho were more productive than those in other parts of the western United States and Alaska (Hatler 1966, Jonkel and Cowan 1971, Poelker and Hartwell 1973, Piekielek and Burton 1975, Lindzey 1976). However, they did not approach the productivity reported for bears in the eastern United States (Spencer 1955, Harlow 1961, Stickley 1961, Erickson and Nellor 1964, Hamilton 1972, Collins 1973). We calculated a reproductive rate of 0.782 (after Craighead et al. 1974) from 5 reproductive cycles representing 4 females.

Alternate-year cub production by females was not consistent. Between 1973 and 1976, a minimum of 5 females over 5 years of age did not produce litters for at least 2 consecutive years.

Between 1973 and 1976, bears had low and high years of cub production as evidenced by the range of 18-54 percent in litter frequencies. However, because of inconsistencies in minimum breeding age and lack of a regular alternate-year breeding cycle, our data indicate that black bears in west-central Idaho have not established a synchronous breeding pattern as described by Free and McCaffrey (1972).

The relative effects of nutrition versus social behavior and spacing on population processes such as minimum breeding age, breeding success, growth, and survival, have been widely studied, and the opinions as to which factor is most influential remain divided (Watson and Moss 1970). Both nutrition and social behavior may influence populations concurrently, and the latter may be mediated through the former (Watson and Moss 1971).

Because effects of nutrition, social behavior, and spacing are complex, it is difficult to assess their relative effects on reproductive success and minimum breeding age in wild, free-ranging populations. However, there is evidence that regional differences in black bear minimum breeding age and reporductive rate may be primarily due to diet and nutrition (Spencer 1955, Harlow 1961, Erickson and Nellor 1964, Barnes and Bray 1967, Jonkel and Cowan 1971, Hamilton 1972, Collins 1973, Piekielek and Burton 1975, Rogers 1976, this study).

Rogers (1976) reported that captive black bears on a rich diet, even though dominated by larger bears, developed more rapidly than wild ones and commonly bred at 2.5 years of age. In contrast, wild black bears seldom breed at that age. The few reported cases of early breeding have come from the eastern United States (Hamilton 1972, Collins 1973), where nutrient-rich mast is a major food item. Rogers (1976) also reported that reproductive success was positively correlated with the fall weight of female black bears in Minnesota and, like Jonkel and Cowan (1971), he noted increased reproductive success after years of abundant food and decreased success after years of poor food. In general, accumulated data indicate an apparent latitudinal gradation in black bear minimum breeding age and reproductive rate that may be related to nutrition. In the eastern United States, where a mast diet is common, bears have a lower minimum breeding age, higher reproductive rate, and larger mean adult body weight (Spencer 1955, Harlow 1961, Erickson and Nellor 1964, Hamilton 1972, Collins 1973) than in the western United States (Barnes and Bray 1967, Jonkel and Cowan 1971, Piekielek and Burton 1975, this study (where a less rich diet of grasses, forbs, and berries is most common.

Behavioral differences between populations with differing densities and/or age structures may also influence reproductive rate and minimum breeding age. However, in the studies reported, nutrition appeared to account for most of the variability in these population processes.

Denning Activity. — Time of entrance into and emergence from dens was highly variable among bears between years. The nondenning season for black bears on our study area extended from about the second week of April to about the last week of November. In 1975, all instrumented bears denned between 27 October and 25 November (Table 6). In 1976, denning began on 15 October and was completed by 16 November.

Table 6. Denning dates for black bears in west-central Idaho, 1975-76.

1976 sex- and age-class	Sample size		Denning dates			
			1975		1976	
	1975	1976	Mean	Range	Mean	Range
Male						
Adult	7	2	9 Nov.	27 Oct.-25 Nov.	5 Nov.	2 Nov.-7 Nov.
Subadult	1	-	22 Nov.	-	-	-
Yearling	-	5	-	-	3 Nov.	22 Oct.-16 Nov.
Female						
Adult	7	7	17 Nov.	6 Nov.-24 Nov.	26 Oct.	15 Oct.-8 Nov.
Yearling	-	2	-	-	27 Oct.	20 Oct.-2 Nov.

The average date of denning in 1976 (30 October) was 15 days earlier than in 1975 (14 November). Because phenological development of food plants was about 2 weeks earlier in 1976 than in 1975, the availability of food in fall differed between the years. In 1975, some bears foraged actively even after several inches of snow had accumulated. In contrast, in 1976 all instrumented bears denned earlier than in 1975, even though daily temperatures were unusually mild and no appreciable amount of snow had fallen. Therefore, the earlier denning in 1976 may have been a response to the lack of food. Erickson and Youatt (1961) reported that prolonged feeding delayed denning of captive bears but that denning occurred promptly when feeding was terminated.

In both years, the dates of denning of adult males and females differed. Males denned first in 1975 ($Z=1.34$, $P>0.20$, Wilcoxon Rank-Sum Test), but females were the first to den in 1976 ($Z=-1.46$, $P>0.15$). Females denned on the average 8 days later than males in 1975 but 10 days earlier than males in 1976. Because of small sample sizes and high variability of denning dates, it may have been coincidence that females denned later than males in 1975 and earlier than males in 1976. However, it is more probable that their reproductive condition (all were pregnant) in 1976 caused them to den earlier than the males. Lindzey (1976) reported that pregnant females denned before males but he did not mention nonpregnant females.

Mean denning dates of male and female yearlings were about the same, respectively, as for adults (Table 6).

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BLACK BEAR HUNTING TO REDUCE FOREST DAMAGE

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Abstract: Before 1973, the State of Washington had a spring black bear (*Ursus americanus*) season from 1 April to 30 June throughout most of the area west of the Cascades in an attempt to alleviate damage to forest tree reproduction. Extensive efforts by professional control hunters were still needed to keep damage at an acceptable level. Indications that sport hunting might be more effective in controlling damage resulted in an effort to concentrate sport hunting in problem damage areas. The general spring season was discontinued and a system of special hunts, by unit, was established. The extent of the area open to hunting was reduced by about 75 percent. Success of the program was evaluated by comparing 3 years' data collected under the unit system with 3 years' data from the general open season. The bear kill increased from an average of 503 per year in the general open season to 740 per year under the unit system. Bear tag sales increased by 81 percent during the same period.

The black bear is one of the most important big game species in Washington. The state provides a greater annual harvest of black bears than any other state or province. From a population of 27,000 bears, over 3,400 are taken yearly (Poelker and Hartwell, Washington Game Dept. Biol. Bull. 14, 1973) (Table 1). Over the years, the black bear's status has changed from unprotected varmint to desirable trophy animal and back again. With increased popularity and hunter interest, it appears the black bear's status as a respected and valued member of the big game community is assured both now and for the future.

Table 1. Annual population estimate, sport harvest, and control harvest of black bears in Washington, 1966-75.

Year	Population estimate	Sport harvest	Control harvest
1966	20,000	4,710	460
1967	20,000	3,180	450
1968	22,000	4,150	426
1969	22,000	3,410	419
1970	22,000	3,470	226
1971	22,000	4,100	216
1972	27,000	3,400	227
1973	27,000	2,830	211
1974	27,000	3,910	213
1975	27,000	3,760	192

The black bear is classified as a game animal in Washington. Seasons exist statewide and the annual bag limit is 1 or 2 bears, depending on the area. A tag is required to hunt black bears, and harvested bears must be reported on a card issued to hunters. Each year, the setting of the black bear seasons generates much interest among sportsmen and personnel of the forest industry. The most dynamic and unique aspect of our management program is the spring black bear season. This season is directly correlated with the black bear's propensity to damage second-growth timber in western Washington. Black bears damage trees by tearing off the bark at the base of the tree and exposing the sapwood, which they eat. Trees that are completely girdled die; those partially girdled become infected with fungus, which causes deterioration, or experience a retardation in growth rate. A comprehensive discussion of bear damage is provided by Poelker and Hartwell (Washington Game Dept. Biol. Bull. 14, 1973).

SYSTEM DEVELOPMENT

Although bear damage has been recognized as a problem for many years by foresters and game managers, both have been handicapped by a lack of knowledge, concerning the animal and concerning the long-term effects of bear damage on timber reproduction. In an attempt to gain needed information, the Washington Department of Game established a cooperative black bear research project starting in 1963 (Federal Aid Project W-71-R). Involved in the project with the Game Department were the Washington Department of Natural Resources, the Bureau of Sport Fisheries and Wildlife, the U.S. Forest Service, and private industry. The major goal of the project was to obtain data upon which an objective bear management program could be based.

Data obtained during the Cooperative Black Bear Study showed that a specific black bear could normally be expected to inhabit the same genreal area from 1 year to the next during a particular season. This occupied area was smaller than expected, averaging approximately 50 km^2 for males and 5 km^2 for females (Polker and Hartwell, Washington Game Dept. Biol. Bull. 14, 1973). During the study, the possibility of alleviating bear damage by seasonal regulation of the sport harvest was often expressed. With this objective in mind and information on areas occupied by black bears, a plan evolved through which it was hoped that both an increase in recreational opportunity for sportsmen and a reduction in bear damage might be obtained.

SYSTEM DESCRIPTION

The plan devised resulted in a major revision of black bear hunting seasons at the January 1973 Game Commission meeting (Washington State Game Comm. 1973). The plan, developed by the Department of Game in cooperation with other state agencies, sportsmen's groups throughout the state, and private industry, involved the establishment of spring damage units open to black bear hunting from 1 April to 30 June. Selection of units was based on the existence of bear damage, accessibility to sport hunters, and suitability for sport-hunting efforts. Areas outside the spring damage units were closed to bear hunting, thus concentrating spring bear hunting in current damage areas. Spring bear seasons in the past were established solely to alleviate bear damage. Since these seasons were generally open throughout much of western Washington, the concentration of effort necessary to reduce damage was not achieved. It was felt that by concentrating sport hunting in problem areas, sportsmen could be more effective in reducing damage.

The bear kill report card, mentioned previously, is used to provide information on the success of the program. Additional information on reduction of damage is obtained through aerial and ground surveys of damage areas within the spring bear units.

The goal of this program is to involve sportsmen in alleviation of a game damage problem while increasing their own recreational opportunities. As sportsmen's success increases, the necessity for professional control of bear damage decreases.

Because a large proportion of black bears harvested in western Washington are taken with hounds, boundaries of spring damage units are established to facilitate hound hunting. A 3-year trial of this program to evaluate its potential was completed in 1975.

RESULTS

Table 2 shows a comparison of spring bear harvests in western Washington during the past 6 years. The kill for the 1970-72 period was taken from 13 counties in western Washington without regard to bear damage and averaged 503 bears per year, or 0.016 bear killed per km^2, 6 times as great as the unrestricted 1970-72 harvest. During the 1973-75 period, an average of 37 percent more bears per year were taken by sport hunters in only 22 percent of the area formerly open. The highest bear kill per square kilometer recorded for any unit during the evaluation period was 0.844.

Data from the bear kill report, showing sex and age of bears and method of hunting, are given in Table 3.

Table 2. Comparison of sport harvest of black bears, April-June, during 1970-72 and 1973-75 periods.

Year	Bear harvest	Open area (km^2)	Bear kill per km^2
1970	490	30,000	0.016
1971	630	30,000	0.020
1972	390	30,000	0.012
1970-72 average	503	30,000	0.016
1973	650 (87)[a]	6,300	0.103 (0.116)[b]
1974	680 (90)	8,175	0.084 (0.096)
1975	740 (77)	7,758	0.096 (0.104)
1973-75 average	690 (85)	7,411	0.095 (0.104)

[a] Additional kill by control hunters.

[b] Adjusted to include kill by control hunters.

Table 3. Method of hunting and sex and age of black bears, by percent, in spring harvest, 1973-75.

Year	Method		Male		Age		
	Hounds	Other	Hounds	Other	Adult	Yearling	Cub
1973	90	10	48	53	83	15	2
1974	88	11	58	54	86	14	0
1975	91	9	49	40	77	21	2
1973-75 average	90	10	52	49	82	17	1

The higher-than-average take of adult bears in the spring is most likely a combination of the older-aged population characteristic of a damage area and hound-hunter selection for larger bears.

Interest in black bear hunting has increased dramatically since implementation of the unit-based spring season. Yearly average black bear tag sales are 81 percent higher than during the 1970-72 period when about 5 times the area was open.

Table 4. Comparison of bear tag sales, April-June, during 1970-72 and 1973-75 periods.

Year	April	May	June	Total
1970	140	264	278	682
1971	341	278	315	934
1972	178	251	361	790
1970-72 total	659	793	954	2,406
1973	614	596	481	1,691
1974	154	685	611	1,450
1975	270	618	323	1,211
1973-75 total	1,038	1,899	1,415	4,352
Percent increase	57.5	139.5	48.3	80.9

Table 5. Spring black bear harvest, 1970-72 and 1973-75, based on information obtained from returned bear harvest report cards.

Year	April	May	June	Total
1970	16	41	38	95
1971	21	42	44	107
1972	14	31	34	79
1970-72 average	17	38	39	94
Percent of total	18	41	41	100
1973	42	63	45	150
1974	21	42	56	119
1975	7	53	42	102
1973-75 average	23	53	48	124
Percent of total	19	43	38	100
1970-75 total	121	272	259	652
1970-75 average	20	45	43	108
Percent of total	18	42	40	100

Of the 3 months included in the spring bear season, 82 percent of the kill occurred in May and June over the 6-year period (Table 5). Monthly kill patterns were generally the same under the 1973-75 system as in 1970-72.

DISCUSSION

Collected data indicate that the new sport-hunting program is doing a far better job of harvesting bears in damage areas and that bears in nondamage areas are being preserved. This program allows professional control efforts to be directed towards special problem areas as the general control of bear damage is being satisfactorily handled by sport hunters. Field surveys of damage areas by landowners, control hunters, and game department personnel showed that bear damage was reduced or eliminated in most areas where spring seasons were established. Landowners have become more supportive of the spring season as the success of the program became evident.

Evaluation of 3 years' experience with the unit system for spring bear hunting indicates that a successful management option has been developed. This option should remain a permanent program for timber protection in bear damage areas unless satisfactory alternatives are discovered. After 25 years of working with this problem, it is apparent that bear damage is not a passing phase in management of forest land. With increasing dependence on tree farming to sustain the timber industry, land will continually be developing a greater potential for bear damage. The problem facing both foresters and game managers is how best to meet this situation. Knowing this, our management is geared to deal with new damage areas as they develop. Similar sport-hunting seasons were set in 1976 and 1977. Hound hunting is essential for adequate harvesting of damage-causing bears. Professional control by WFPA will take care of areas not hunted by sportsmen.

The Cooperative Black Bear Study has provided participating agencies and the forest industry opportunity for a long, in-depth look at black bear management. A management problem was recognized and cooperative research conducted to identify possible management alternatives. The success of black bear management in Washington in the future will be based almost entirely on the contributions of those who were involved in the many phases of the study.

BLACK BEAR MANAGEMENT IN SEQUOIA AND KINGS CANYON NATIONAL PARKS

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Abstract: Traditionally, black bear (*Ursus americanus*) management at Sequoia and Kings Canyon National Parks has consisted mainly of efforts to remove problem animals. In recent years, the ready availability of human food has been recognized as the real problem. The parks' current bear management program is aimed at eliminating all unnatural food sources in an effort to allow the bears to lead as natural a life as possible.

HISTORY AND BACKGROUND

Bears and associated bear problems have long constituted an important part of the natural resources management program at Sequoia and Kings Canyon National Parks. Little is known about the area's bear population before 1890, when Sequoia was established as this country's second national park. At that time, grizzly bears (*Ursus arctos*) still roamed the area. However, the last grizzly recorded in California was killed at Horse Corral Meadow, near the northwest corner of Sequoia National Park, in 1922 (Grinnell et al., *Fur-bearing Mammals of California,* 1937). Since then, only black bears have frequented the area encompassed by these two parks.

Although total visitor use has steadily increased from 1,265,858 in 1959 to 2,168,477 in 1976, the number of bear incidents, as shown in annual summaries, has not correspondingly increased (Table 1). However, the cost of damage associated with these incidents has increased dramatically (Table 1). This increased cost can be attributed in part to inflation and in part to a greater percentage of incidents involving automobiles, and the subsequent high cost of repairs. The occurrence of bear activity in areas of high visitor use is nothing new. In the 1930s, park rangers fed bears on a regular daily schedule for public viewing (Fig. 1). This practice no doubt helped to attract bears into public use areas.

Through the 1950s and 1960s, after the bear-feeding program was discontinued, habits that had been developed by the program persisted, and it became difficult to keep bears away from people's food. Bear control was emphasized, including trapping problem animals, destroying dangerous ones, and relocating others. By 1972, it was apparent that this approach attacked the symptoms rather than the cause of the problem. A bear management plan was developed that emphasized the elimination of unnatural food sources, education of visitors and employees, enforcement of pertinent regulations, and use of efficient bear-handling procedures. An important part of the plan was the development of an accurate, timely report procedure covering all bear incidents and management actions.

M. Chin provided valuable assistance in developing the parks' bear management program as well as in reviewing a draft of this manuscript.

CONTEMPORARY PROBLEMS

Although natural bear populations undoubtedly existed in these parks before the coming of European man, much of the area is not good natural bear habitat.

Table 1. Annual number of bear incidents and dollar value of damage or loss due to bear incidents in Sequoia and Kings Canyon National Parks. Figures are taken from annual summaries that reflect several reporting procedures. Supporting data are not generally available to explain unusually high or low numbers.

	1959	1960	1961	1962	1963	1964	1965	1966	1967
Incidents	167	277	195	289	64	37	570	66	168
Value ($)	1,922	1,355	1,900	815	1,270	592	1,945	785	1,373

	1968	1969	1970	1971	1972	1973	1974	1975	1976
Incidents	153	87	604	174	204	287	175	230	221
Value ($)	1,565	1,840	4,165	1,877	6,059	5,130	5,856	10,474	10,119

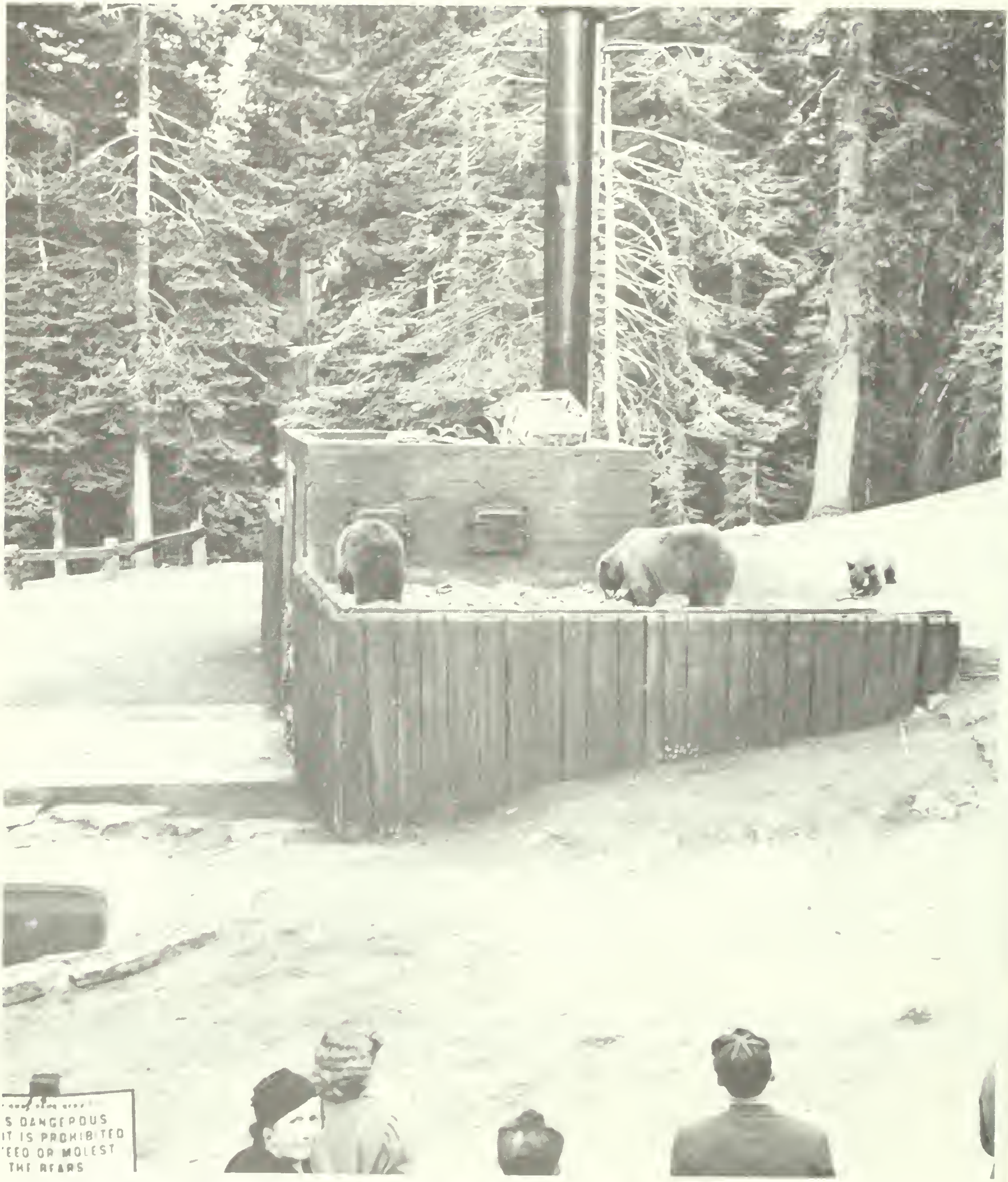

Fig. 1. Bear-feeding operation at Bear Hill in Giant Forest area, Sequoia National Park, 1938.

Vegetation patterns and sighting records indicate that of the 342,166 ha in the two parks, only about 81,000 ha, or 24 percent, appear to be able to support a natural bear population (Fig. 2).

In general, the present distribution of black bears is probably much the same as it was historically. The major exception is that popular camping areas, with readily available unnatural food (i.e., of human origin), have become areas of concentrated bear density, especially large frontcountry campgrounds that are readily accessible by automobile. Approximately 86 percent of all reported bear incidents occur in such locations. Since over 93 percent of Sequoia and Kings Canyon National Parks is relatively inaccessible backcountry, the developed campgrounds, where most incidents take place, are concentrated in that relatively small part of the parks served by the road systems. Most of the management effort is directed at these frontcountry areas of concentrated use.

Most bear incidents in campgrounds involve filching small food items, breaking open portable coolers, or rummaging through improperly discarded garbage. Occasionally bears tear open tents for food. In most cases the tents are unoccupied and food is left inside. Despite prohibiting regulations, it is suspected that some campers intentionally leave food out to attract bears, hoping to get a close view of the animal. Unfortunately, this suspicion is difficult to prove. A few bears have learned to smash auto windows or otherwise gain access to closed vehicles and campers. These bears pose the most serious problems and must be immediately identified and dealt with. Luckily, most campground bears remain shy and relatively unaggressive. Few personal injuries have occurred during campground incidents (e.g., only 2 minor injuries were reported in both 1975 and 1976).

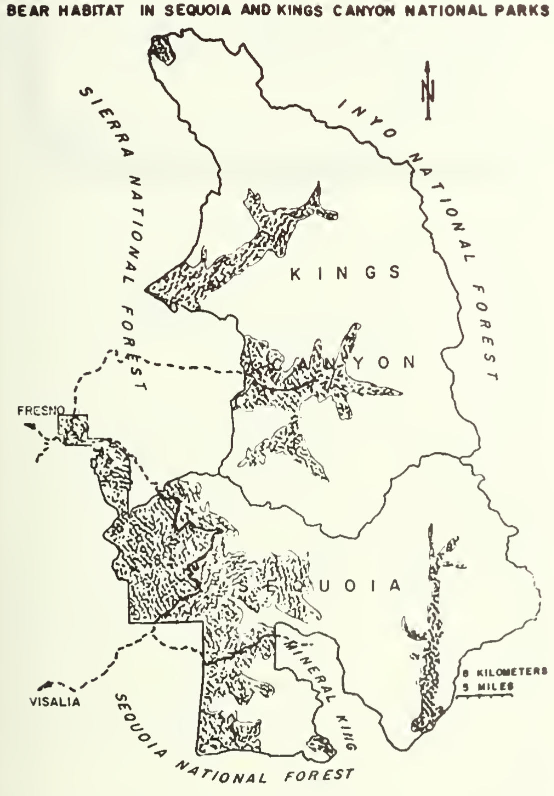

Fig.2. Map of bear habitat in Sequoia and Kings Canyon National Parks based on plant communities and sighting records.

Concession-operated lodging with outdoor tables and food storage has also been a problem. Lodge guests stay in cabins, some of which have outdoor porches with cupboards for dishes and cooking equipment. Food stored in the cupboards attracts bears onto the porches, which frequently results in property damage as well as loss of food. A few bears have learned to enter the cabins for food. These problems will continue until each park visitor realizes the danger and illegality of making food available to bears.

In at least 2 backcountry locations, bears have become an increasing nuisance in recent years. Common activity patterns include tearing backpacks and climbing trees to remove cached food. Loss of food supplies can be serious when hikers are 2 or more days from the nearest trailhead. Delay in reporting these incidents, remoteness of location, and poor identification of individual bears make these situations difficult to deal with.

THE MANAGEMENT PROBLEM

The bear management program at Sequoia and Kings Canyon in the past 3 years has developed 5 elements: waste disposal, education, reporting, enforcement, and management of individual bears. Since improper waste disposal has generally been the major cause of bear incidents, a concerted effort has been made to install bearproof garbage cans at all locations in both parks. To date, nearly 900 cans with concrete bases and heavy metal tops have been installed throughout the parks. In addition, all large dumpster bins have been modified with effective hasps and catches. Garbage pick-up schedules have been arranged as late as possible each day to avoid overflow conditions during the evening hours when bears are most active.

Educational efforts have included placing bear caution signs (Fig. 3) in all campgrounds and restrooms. A 2-minute illustrated slide program with a taped script is

WARNING BEAR HABITAT

PROTECT YOUR PROPERTY AND YOURSELF

1. Store all food in a vehicle trunk, if no trunk available, keep food and food containers covered and out of sight inside the vehicle.
2. Deposit all garbage in the nearest refuse container.

DO NOT

1. Store food in tents.
2. Leave food, food containers, cooking utensils, or table scraps in the open.
3. Leave vehicles unattended with windows cracked open.

—PLEASE—

PARK REGULATIONS (AND GOOD SENSE)
REQUIRE THAT YOU DO NOT FEED OR LEAVE FOOD
OUT FOR PARK ANIMALS

Fig. 3. Painted 23-cm x 30-cm pressed wood sign placed in restrooms and other highly visible campground locations.

shown nightly at each of the 5 locations where campfire talks are given. The program illustrates proper storage of food and disposal of waste and requests visitor cooperation. Attempts are also made to establish verbal contact with all campers when rangers make their evening campground patrols. Finally, brochures that explain the bear problem are given to visitors at park entrance stations and at each campground. This past year, a new attraction-getting brochure was distributed. It calls attention to a serious problem by a simple and direct comic approach. If we can reach everyone who enters the parks with a hard-hitting educational message about the danger and illegality of making food available to bears, our goal of greatly reducing the number and severity of bear incidents will be more easily achieved.

The reporting of bear incidents has developed from the monthly report of past years to a daily report, using the standard National Park Service Case Incident Report Form. A system of immediate reporting by radio or telephone to a central dispatcher who would coordinate the reports for computer storage and analysis is planned for the future. Timely, accurate reports are necessary to gain mastery of bear problems. The active bear season lasts only from April or May through October, and a flexible approach based on a sound reporting system can quickly resolve problem situations.

In 1976, a federal regulation making visitors responsible for protecting food and waste from bears became effective. Warnings were issued in its introductory season. Stricter enforcement, with citations for violations, was carried out in 1977. We hope that gradually intensified application of the regulation along with other elements of the bear management program will change the habits of both people and bears.

Management of individual problem bears is rapidly becoming a sophisticated science that requires the ability to identify individual animals as well as training in the use of controlled drugs. Decisions on the fate of a problem-causing bear are made only after careful deliberation of past offenses as well as circumstances attending the bear's offenses. Each case is individually considered by a group of park managers and biologists.

Attempts are made to capture specific bears identified as those causing problems. Whenever possible, the capture is made with a baited culvert trap. One problem with this technique is that innocent bears may be inadvertently trapped. Advantage is taken of this situation to mark all trapped bears with readily visible ear tags. Innocent bears are released whether they have been previously marked or not. Having most of the bears that frequent the visitor use areas so tagged has greatly facilitated the identification and capture of individual culprits. In the past, many innocent bears are thought to have been sacrificed in attempts to remove the offending one. Culvert traps present a second problem in that some bears become trap-shy. In such cases, the offender is taken with a Cap-chur gun using Sernylan (phencyclidine hydrochloride). After succumbing to the drug, the bear is placed in a culvert trap to await management action. A high degree of success has been achieved with this method. Snare traps have been used on only 2 occasions in recent years, when individual bears eluded other methods of capture.

If a guilty bear is a first offender or its offense is minor or the result of park negligence, attempts will usually be made to relocate it in some remote area of the parks in hopes of rehabilitation. It is unfortunate that with the limited road access to most parts of these parks, bears cannot easily be moved by mobile traps far enough to challenge their return capabilities. In several instances, relocated bears have returned from as far away as 56 km within 2 weeks. Some bears that have not returned have left the park to become problems elsewhere. As an alternative, helicopter relocations have been made 5 times in the last 2 years. Despite arguments of potential danger in the backcountry from relocated bears, we have no evidence that these animals have caused any problems. In the future, radiotelemetry equipment will be used, where possible, to follow the movement and activities of relocated bears.

Although one of our goals is to minimize the killing of bears, we recognize that it may sometimes by necessary. Bears whose behavior falls within one of the following categories are now considered for immediate destruction: (1) Bears that attack or injure people without provocation. (2) Bears that growl at, rush, chase, or otherwise threaten people without provocation. (3) Bears that enter occupied areas to take food despite people's actions to chase them away, and are trapped and relocated only to return repeatedly and resume their previous habits. When 1 or more of these criteria are met, park managers decide whether the bear must be destroyed. Since 1974, 4 bears have been destroyed. There may be a transition period of several years during which individual problem animals adjust to the unavailability of unnatural food sources. In the long run, proposed management plans should lead to a more natural bear population.

RESEARCH

Along with an aggressive management program, the parks are sponsoring comprehensive research designed to provide valuable basic information on the ecology of black bears. Under the direction of workers from the University of California, Berkeley, work completed to date has included an intensive capture, mark, and reobservation program as well as scat collection and analysis of naturally occurring food availability (Walraven and White, Unpubl. Prog. Rep. to Natl. Park Serv., 1976). These studies have so far provided a valuable basis upon which to begin to monitor the effectiveness of the management program. The final report on this research has not yet been received but should contribute pertinent information on the relationship between the availability of natural foods and the level and intensity of bear incidents (M. Walraven, personal communication).

The first phase of this research funding has expired. Important continuation studies have been proposed. These studies will include an evaluation of the effects of relocating a bear, both on the bear and on bears that are already in the area in which it is released. Studies of movement and denning patterns, social interactions, and food preferences are also proposed. Extensive use will be made of radiocollars for tracking individual bears.

DISCUSSION

For many years, bear management at Sequoia and Kings Canyon National Parks consisted of little more than efforts to remove problem animals. The real problem of readily available human food, although recognized for some time, has been systematically attacked only during the last 3 years. The current bear management program is based on (1) elimination of unnatural food sources, (2) education of all park visitors and employees, (3) complete and timely reports of all incidents, (4) enforcement of applicable regulations, and (5) positive identification and effective management of problem bears. Although, as mentioned, the final report from the complementary research study is not yet available, interim recommendations from the study have helped to shape this program.

The systematic approach to the problem has resulted in increasingly effective bear management, but there are still some areas in need of immediate improvement, namely, reporting of bear incidents, identification of individual animals, and impressing upon visitors the importance of not making foods available to bears. Effective implementation of the outlined bear management program should allow the parks' bears to live as natural a life as possible, with minimum interference by humans.

SOME POPULATION CHARACTERISTICS OF TWO BLACK BEAR POPULATIONS IN IDAHO

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Abstract: Two geographically discrete populations of black bears (*Ursus americanus*) in Idaho were studied during 1973-76. The Council population, located in west-central Idaho, has a history of heavy hunting pressure, accessibility, and liberal hunting seasons. The Lowell population in north-central Idaho has relatively light hunting pressure, poor accessibility, and liberal hunting seasons. An analysis of the male and female age structures indicated that adult males were more susceptible to hunting than other segments of the population. Sex composition differed significantly between subadult and adult segments of the 2 populations, but not between populations. Mean litter size was 1.9 at Council and 1.7 at Lowell. Productivity (number of young produced per year) appears to be density-independent and a function of habitat quality and the number of adult females present in the population.

Although several recent reports concern population parameters of bears, no data have been published comparing density, age and sex compositon, and reproductive biology of exploited and unexploited populations of black bears (Jonkel and Cowan 1971, Kemp 1972, Craighead et al. 1974, Pearson 1975). In 1973, the Idaho Department of Fish and Game initiated a black bear study in the area of Council, Idaho. The objectives of this study were to ascertain the density, sex and age structure, movements, breeding biology, denning ecology, and food habits of an exploited black bear population in the southwestern part of the state. A second black bear study was begun in 1975 in the Lowell area of Idaho in conjunction with a mortality study of calf elk (*Cervus elaphus*). The objectives of this second study were to determine the density, sex and age composition, reproductive biology, and food habits of an unexploited black bear population. Some population characteristics of these geographically discrete black bear populations are reported here.

A number of persons provided valuable assistance during the course of this study. A. Nicholson, A. Ogden, D. Rhodenbaugh, M. Luque, J. Brown, T. Rinkus, and J. Pope worked as field assistants and S. Amstrup and D. Reynolds as graduate assistants. I also wish to thank the following personnel of the Idaho Department of Fish and Game: L. Oldenburg for administrative supervision, C. Prentice for preparing teeth for aging, C. Nellis for reviewing the manuscript, and especially M. Schlegel for his assistance on the Lowell area. I also express appreciation to my wife, Denise, for her support during my frequent and often long absences from home. This study was a contribution of Federal Aid in Wildlife Restoration Project W-160-R.

STUDY AREA

Black bear populations occur primarily in the northern two-thirds of the state, with isolated populations in eastern Idaho along the Montana and Wyoming state lines (Fig. 1).

The Council study area is located approximately 16 km southeast of Council, Idaho. The predominant geographic features of the area are Council Mountain and West Mountain Ridge. Elevations range from 1,040 m to over 2,470 m on Council Mountain. The area trapped was approximately 130 km^2.

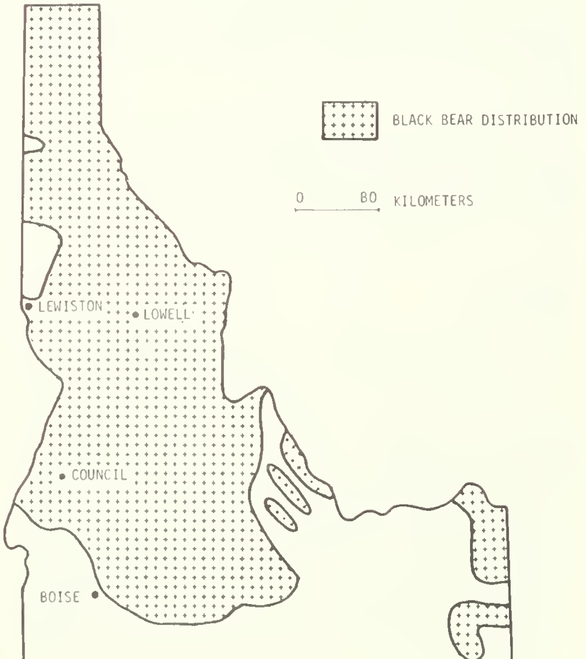

Fig. 1. Map of Idaho showing location of Council and Lowell study areas and distribution of black bears in the state.

Timber stands on the area range from dense to open with some natural bare areas. Dominant tree species are grand fir (*Abies grandis*), subalpine fir (*A. lasiocarpa*), Engelmann spruce (*Picea engelmannii*), ponderosa pine (*Pinus ponderosa*), and Douglas fir (*Pseudotsuga menziesii*). Logging and cattle grazing are the major land uses in the area.

The Council area was chosen for study because of a concern for the status of its black bear population. This area has a history of heavy hunting pressure, accessibility, and liberal hunting seasons.

The Lowell study area encompasses 260 km^2 and is located approximately 160 km east of Lewiston, Idaho. The predominant feature of this area is Coolwater Ridge, which bisects the area from west to east. Elevations range from 460 m to 2,135 m.

The Lowell area has a long history of fire dating back to the 1750s and, as a result, contains vast areas of seral brushfields. Most timber stands are relatively dense and contain ponderosa pine, Douglas fir, and grand fir at lower elevations. Engelmann spruce, subaline fir, and western red cedar (*Thuja plicata*) are found at higher elevations and on the more mesic sites. Cattle grazing is the major land use in the area. Only 1 road enters the study area. The Lowell area has light hunting pressure, poor accessibility, and liberal hunting seasons.

The climates of the 2 areas are influenced primarily by maritime air from the Pacific Ocean and are characterized by moderately long, cold, wet winters and dry, hot summers. Precipitation averages 81 cm.

METHODS

Several black bears were captured on the Lowell area in 1975 by tranquilizing them with a Cap-chur gun and dart from a Hiller 12-E helicopter. Most bears, however, were captured with Aldrich spring-activated snares in or adjacent to cubby sets baited with spawned-out salmon (*Oncorhynchus tshawytscha*) or steelhead (*Salmo gairdneri*). The snares were usually attached to green drag logs placed beside the cubby. In 1976, all snares set on the Lowell area were attached to live trees to facilitate the removal of the bears from that study area by helicopter.

A syringe mounted on the end of a 2-m jab stick was used to inject Sernylan (phencyclidine hydrochloride; dosage rate approximately 1.3 mg/kg of body weight) into all snared bears to immobilize them. A standard 300-mg dose of Sernylan was used on adult bears shot from the helicopter.

All captured bears were tagged with numbered aluminum ear tags. In addition, they were tattooed with corresponding numbers in the right ear and upper right lip. Forty-five bears were radio-marked on the Council area. Most captured bears were weighed, and physical measurements were taken on all bears.

Bears in the Lowell study area were trapped during June and early July in 1975 and 1976; bears in the Council area were trapped from May until mid-August during 1973-76. Only those data collected at Council from May until mid-July in 1973 and 1974 were used to compare with Lowell information so that the periods of data collection on the 2 areas would be comparable.

RESULTS AND DISCUSSION

Density

Black bears in Idaho tend to move to lower elevations shortly after emerging from their dens in the spring (Amstrup and Beecham 1976). As a result, density estimates derived from spring and early-summer trapping may be slightly inflated, but any bias should be similar on the 2 areas.

Preliminary life-table data indicate substantial ingress and egress of subadults ($\leq$ 3 years of age) at Council (Beecham, unpublished data). Because this movement would influence marked-unmarked ratios and inflate population estimates, we computed the density of the relatively stable adult segment of the population by using the Lincoln Index technique. To this figure we added the number of subadults, calculated from the ratio of subadults to adults, to give a total population estimate. This technique was applied to data collected on both areas.

A total of 47 individual bears were captured 58 times at Council and 100 individuals 120 times on the Lowell study area.

The estimated density of black bears on the Council and Lowell study areas was 1 bear per 2.1 km^2 and 1 bear per 2.3 km^2, respectively. Similar densities were found in Alberta (1 per 2.6 km^2; Kemp 1972:27) and Montana (1 per 2.1-4.4 km^2; Jonkel and Cowan 1971:41) and somewhat lower densities in a Michigan study (1 per 8.8 km^2; Erickson and Petrides 1964:48).

Age Composition

Few data are available that demonstrate how the age composition of an unexploited bear population changes under the influence of increased hunting pressure. The heavily hunted Council population had a 50:50 subadult-adult ratio, whereas the relatively unhunted Lowell population showed a preponderance of adult bears in the population (Table 1). An analysis of the

Table 1. Sex and age composition of black bears captured at Council (1973-74) and Lowell (1975-76), Idaho. Numbers in parentheses are percentages.

Location	Number of males			Number of females			Total	
	Subadult	Adult	Total	Subadult	Adult	Total	Subadult	Adult
Council	14 (58)	10 (42)	24 (51)	8 (35)	15 (65)	23 (49)	22 (47)	25 (53)
Lowell	20 (36)	35 (64)	55 (55)	9 (20)	36 (80)	45 (45)	29 (29)	71 (71)

male and female age structures indicated that adult males were the most susceptible segment of the population to hunting. Ingress and egress of subadult males were primarily responsible for maintaining population numbers at Council, although some subadult females also moved into and out of the area.

Most investigators have reported subadult-adult ratios approaching 50:50 (Erickson and Petrides 1964, Jonkel and Cowan 1971, Kemp 1972).

Sex Ratios

Sex ratios reported for cub black bears have not differed significantly from 50:50 (Jonkel and Cowan 1971, Kemp 1972). Sex ratios for adult black bears, however, have ranged from 50:50 to being skewed towards males (Raybourne 1976), depending on the method of collection.

Sex ratios obtained from capture data on the Council and Lowell study areas did not differ from 50:50. Sex composition data differed significantly between subadult and adult segments of the 2 populations, but not within each component (Table 1).

Radiotracking of all sex- and age-classes of black bears at Council (Amstrup and Beecham 1976, Reynolds and Beecham 1980) revealed that subadult and adult males traveled more extensively than other age- and sex-classes of bears. This behavioral trait undoubtedly increased their vulnerability to trapping and hunting and inflated our estimates of their numbers. As a result, the actual sex ratio of both populations may slightly favor females. Our data suggest that bear hunters in Idaho are unable to distinguish between males and females in the field before killing them. Thus, any bias in our harvest data would come from differential vulnerability of the sexes.

Reproductive Biology

The reproductive potential of a specific bear population becomes increasingly important as hunter pressure and other mortality factors increase. Habitat quality appears to be a significant factor determining both minimum breeding age and litter size of black bear populations (Erickson and Nellor 1964, Jonkel and Cowan 1971).

We were able to determine the minimum breeding age for 8 females bears at Council (Reynolds and Beecham 1980). Three bears successfully bred at 3.5 years of age, 4 at 4.5 years, and 1 at 5.5 years. At Lowell, 2 female black bears bred at 3.5 years of age and 4 bred at 4.5 years; 1 female 5.5 years old had not successfully bred. Jonkel and Cowan (1971) reported females in estrus at 4.5 years of age, but no litters were produced until 6.5 years.

Mean litter size at Council was 1.9 and at Lowell was 1.7 (Table 2). Jonkel and Cowan (1971) reported that average litter sizes in Montana ranged from 1.5 to 1.8. Spencer (1955), Stickley (1961), and Erickson and Petrides (1964) all reported mean litter sizes exceeding 2.1.

Table 2. Litter size in black bear populations, Council (1973-74) and Lowell (1975-76), Idaho.

Area	*N*	Litter size			Mean
		1	2	3	
Council	11	1	10	-	1.90
Lowell	23	10	11	2	1.65
Total	34	11	21	2	1.74

Jonkel and Cowan (1971) commented that the late minimum breeding age and low mean litter size they observed in a Montana black bear population were due to poor nutritive status. We observed somewhat lower minimum breeding ages and a larger mean litter size ($P < 0.10$) at Council. We concur with Jonkel and Cowan (1971) that minimum breeding age and mean litter size are functions of habitat quality. We believe that the larger litter size observed at Council was not a compensatory response to excessive adult mortality. Craighead et al. (1974) suggested that increased reproductive rates and increased survival of subadults may compensate for excesses in adult mortality. Our data indicate that increased survival and ingress of subadult bears may partially offset adult mortality. Reproductive rates, however, appear to be independent of density (Beecham, unpublished data).

Population-regulating Mechanisms

The causes of natural mortality in bear populations remain largely unknown. If we assume that habitat is probably the ultimate factor operating to control bear populations, social intolerance with the resultant dispersal of subadults appears to be the proximate mechanism that was regulating bear populations on the study areas. Stokes (1970) and Kemp (1972) concluded the same for grizzly (*Ursus arctos*) and black bears, respectively.

Despite the difficulty of documenting specific cases of subadult mortality, limited evidence indicates that adult males do kill other bears. Pearson (1975) reported 2 separate cases where an aged grizzly bear and a subadult (4.5 years) were killed by other grizzlies. Jonkel and Cowan (1971) documented the killing of a yearling black bear in 1 of their traps by a large black bear or a grizzly bear. In 1975, shortly after a 3.5-year-old female black bear was released from a trap, it was killed and partially eaten by a large black bear at Lowell. Although predation by adult bears on subadults has been documented, we feel that dispersal of subadults, primarily males, is the more important regulating mechanism operative in the black bear population at Lowell. Capture rates of untagged, ingressing subadult males at Council support this conclusion (Beecham, unpublished data).

Pearson (1975) captured 2 male grizzly bears with large, infected wounds that he felt could have been inflicted only by another grizzly. Fresh wounds and scarring were commonly observed on adult male black bears captured at Lowell but were recorded only occasionally for adult males at Council. We believe this strife is a function of the aggressiveness of older-aged bears rather than the result of spatial mechanisms operative in the respective populations. Radiotracking of adult bears at Council supports this conclusion by demonstrating an average overlap of 85 percent in the home ranges of several adult males (Reynolds and Beecham 1980).

MANAGEMENT CONSIDERATIONS

Our data indicate that the productivity (number of young born per year) of a black bear population is density-independent and is a function of habitat quality and the number of adult females present in the population. Therefore, the game manager cannot expect increased productivity as a compensatory factor resulting from the heavy harvest of a black bear population.

Second, without reservoir areas nearby to produce highly mobile subadult bears, heavy hunting pressure can be expected to reduce bear densities.

Third, a decrease in the average age of the bear population indicates decreased opportunity to provide trophy bears. Adult male black bears on the Council and Lowell study areas appear more aggressive and are more mobile than their female counterparts and are therefore more vulnerable to hunting.

We concur with Craighead et al. (1974) in recommending conservative bag limits and bear hunting seasons.

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BLACK BEAR MANAGEMENT IN YOSEMITE NATIONAL PARK

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Abstract: Conflicts between park visitors and the American black bear (*Ursus americanus*) in Yosemite National Park pose serious management problems for the National Park Service and often result in extreme inconvenience and monetary losses to park visitors. Food-reward associations with humans have resulted in the loss of the black bear's instinctive fear of people and in the development of highly sophisticated patterns of depredation. A management program consisting of 5 basic elements was implemented in the spring of 1975 to meet bear management objectives of the National Park Service. The effects of management on bears and park visitors were evaluated by monitoring the patterns of damage that bears displayed before and during the program. Analyses of data accrued from property damage, personal injuries, and control of problem bears were also made. The results of these analyses are discussed and their implications applied to management practices and research needs. Comparisons of data accrued before and through the first 2 years of the program appear to support the hypothesis that the program is achieving its stated objectives.

The natural behavior, foraging habits, distribution, and numbers of black bears in Yosemite National Park have been significantly altered by habituation to human-supplied food sources. During the past 6 decades of food-reward associations with people, bears have evolved deeply ingrained, sophisticated patterns of depredation.

The Yosemite Human-Bear Management Program was implemented in 1975 to meet bear management objectives of the National Park Service with minimum adverse impact on the black bear population and environment. This paper summarizes the management problem and management activities, describes evaluation procedures, presents preliminary results, and brings together data that may be used for future program analysis.

The conflict between bears and people and the effects of people upon bears are seen nowhere more dramatically than in Yosemite National Park. Extensive development, high levels of visitor use, and patterns of visitor use are key factors contributing to the conflict. Visitation has exceeded 2.25 million people since 1968 and 2.7 million in 1976 (Table 1). Levels of backcountry use tripled in less than 10 years. Recorded visitor-nights of use increased from 77,654 in 1967 to 169,924 in 1976. In 1976, 64,606 people spent nights in the backcountry.

Extensive development including campgrounds, hotels, restaurants, stores, swimming pools, tennis courts, golf courses, a ski area, and 5 backcountry High Sierra Camps concentrates human use in available bear habitat, increasing the potential for encounters with bears. Stokes (1970) found that repeated visits of bears to developed areas and garbage disposal sites to obtain food represent reward-reinforced behavior.

Through food-reward association, bears have learned the relationship between vehicles and food stored in them. In the last 3 years, 1,493 vehicles were damaged or broken into by bears seeking food — 65 percent of the 2,293 recorded bear incidents. Bears have also learned the association between backpacks or foodsacks suspended from trees and the ropes holding them up. Today, the average backpacker finds it increasingly more difficult to suspend food supplies in a manner that prohibits bears from reaching them. In the past 2 years, it is estimated that 3,840 bear incidents occurred in the backcountry. The level of sophistication shown by bears in their patterns of depredation appears to be increasing as their instinctive fear of people decreases.

After review of available information, the Superintendent of Yosemite National Park directed that a program be implemented to (1) restore and maintain the natural distribution, abundance, and behavior of the endemic black bear population; (2) provide for the safety of park visitors and their property; and (3) provide opportunities for visitors to observe, understand, and appreciate the black bear in its natural habitat.

METHODS

Methods employed included (1) public information and education, (2) removal of all artificial food sources, (3) enforcement of regulations regarding proper food storage and the feeding of wild animals, (4) control of problem animals, and (5) research and monitoring.

Public information systems and steps taken to increase the public's awareness of the program and compliance with its provisions included (1) distribution of bear brochures to both frontcountry and backcountry users; (2) permanent warning signs at park entrances, campground entrances, parking lots, and park restrooms; (3) articles regarding bears and people in each

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Table 1. Property damages and personal injuries attributable to black bears, Yosemite National Park, 1966-76.

Year	Park visitation	Damage incidents[a]		Decrease/increase of incidents from previous year (%)	Number of personal injuries	Number of visitors per injury	Control actions[b]
		Number	Estimated value ($)				
1966	1,817,000	49	1,888	-	29	63,000	47 (24)
1967	2,201,500	72	2,843	47	11	200,000	48 (17)
1968	2,281,100	49	2,670	−47	6	380,000	16 (4)
1969	2,291,300	86	6,360	76	12	191,000	38 (4)
1970	2,277,200	27	4,730	−69	3	759,000	40 (6)
1971	2,416,400	103	11,835	282	10	242,000	61 (13)
1972	2,266,600	262	28,588	154	3	746,000	81 (17)
1973	2,339,400	246	24,367	−6	16	146,000	43 (9)
1974	2,343,100	613	80,248	149	28	84,000	26 (1)
1975	2,619,000	975	113,197	59	15	175,000	135 (10)
1976	2,753,100	688	66,294	−29	12	229,000	147 (16)

[a] Not including personal injuries.

[b] Numbers of bears killed given in parentheses.

summer issue of the park newspaper; (4) increases in the numbers of ranger patrols and interpretive programs about bears; and (5) an AM taped radio broadcast receivable on all roads entering Yosemite Valley informing the public about bears.

Open garbage pit dumps were sources of artificial food until 1969 and 1970 when land dumps were closed and a solid waste collection system was adopted. Despite the conversion, bears continued to feed on garbage provided by the non-bearproof dumpsters. In the spring of 1975, all dumpsters in use in the park were bearproofed. Cables from which park visitors could suspend their food supplies out of reach of bears were installed in selected backcountry areas and frontcountry walk-in campgrounds.

Efforts to insure denial of human food sources and to have visitors store food so as not to lure bears into campgrounds were aided by the adoption of Special Regulation S7.16e (3) CFR 36 requiring proper food storage methods. The level of enforcement varied from verbal warnings to arrest and/or impoundment of property.

One control action was recorded each time a bear was either captured and transplanted, shipped to a zoo, or destroyed. Efforts to remove bears promptly from park developments when property damage or injuries were occurring were intensified. Bears were captured, while free-ranging, with Sernylan (phencyclidine hydrochloride) administered by projectile-syringe, with baited culvert traps, and with Aldrich snares. Measurements, weight, sex, and age were recorded, and a blood sample was collected. Bears were tagged with metal cattle ear tags with vinyl streamers attached.

Bears were relocated 13-48 airline km from their capture sites and released at predesignated release sites. To control bear densities in each release area, a minimum interval of 7 days was allowed between successive releases in each area: this 7-day release interval was violated only when all other release sites were full.

Bears were intentionally destroyed using pentobarbital sodium and processed as scientific specimens if they had been relocated twice, captured a third time, *and* their individual trapping records showed conclusively that they were confirmed rogue animals or were responsible for personal injuries. Bears twice relocated and captured a third time that were not serious problem animals were relocated a third time.

The Division of Resources Management maintained a central monitoring system that recorded human injuries, property damage incidents, and all bear control actions on a daily basis. Thus, current information for guiding the overall program and data for evaluation studies were available.

A 2-year research study on the population ecology of the black bear in Yosemite National Park was contracted to the University of California, Berkeley, in 1974 and has since been extended to cover a 4-year period ending September 1978.

The success of the program depends on the validity of the hypothesis that removal of unnatural foods will restore a natural population of bears, thereby reducing the need to control (capture and transplant or destroy) bears to protect humans and their property. Data accrued from problem bear control, property damage, personal injuries, and research on population dynamics will be used to test the following hypothesis:

> Bear control procedures, law enforcement, public information systems, and management actions to

eliminate unnatural food sources, applied under the 1975 Human-Bear Management Program, will (1) restore a more natural black bear population than exists at present, as evidenced by fewer bears using developed areas and by progressive reduction in the numbers of bears controlled or destroyed; (2) reduce the number of property damage and human injury incidents from previous levels; and (3) not prevent the park bear population from stabilizing at the natural carrying capacity of the park.

RESULTS

Property Damage Incidents

Removal of artificial food sources in the spring of 1975 marked the beginning of a transition period in which bears are expected to resort primarily to natural foraging for energy requirements. In the first year after artificial foods were eliminated, incidents increased to a high of 975 but decreased to 688 in the second year (Table 1). Plotting property damage incidents (PDs) on a graph showed that the number of PDs increased exponentially from 1961 through 1975. The number of PDs fitted to a regression line with a square-root transformation as the dependent variable and with time as the independent variable (Fig. 1) shows that PDs increased significantly with time ($t = 5.73$, df = 9, $\alpha = 0.01$, $r = 0.89$). A 95 percent confidence interval is constructed around the regression line as graphically portrayed by the dashed lines in Fig. 1. The 975 and 688 incidents recorded in 1975 and 1976, respectively (after removal of unnatural foods), fall within these boundaries, indicating that they do not differ significantly from the exponential growth trend. However, incidents in 1976 decreased 29 percent from those of the previous year. We expect further decreases in incidents as young bears without human-altered behavior progressively replace incorrigible animals and the population readjusts to natural carrying capacity levels.

Patterns of damage and changes in patterns that bears display may be useful in determining the effects on both bears and people of removing unnatural foods. Patterns monitored included (1) time of incidents, (2) location, (3) type of property damage, and (4) the relation of food and food storage to incidents.

The time that incidents occurred in 1974 through 1976 (month; weekend vs. weekday; hour) remained relatively unchanged; 70 percent of the damage occurred in June, July, and August; and 18 percent occurred in September, October, and November. The percentage of incidents that occurred in the daytime (15 percent) and at night (74 percent) also remained the same, suggesting that the bearproofing program has not altered the bears' crepuscular activities (times of occurrence for 11 percent of the incidents were unkown).

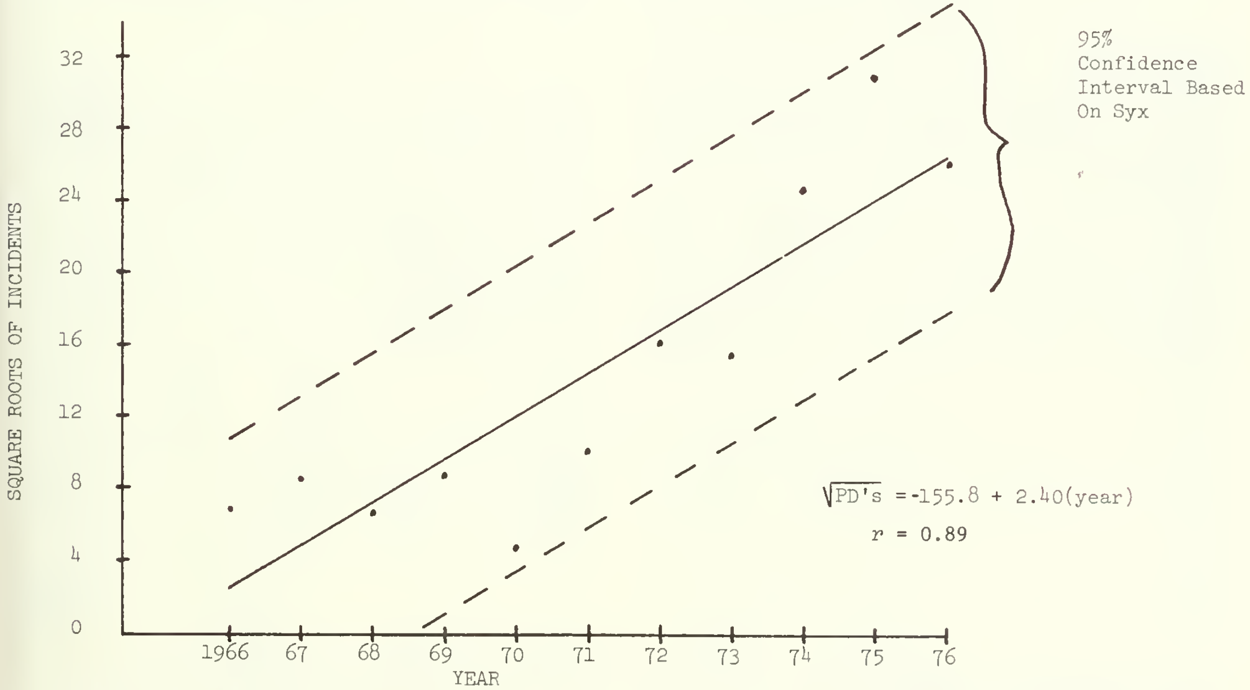

Fig. 1. Property damage incidents fitted to a regression line using a square-root transformation as the dependent variable and time as the independent variable.

The percentage of incidents that occurred in campgrounds decreased from 71 percent in 1974 to 46 percent in 1976 but the percentage of incidents in parking lots increased 15 percent. This shift suggests to some degree the effectiveness of the new program. The percentage of incidents in all other locations except backcountry areas remained the same.

Food rewards associated with people or with objects that contain food have resulted in deeply ingrained patterns of depredation. Some forms of bear behavior appear to be conditioned responses from past experiences that resulted in positive food rewards; examples are smashed windows of vehicles that contained no food, tree limbs or ropes chewed into to retrieve suspended food, and false charges at people. Behavior that resulted in bear incidents due to conditioned responses and in which no human error precipitated the incident is referred to in this paper as *conditioned bear behavior*.

Smashing vehicle windows and pulling out window and door frames to gain entry into vehicles for food represent a behavior pattern that characterizes the Yosemite population. Methods of food storage in a vehicle are critical factors in determining the likelihood of bear damage to the vehicle (Table 2). Vehicles that had food in the passenger sections either because they lacked trunks or because people neglected to store food properly sustained 68 percent of the total vehicular damage incidents in 1976. Vehicles with properly stored food represented only 18 percent of the incidents. Fourteen percent of the damaged vehicles had no food in them. Over $54,000 damage to vehicles occurred in 1976, a decrease of 43 percent from a high of $96,594 recorded in 1975. An indication of a favorable trend is that the percentage of incidents involving vehicles declined from 70 percent in 1974 to 57 percent in 1976.

To determine the cause of incidents, causative factors were assigned to each incident investigated (Table 3). Unstored food and improperly stored food were major causative factors for 48 percent of frontcountry incidents in 1976. Forty-six percent of the incidents were attributed to conditioned bear behavior.

Backcountry Incidents

Surveys by backcountry rangers checking compliance with wilderness permits showed the number of

Table 2. Analysis of bear incidents relating food and food storage to property damage, Yosemite National Park, 1974-76.

	Food in trunk of vehicle	Food in passenger section; vehicle with trunk	Food in passenger section; vehicle without trunk	No food present	Food storage unknown	Food present	Food left in open	Food hung from tree/cable	Total[a]
Vehicles									
1974	64(15)[b]	163(37)	93(21)	33 (8)	86(20)	-	-	-	439(70%)
1975	132(20)	205(31)	237(36)	87(13)	-	-	-	-	661(68%)
1976	70(18)	124(32)	143(36)	56(14)	-	-	-	-	393(57%)
Towed units									
1974	-	-	-	-	-	-	-	-	-
1975	-	-	-	1 (6)	-	15(94)	-	-	16 (2%)
1976	-	-	-	1(10)	-	9(90)	-	-	10 (2%)
Tents									
1974	-	-	-	26(46)	11(20)	19(34)	-	-	56 (9%)
1975	-	-	-	19(46)	-	22(54)	-	-	41 (4%)
1976	-	-	-	11(39)	-	17(61)	-	-	28 (4%)
Backpacks									
1974	-	-	-	-	4 (6)	-	20(27)	49(67)	73(12%)
1975	-	-	-	-	8 (6)	-	38(26)	100(68)	146(15%)
1976	-	-	-	-	18 (9)	-	28(13)	165(78)	211(31%)
Ice chests									
1974	-	-	-	-	-	-	26(100)	-	26 (4%)
1975	-	-	-	-	7(10)	-	58(88)	1 (2)	66 (7%)
1976	-	-	-	-	16(27)	-	41(69)	2 (3)	59 (9%)
Other									
1974	-	-	-	-	-	-	-	-	36 (6%)
1975	-	-	-	-	-	-	-	-	71 (7%)
1976	-	-	-	-	-	-	-	-	94(14%)

[a] Percent given as percent of total incidents

[b] Percent of damaged items given in parentheses.

Table 3. Causative factors for property damage incidents in Yosemite National Park, 1975-76. Table gives the percentage of incidents assigned to each factor.

	Feeding/ baiting (intentional)	Food left in open	Improper food storage	Improper disposal of garbage	Accidental encounter	Conditioned bear behavior	Unknown
Frontcountry							
1975	1	9	35	0	0	54	1
1976	0	12	36	1	0	46	5
Backcountry							
1975	0	8	16	0	1	75	0
1976	0	10	8	0	0	74	8

reported incidents to be low and unrepresentative of actual backcountry bear encounters. The number of backcountry incidents can be estimated from the percentage of parties contacted that suffered incidents and from data on wilderness permit compliance. The level of incidents expressed as incidents per thousand visitor-nights decreased from 13.5 in 1975 to 7.0 in 1976 (Table 4).

The reduction in backcountry incidents is attributed largely to information systems, enforcement of food storage regulations, and the installation of food suspension cables in selected high-problem areas. However, it is clear from the number of incidents and from personal observation that the large majority of backcountry users underestimate the cleverness and ability of bears to retrieve food suspended from or between trees. Aversive conditioning of bears may be required to reinstill an avoidance of people and minimize backcountry conflicts.

Injuries

A reduction in injuries occurred each year after the program was implemented (Table 1). The 12 injuries recorded in 1976 represent decreases of 57 and 20 percent from the 28 and 15 injuries recorded in 1974 and 1975, respectively. Two of the injuries in 1975 and 9 of the injuries in 1976 occurred in backcountry areas. Four of the backcountry injuries in 1976 occurred in 1 night and were attributed to a single yearling bear seeking food in an area of high visitor use. The bear was destroyed the next day.

Problem Bear Control

Cooperative efforts between contract researchers from the University of California, Berkeley, and park rangers and biologists have served to accentuate both research and management programs. Since 1974, 202 individual bears have been captured and marked. Intensified efforts to keep bears out of developed areas increased the number of control actions sharply in 1975 and 1976 and yielded many data useful in evaluating currently accepted management practices regarding control of problem bears. Under the criteria outlined in the mangement plan, 26 bears were killed in management actions in 1975 and 1976. The effects of management-induced mortality on the population will be analyzed when results of current research on population dynamics become available.

Relocation of problem bears resolved immediate problems only temporarily. During 1976, 98 different bears were relocated within park boundaries a total of 131 times. Observation of bears returned and/or recaptured at the same or another developed area indicated a 38 percent return rate (31 percent returned to their original capture sites). In 1975, the rate of return to developed areas for 100 bears relocated 125 times was 26 percent (21 percent returned to their original capture sites); in 1974 the rate was 8 percent for 23

Table 4. Levels of visitor use, bear incidents, personal injuries, and control actions in Yosemite's backcountry, 1973-76.

Year	Recorded visitor-nights	Estimated number of bear incidents	Incidents per thousand visitor-nights	Recorded incidents	Recorded damage ($)	Personal injuries	Control actions
1973	141,464	-	-	-	-	-	-
1974	192,180	-	-	61	2,145	2	0
1975	196,565	2,654	13.5	96	5,762	2	2
1976	269,924	1,186	7.0	160	4,471	9	3

Table 5. Summary of black bear captures/relocations and return rates to developed areas for 1-, 2-, and 3-year intervals, 1974-76.

Year	Total number of captures	Total number of new animals	Sex ratio M:F	Cumulative new animals	Number of times captured					Total number of individuals
					1	2	3	4	5	
1974	55	42	21:19	42	32(76%)	7(17%)	3 (7%)	0 (0%)	0 (0%)	42
1975	160	93	50:61	135	78(69%)	25(22%)	8 (7%)	2 (2%)	0 (0%)	113
1976	172	67	55:58	202	75(66%)	23(20%)	10 (9%)	4 (4%)	1 (1%)	113

Year	Total relocations	Number of times each individual relocated				Total number individuals relocated	Recaptures			Return rates[a]		
		1	2	3	4		First year	Second year	Third year	1-year interval	2-year interval	3-year interval
1974[b]	25	21	2	0	0	23	2	8	3	8% (0%)	40%	52%
1975[b]	125	76	23	1	0	100	33	31	-	26%(21%)	51%	-
1976[b]	131	71	23	3	1	98	44	-	-	34%	-	-
1976[c]	-	-	-	-	-	-	49[d]	-	-	38%(31%)	-	-

[a] Numbers in parentheses indicate return rates to original capture sites.

[b] Return rates based on recapture data only.

[c] Return rates based on recaptures and observations.

[d] Includes observations of 5 bears returned but not captured.

bears relocated 25 times. Table 5 shows the successive increases in the return rate as the time interval after relocation increased. The tendency for bears to return to their original capture sites, the geographical distribution of developed areas in Yosemite, and insufficient land area for relocation all served to negate the effectiveness of transplants.

Transplant success in 1975 was shown to be related to the distance transferred from the capture site (Harms 1976). The transplant success (85 percent) for bears transferred 37-48 km was significantly greater ($P <$ 0.05) that the success (65 percent) for bears transferred 13-20 km. However, in 1976, no significant difference could be shown between success rates and transfer distances (Table 6). This lack of significance may be explained in part by the fact that many bears relocated in 1976 had also been relocated one or more times in 1974 and/or 1975 and may have improved their homing abilities.

When return rates to developed areas were analyzed by age-class (Table 6), yearlings and subadults showed successes of 29 percent and 11 percent, respectively, as compared with 42 percent for adults. Optimistic interpretation of these data suggests that successful rehabilitation of these age-classes may be occurring. It is recognized, however, that the stress of the relocation in terms of placing a subdominant animal in an area in which the natural carrying capacity is already exceeded may increase the mortality rates for these age-classes. Jonkel and Cowan (1971), studying a black bear population in Montana, found that young bears over 1.5 years of age rapidly disappeared from the population. No difference was observed in return rates between females and males relocated in Yosemite.

Table 6. Black bear return rates, by age-class, in relation to relocation distances, Yosemite National Park, 1976.

Relocation distance (km)	Number released					Number returned to developed areas					Return rate
	Cub	Yearling	Subadult	Adult	Total	Cub	Yearling	Subadult	Adult	Total	
1.0-17.9	2	7	0	7	16	0	2	0	4	6	38%
18.0-33.9	10	9	3	24	46	3	4	1	10	18	39%
34.0-49.9	23	5	6	35	69	11	0	0	14	25	36%
Total	35	21	9	66	131	14	6	1	28	49	38%
Return rate by age-class						40%	29%	11%	42%	38%	

Females with cubs showed the strongest homing instincts. All females with cubs that were relocated and recovered in 1976 returned to their original capture sites at an average rate of 2.75 km/day (Table 7) with an average recovery time of 21 days. The rate of return for adult males averaged 1.61 km/day with an average recovery time of 38 days.

Table 7. Transplant/recovery distances (airline km) and rates of return to original capture sites for 41 black bears by sex and age-class, 1976.

Age-class	Transplant/recovery distance (km)		Rate of return (km/day)		Elapsed time (days), release to return	
	Male	Female	Male	Female	Male	Female
Adult						
$\bar{X}$	29.45	33.69	1.61	2.44	38.18	21.77
N	11	13	11	13	11	13
SD	10.59	10.56	1.26	2.02	40.99	16.88
Subadult						
$\bar{X}$	-	-	-	-	-	-
N	0	0	0	0	0	0
SD	-	-	-	-	-	-
Yearling						
$\bar{X}$	10.33	-	1.24	-	17.00	-
N	3	0	3	0	3	0
SD	5.13	-	0.21	-	6.92	-
Cub						
$\bar{X}$	35.86	38.29	2.75	2.75	20.43	21.57
N	7	7	7	7	7	7
SD	7.84	6.45	1.27	1.40	21.31	20.90

Emigration and dispersion of bears as a result of the relocation program and/or removal of artificial food sources have been observed. Some bears made substantial treks beyond park boundaries after being transplanted. The greatest distance traversed from the release site was approximately 100 km. One adult male traversed 97 km in 14 days. A female with a cub was observed near Kings Canyon National Park, a distance of 77 km, 13 days after being released. All bears that made long treks in short periods of time continued to travel in the same approximate direction as their transplantation, e.g., bears relocated southward continued moving south (Graber and White 1976). These movements are contrary to the typical response in which 31 percent of the bears relocated in 1976 returned to the exact locations of their capture. Perhaps these bears were completely confused in their "compass orientation" and moved long distances in an attempt to find their home territories or familiar landmarks.

Population Levels

Present population levels greatly exceed past reported natural levels. Grinnell and Storer (1924) estimated 125 bears in 1920. Until current research shows otherwise, this figure represents out best estimate of the natural carrying capacity of the park. The present population is estimated to be between 220 and 350 animals; this estimate is based upon density levels of 0.13-0.19 bear/km^2 of available bear habitat. The number of bears tagged (202) since 1974 indicates the minimum estimate of 220 to be low.

As artificial food sources are removed and natural carrying capacities restored, the population is expected to decrease. Through scat analysis, Graber and White (1976) showed that the use of human foods by bears in Yosemite Valley during the spring of 1976 (17 percent by volume, 17 percent by frequency) was substantially reduced from the summer of 1974 (48 percent by volume, 63 percent by frequency). Continued research on food habits and population dynamics should detect responses of the population to the restoration of natural carrying capacities.

CONCLUSIONS

The basic premises of Yosemite's black bear program follow those for grizzly bears in Yellowstone National Park (Cole 1976). These premises include: (1) The "right" number of bears is the number that occurs naturally (i.e., without human influences on bear behavior, habits, or population dynamics). (2) Removals of unnatural food and incorrigible animals will allow young bears without human-altered behavior or habits to progressively replace incorrigible animals in the population. Once replacement is accomplished, (3) the control of human influences alone will prevent corruption of new bears and will thereby supersede control of bears. Since the program has been in effect only 2 years, statistical analysis of the effects of the program is confined to the limitations set by the sample size. Personal injuries decreased in both years of the program but it is difficult to show that the reductions were significant. However, the hypothesis that the program will reduce injuries need not be rejected. The alternative hypothesis that the program will increase injuries, or the null form that it had no effect on injuries, is not supported by the preliminary data.

Regression analysis correlating incidents with time showed a significant positive relationship before the program's implementation. The equation of the lines allows forecasts of the number of incidents in future years. The difference between actual values and predicted values can be tested to determine whether the observed values differ significantly from the trend line. Neither the increase in incidents after program implementation nor the decrease that occurred in the second year differed significantly from the trend line. Four hundred or fewer incidents in 1977 would represent a significant reduction.

Experience in several national parks demonstrates that relocation programs have limited success unless the homing abilities of the bears can be overcome through transplant distances of 80 km or more. Relocation at great distances is physically impossible at Yosemite if bears are to be released inside park boundaries. Information on recovery times and on rates of return for relocated bears in Yosemite suggests that preventive programs of sanitation, information, law enforcement, visitor control, and perhaps aversive conditioning should preclude bear control in the priorities of responsive management tools.

Levels and patterns of visitor use continuously expose artificial food sources to bears and provide food-reward associations with people. Human-altered behavior has become deeply ingrained in the majority of the bear population as evidenced by the high number of incidents despite intense control efforts. Visitor use levels and patterns in Yosemite may preclude the possibility of achieving a wholly natural black bear population. That goal however, should not be reduced. Instead, managers should seek to apply new techniques and methods in addition to following currently accepted management practices. Aversive conditioning, area closures, restricted visitor use, and use of individual food lockers in both backcountry and frontcountry areas are possible methods yet to be tried. In the final analysis, however, the priority that Park Service administrators place upon achieving *naturalness* in the black bear population will determine the level and nature of future management programs.

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HARVEST AND POPULATION CHARACTERISTICS OF BLACK BEARS IN OREGON (1971-74)[1]

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Abstract: Sixty-six percent of black bears (*Ursus americanus*) harvested in Oregon during the 1971-74 sport-hunting seasons were killed by persons hunting other game at the time. Male bears, however, were harvested most heavily during the months when the majority of bears taken were killed by persons hunting exclusively for bears. Most females bred as 3- or 4-year-olds but produced fewer cubs in their first litter than were produced by bears older than 5 years. Survival of females in age-classes 1-5 was significantly higher than survival of males in the same age-classes. Survival did not differ between sexes in bears older than 6 years.

In 1961, the state legislature granted to the Oregon Department of Fish and Wildlife the authority to manage the black bear. The initial management authority excluded those areas of the state where bears could be expected to damage trees. Although the Department has gradually increased its control over management to its present statewide basis, liberal damage control policies still prevail. Biological knowledge necessary for proper management of the bear did not increase proportionately to the Department's increased management authority. Management decisions were based largely on harvest levels of the previous years.

This paper describes characteristics of the annual harvest and demographic characteristics of the hunted population in Oregon between 1971 and 1974 and discusses biases encountered in the analysis of data collected from hunter-killed bears.

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METHODS

Between September 1971 and September 1974, teeth and reproductive tracts were collected from black bears killed in Oregon. Taxidermists, sportsmen's clubs, persons involved in bear damage control programs, and individual sportsmen cooperated by saving either teeth or teeth and reproductive tracts. Questionnaires, requesting information on sex, age, and date and location of kill, were mailed annually between 1972 and 1974 in February or March to persons known to have killed a bear during the preceding sport-hunting season. The sport season for black bears extended from 1 August to 31 December. Most damage control hunting was done between April and August.

The maximum length and thickness of the root of each canine tooth were measured to determine sex of the bear (Sauer 1966, Guenther 1970). Teeth were decalcified and sectioned (Lindzey and Meslow 1972) and age was assigned to each bear on the basis of counts of dark-staining bands in the cementum (Marks and Erickson 1966, Stoneberg and Jonkel 1966).

Reproductive tracts were frozen or preserved in Bouin's fluid until examined. Ovaries were examined macroscopically for rupture sites and then serially sectioned with a razor blade. Measurements were made of corpora lutea and largest follicles. Each cornu of the uterus was cut open and examined for placental scars (Erickson and Nellor 1964, Poelker and Hartwell 1973).

RESULTS AND DISCUSSION

Characteristics of the Annual Harvest

Of the 585 completed questionnaires returned during the study, 66 percent were from persons whose names had been furnished by taxidermists, and the remainder were from persons who had written to us or had responded positively to the bear section of the annual big game harvest questionnaire sent out by the Oregon De-

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partment of Fish and Wildlife. Because we felt that these returns may have been biased if persons tended to take only bears of a certain age or sex to taxidermists, we compared the frequency of reported cub, yearling, and adult bears and the frequency of males and females in the taxidermist portion of questionnaires to similar frequencies in the remainder of the questionnaires. Because we found no significant difference in either sex ($P > 0.05$, $X^2 = 0.12$, df = 1) or age ($P > 0.05$, $X^2 = 2.04$, df = 2) frequencies between the two segments, the entire sample was considered representative of the annual harvest.

Between 1971 and 1973, 65.8 percent of bears killed were taken by persons hunting other game animals at the time (incidental harvest). The incidental harvest made up the greatest percentage of monthly kill in October and November, months that included the deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) seasons. Willey (1971:6) found that a sizable percentage of Vermont's annual kill of black bears occurred during the first weekend of the white-tailed deer (*O. virginianus*) season.

Analysis of questionnaire returns indicated that the largest percentages of male bears in monthly harvests occurred during August and December (Table 1), the months with the largest exclusive harvests (94 and 80 percent — bears killed by persons hunting only for bears). Active selection by the hunters for larger bears and increased vulnerability because of feeding habits (Willey 1971:10) undoubtedly contributed to the unequal sex ratio. The tendency of male bears to enter dens later than females (Erickson 1964, Lindzey and Meslow 1976) makes them proportionately more available to hunters during the latter part of the season. The proportions of males and females in the monthly harvests between September and November remained relatively constant. Willey (1971:6) concluded that during the deer season, differential vulnerability was not expressed because bears may simply be shunted from one hunter to another until shot.

Table 1. Sex of black bears and month of harvest in Oregon as reported in questionnaires (1971-73).

Month	Male		Female	
	Number	Percent	Number	Percent
August	38	70.1	16	29.9
September	53	60.9	34	39.1
October	181	63.3	105	36.7
November	51	64.6	28	35.4
December	7	77.8	2	22.2
Total	330	64.1	185	35.9

Although more male bears were reported to have been killed than females (178:100), we found, as did Erickson (1964:86) in Michigan, that hunters tended to report females as males. Corrected to account for this bias (see below), the proportion of males to females reported in the questionnaires no longer differed significantly from 1:1 ($P > 0.05$, $X^2 = 1.87$, df = 1). This fact, however, assuming that sex report bias is constant through the season, does not negate the apparent differences in harvest levels of the sexes among months.

Reports of age (cub, yearling, adult) on questionnaires are undoubtedly biased (Poelker and Hartwell 1973:126). If we assume that the magnitude of this bias also remains constant through the season, age compositions of the monthly harvest may be compared (Table 2). Few cubs and yearlings were killed during August and December. This result was to be expected if hunters selected for larger bears during these months. Earlier den entrance by yearlings (Lindzey and Meslow 1976) would make them less available to the hunter than adult males during the last part of the hunting season.

Table 2. Age of black bears and month of harvest in Oregon as reported in questionnaires (1971-73).

Month	Cub		Yearling		Adult	
	Number	Percent	Number	Percent	Number	Percent
August	1	1.9	5	27.8	38	70.4
September	4	4.7	34	39.5	48	55.8
October	14	4.9	89	31.3	181	63.7
November	6	7.7	18	23.1	54	69.2
December	0	0	1	11.1	8	88.9
Total	25	4.9	157	30.7	329	64.4

Collection of Teeth

Teeth were collected from 349 black bears killed during the 1971-73 sport-hunting seasons and from 150 additional bears killed during damage control programs. Because we lacked data on location of kill for many of the bears, we were unable to divide the sample on the basis of geographical regions of the state. However, over 90 percent came from the region west of the Cascade Mountains.

The possibility of differences in behavior between the sexes, that could cause survival rates to differ (Erickson and Petrides 1964, Jonkel and Cowan 1971, Willey 1971:6), necessitated partitioning the sample into males and females. We tested the validity of using Guenther's (1970) maximum root length measurement for determining sex of bears in a sample. We compared measurements he reported (males = 48-60 mm females = 37-49 mm with measurements of teeth in our sample that were accompanied by a reproductive tract and thus of known sex. Of these comparisons ($N = 61$), 95.1 percent agreed; the 3 comparisons that disagreed were of teeth accompanied by male reproductive organs but were determined to be those of females by canine root measurement. These samples may have been incorrectly packaged by cooperators, because the maximum root measurement of each (36.0, 34.3, and 43.5 mm) was less than the minimum measurements for males; these bears were 20, 13, and 3 years old, respectively.

Sex was determined for bears represented by teeth in the collection on the basis of the maximum canine root measurement. If the bear was represented in the collection by only an incisor or premolar, or the canine root was shattered or not closed, sex was determined by the following criteria in this order: (1) the reproductive organs that accompanied the tooth, (2) sex recorded by the sportsman or taxidermist, (3) sex reported on questionnaires. Seventy-three teeth, however, either did not have closed canine roots or their maximum root measurements were in the area where measurements for the 2 sexes overlapped and other criteria for determining sex of these bears were not available. Of these teeth, 46 (63 percent) were those of nonreproducing (see below) 1- and 2-year-olds; 11 (15 percent) were from 3-year-olds; and the remainder (22 percent) were from bears 4 years old or older. These 73 bears were apportioned as to sex on the basis of the proportions of males and females already in the respective age-classes.

Because collections of samples from game animals are frequently provided by hunters, and possibly subject to active and inactive biases, we compared sex as based on canine root measurements with hunter reports in an effort to determine where biases occurred and how large they were. Sex of bears as recorded by taxidermists and individual sportsmen ($N = 61$) agreed with our determinations of the bears' sex 80.3 percent of the time. We found, however, only a 75 percent agreement between sex of bears as reported on questionnaires and our determinations; 80 percent of these discrepancies involved females recorded as males. Hunters taking part in damage control programs were requested either to collect teeth from both sexes but only female reproductive organs or to collect teeth and reproductive organs from both sexes. Of the teeth from the first collecting scheme (not accompanied by reproductive tracts, $N = 28$), only 60.7 percent of the reports of sex of bears by hunters agreed with our determinations. All disagreements were of bears recorded as males by hunters but classified as females by canine root measurement. Damage control hunters that were requested to collect only female reproductive organs but teeth from both sexes presumably recorded a female bear as a male if they had lost or failed to collect the reproductive organs. The sex of bears recorded by hunters requested to collect reproductive organs and teeth from both sexes agreed 95 percent of the time with our determinations of sex, which suggests a 5 percent error in marking and packaging such samples.

Age Composition of Sample

Because we found no significant difference in the frequencies of 1- and 2-year-olds and older bears among the 2 samples from control programs and the sample from the sport-hunting seasons ($P > 0.05$, $X^2 = 1.39$, df = 2), the 3 subsamples were combined (Table 3). Cubs and yearlings (1-year-olds) combined represented 21 percent, and older bears 79 percent, of the total sample. Analysis of the questionnaires indicated that cubs and yearlings combined made up 36 percent and adults 64 percent of the annual harvest. On the assumption that hunters tended to report cubs as yearlings and yearlings as older bears (adults), but not older bears as cubs or yearlings, the difference between the number of cubs and yearlings in our sample and the number actually harvested, as indicated by questionnaire analysis, may have been even greater than the difference indicated.

For their proportion in the sample to equal the proportion they constituted in the annual harvest (questionnaire), 124 additional bears were required in the cub and yearling age-classes combined. We considered the addition of 124 bears to our sample as a conservative correction of the sample to make it more representative of the annual kill in the cub and yearling age-classes. These 124 bears were distributed equally (31) among the male cub, female cub, male yearling, and female yearling segments of the sample (Table 3).

Reproduction and Recruitment Rates

Age at first breeding, frequency of litters, and litter size are basic reproductive parameters that influence the reproductive potential of a population. Each of these appears variable for the black bear among regions of North America. Female black bears were observed to breed at 3 years of age by Erickson and Nellor (1964), Poelker and Hartwell (1973), and Lindzey and

Table 3. Time-specific life tables for 250 male and 248 female black bears killed in Oregon, 1971-74, and survival rates for males and females combined. Sample data were entered in the d_x column.

Age in years	Males					Females					Males + females	
		d_x	l_x	s_x			d_x	l_x	s_x		s_x	
0	12	43[a]	312	0.862		12	43[a]	310	0.861		0.862	0.785[b]
1	48	79[a]	269	0.706		32	63[a]	267	0.764		0.735	
2		51	190	0.732			33	204	0.838		0.787	
3		36	139	0.741			36	171	0.790		0.768	
4		18	103	0.825			19	135	0.859		0.845	
5		18	85	0.788			19	116	0.836		0.816	
6		18	67	0.731			16	97	0.835		0.793	
7		9	49	0.816			16	81	0.803		0.801	
8		9	40	0.775			11	65	0.831		0.810	
9		7	31	0.774			5	54	0.907		0.859	
10		7	24	0.708			13	49	0.735		0.726	
11		4	17	0.765			6	36	0.833		0.811	
12		3	13	0.769			7	30	0.767		0.767	
13		4	10	0.600	0.772[c]		7	23	0.696	0.811[c]	0.667	0.791[c]
14		1	6	0.833			6	16	0.625		0.682	
15		0	5	1.000			2	10	0.800		0.867	
16		1	5	0.800			2	8	0.750		0.769	
17		0	4	1.000			2	6	0.667		0.800	
18		1	4	0.750			0	4	1.000		0.880	
19		0	3	1.000			1	4	0.750		0.857	
20		0	3	1.000			0	3	1.000		1.000	
21		0	3	1.000			1	3	0.667		0.833	
22		2	3	0.333			1	2	0.500		0.400	
23		1	1	0.000			0	1	1.000		0.500	
24							0	1	1.000		1.000	
25							0	1	1.000		1.000	
26							0	1	1.000		1.000	
27							1	1	0.000		0.000	
Total		312					310					
			$s = 0.775$[d]					$s = 0.818$[d]			$s = 0.798$[d]	

[a] Corrected values to account for bias in the sample (see text).

[b] Survival rate if deaths of orphaned cubs are included (see text).

[c] Average annual survival rate of bears 5 years old and older.

[d] Average annual survival rate.

Meslow (1977), but Stickley (1961) observed a female that bred as a 2-year-old, and Jonkel and Cowan (1971) observed no females younger than 4.5 years of age in estrus or females younger than 6.5-7.5 years of age with cubs. Although female black bears have the potential of producing cubs biennially after their first litter, this frequency may not be realized. Jonkel and Cowan (1971) observed 9 adult females that did not have litters for 3 consecutive years. Size of litters may vary between 1 and 6 cubs (Rowan 1945).

Corpora lutea, mature follicles, and placental scars have been used as estimators of ovulation rates and conception rates, respectively. Erickson and Nellor (1964:34) concluded that it was unlikely that paracorpora lutea or accessory copora lutea would be included in corpora lutea counts, suggesting that counts of corpora lutea should indicate numbers of ova shed. They futher concluded that both ova loss and intrauterine mortality of embryos and fetuses were low. The counts of corpora lutea should provide a relatively unbiased estimate of primary production (cubs born). Jonkel and Cowan (1971) concluded that counts of mature follicles could overestimate ovulation rate. This conclusion was based on finding both atretic and mature follicles and corpora lutea in the ovaries of 2 female bears. The presence of mature follicles may, however, be used as an indicator of sexual maturity of that female, and the frequency of females with mature follicles can indicate the timing of the breeding season.

Erickson and Nellor (1964:23) used counts of placental scars as indicators of conception rates. They found no bear in which the count of recent placental scars was fewer than the young known to have been produced by the female. Hensel et al. (1969:364) found, however, evidence of placental scar disappearance in brown bears (*U. arctos*). They were unable to identify placental scars in the uteri of 2 females killed 8 and 21 months postpartum, whereas scars were obvious in the uteri of 4 females killed 4-15 months postpartum. Although placental scars are valid indicators of previous pregnancies, and, with bears pregnant only once, are valid indicators of the size of the one litter, we feel that the absence of dark placental scars should be cautiously interpreted as indicating that the bears were not pregnant in the preceding 2 years.

Between 1972 and 1974, we collected reproductive tracts from 77 female black bears; about 70 percent of these came from the northwest part of the state. We found no mature follicles (≥ 8 mm, Poelker and Hartwell 1973:77) in ovaries of bears killed before 14 June or after 19 July, or corpora lutea in ovaries of bears killed before 22 July. The peak frequency of occurrence of mature follicles in ovaries was during the first week in July. The youngest bears in which we observed corpora lutea or mature follicles were 3-year-olds, suggesting that females may breed first as 3-year-olds but not before. The average number of corpora lutea in ovary pairs of pregnant females (n = 17) was 2.18. This average is below that found in Michigan (2.42, Erickson and Nellor 1964:37) but above the average in western Washington (1.9, Poelker and Hartwell 1973:83) and Montana (1.8, Jonkel and Cowan 1971:27). The average number of corpora lutea per ovary pair was 1.21 in all females 3 years old and older collected after 21 July. All 5-year-old females except 1 had placental scars in their uteri, suggesting that most, if not all, 5-year-old females had been pregnant either as 3- or 4-year-olds. Ovary pairs of the 2 4-year-old females in our collection contained either corpora lutea or mature follicles, indicating that they had or would have bred as 4-year-olds. Uteri of neither of these females, however, contained placental scars to indicate that they had bred as 3-year-olds. Placental scars in these females would have had to persist only 5 and 6 months (parturition occurs about 1 January).

If all female black bears breed either as 3- or 4-year-olds, then the number of 4-year-olds that bred is indicative of 3-year-olds that did not breed. In our sample, we found that a minimum of 22.2 percent (2 of 9) of 3-year-old females did not breed. If we assume that the presence of follicles greater than 4 mm in size (maximum follicle size of bears younger than 3 years) in ovaries of females collected after 12 May (earliest date 4-mm follicles were observed) indicated that a bear would have bred that breeding season, 1 of 7 3-year-olds (14.3 percent) did not breed. The inclusion of a female with follicles only 4.5 mm when collected on 19 June as a nonbreeder would, however, increase the percentage of nonbreeding 3-year-olds to a minimum of 28.6 percent. If the criterion of follicle size is applied to 5-year-olds, 2 (28.6 percent) would not have bred, presumably because they bred as 4-year-olds. The average of the 4 estimates of the percentage of 3-year-old females that did not breed was 23.4

Litter size of 3- or 4-year-old females appeared smaller than that of older females. The average number of placental scars in 5-year-old females, produced by the 1 previous pregnancy, was 1.14. Mean number of corpora lutea per ovary pair was 2.29 in pregnant females 5 years of age and older. The average ovulation rate of all 5-year-old and older females collected after 22 July (15) was 1.07; 47 percent of these females had ovulated. Ransom (1967:118) found yearling white-tailed deer does to have significantly lower ovulation rates than older does. Provost (1958:47) concluded that beavers (*Castor canadensis*) had smaller litters during the first and second years of their reproductive life than later.

Reproductive rate of females 5 years of age and older, based on corpora lutea counts, was 1.07 cubs per female. Younger females, however, bred either as 3- or 4-year-olds and produced an average of 1.14 cubs. Reproductive rates for these age-classes, apportioned on the basis of the frequency of females breeding in each age-class (76.6 percent for 3-year-olds and 23.4 percent for 4-year-olds), were 0.97 and 0.27, respectively.

Although females with cubs were not protected during the term of the study, our experience indicated that many hunters would not shoot females with cubs. Thus, because we relied on hunters to collect reproductive tracts, pregnant females may have been over-represented in the sample, resulting in overestimation of reproductive rates. We received reproductive tracts from only 2 4-year-olds, the age-class that presumably would include the largest percentage of females with young, while receiving 9 from 3-year-olds and 7 from 5-year-olds. Behavioral traits that may contribute to differing vulnerability of females with and without cubs would similarly bias the determination of percentage of females breeding and therefore bias estimates of total production.

Survival Rates

The time-specific or vertical life table was used to calculate survival rates. The assumptions of stable age distribution and stationary population size were made in the absence of quantitative data to the contrary. We assumed our sample to be a representative sample of ages at death, and thus entered it in the d_x column (Table 3). Implicit in the assumption that this hunter-killed sample represented frequencies of ages at death is that bears dying of other causes die in the same frequency with respect to age-classes. We feel that this assumption was probably not met in the 0 (cub) age-class but was valid for older-aged bears. Natural mortality (mortatlity other than hunter-caused) is difficult to estimate in a hunted population. Lindzey and Meslow (1977), however, observed no natural mortality of bears older than 1 year on an island in southwestern Washington where bears were hunted with bow and arrow. Compensatory mechanisms probably act to decrease natural mortality in a hunted population. We feel that hunting — sport hunting, and damage control hunting combined — is the dominant cause of death of bears older than 1 year in Oregon. Also, we have no reason to suspect that natural mortality would be different from hunter-induced mortality as it affects bears older than 1 year.

Jonkel and Cowan (1971:31, 40) estimated survival rates of black bears between 0.5 and 1.5 years of age as 95 percent when research and hunting mortalities were excluded but as 86 percent when deaths by these causes were included. They estimated an annual survival rate of adults of 86 percent from bears marked as adults or subadults and observed later, and an average annual survival rate of 77.5 percent for the entire population, which included subadults; hunting and handling mortalities were also excluded when these survival rates were calculated. Kemp (1972:30) estimated black bear survival rates in an unexploited population in Alberta, based on a trap-retrap program, to be 73.3 percent, 63.3 percent, and 62.5 percent for cubs, 1-year-olds, and 2-year-old bears, respectively; the average annual adult (over 3 years) survival rate was 87.5 percent. In Michigan, Erickson and Petrides (1964:66) estimated maximum annual survival rates of tagged cubs, yearlings, and older bears of 74, 96, and 79 percent, respectively, and a maximum annual survival rate for the population of 81 percent. Tags returned after the bears had been killed either as nuisances or during the sport-hunting season provided the basis for these calculations. Poelker and Hartwell (1973:129) estimated annual average survival to be between 82 and 85 percent for a tagged sample of black bears killed in Washington.

The average annual survival rate for the population of bears that we sampled was 79.8 percent (Table 3). Survival rates for 2- and 3-year-old bears were 78.7 percent and 76.8 percent, respectively; the average annual survival rate for bears 5 years and older was 79.1 percent. We feel that the survival rate for cubs (86.2 percent) may be an overestimate. Cubs are probably subjected to greater natural mortality, not compensated for by hunting mortality, than older bears and thus the sample of cubs that we collected was probably not proportional to the total deaths of cubs incurred from all causes of mortality. Although Erickson (1959) observed that some cubs orphaned at 6 months of age may live up to 117 days and that 1 cub abandoned at 7.5 months survived for a year, many orphaned cubs undoubtedly die. If we assume that half of the cubs orphaned when their mothers were killed died and were, therefore, not present as 1-year-olds on the next anniversary date (1 April), then cubs produced ($\Sigma y_x = 640$) were exposed to one-half the age-specific mortality rate of their mothers ($y_x \cdot 1 - s_x \cdot 0.5$). For the purpose of this calculation, survival rates were assumed equal for females with and without cubs. We considered these deaths ($N = 60$) additive to those previously accounted for and included them in the d_x entry of age-class 0 (Table 3). Accounting for deaths of orphaned cubs in this manner resulted in a reduction of survival rates for the cub age-class to 0.785.

Survival of females in age-classes 1-5 was significantly higher ($P < 0.05$, $X^2 = 10.19$, df = 1) than that of males in these same age-classes (Table 3). Survival did not differ significantly, however, between the sexes ($P > 0.05$, $X^2 = 1.51$, df = 1) in bears 6 years old and older.

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HABITAT UTILIZATION BY BLACK BEARS IN NORTHERN CALIFORNIA

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Abstract: A study was conducted during May-September 1974 as an integral part of a comprehensive population analysis of black bears (*Ursus americanus* Pallas) in Trinity County, California, by the California Department of Fish and Game. Habitat types on the study area were delineated and evaluated, and the selection and use of each type by black bears were estimated from all fresh bear sign encountered during trapping and radiotracking activities. Scats were collected and analyzed for frequency of occurrence and percentage volume of food items. Bear sign in wet meadows accounted for 55 percent of all sign found during May although wet meadows comprised less than 1 percent of the study area. Mixed conifer forest received heavy bear use during all periods except late August, when bears foraged for insects in decayed logs and stumps in high-elevation partial cuts. Black bears used manzanita (*Arctostaphylos* spp.) brush habitats extensively during late summer and fall to feed on manzanita berries. A failure of the manzanita berry crop in 1973 was believed to have caused a higher rate of subadult mortality and a lower rate of cub production in 1974.

Current land-use decisions in northern California are being made with little concern for black bears. Increasingly intensive silvicultural practices are disrupting black bear habitat — sometimes critical habitat. Few studies have dealt specifically with habitat use by black bears. Jonkel and Cowan (1971) measured habitat selection by relative trapping success in various habitat types in Montana. In western Oregon, McCollum (1973) based his investigation of habitat selection by black bears on tracks and other bear sign. Amstrup and Beecham (1976) studied habitat relationships of black bears in Idaho, and Poelker and Hartwell (1973) investigated the effects of sapwood and cambium feeding by black bears on commercial timber production in western Washington.

Objectives of this study were to delineate and quantitatively describe the habitat types in an area currently supporting a high density of black bears and to determine, by month, their selection and use of each type. Field work extended from May to late September 1974, with incidental observations being made well into November. This investigation was part of a more comprehensive black bear population study conducted by the California Department of Fish and Game (Kelleyhouse 1975).

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STUDY AREA

This study was conducted in a 192-km^2 area in Trinity County, California (Fig. 1). The area is bounded by the Stuart Fork of the Trinity River on the west, the East Fork of the Stuart Fork on the east, the Trinity Alps Wilderness Area on the north, and Lewiston Lake on the south. To expedite field work and data analyses, the study area was separated by Claire Engle Lake into the 83-km^2 Stuart Fork Unit and the 109-km^2 Buckeye-Lewiston Unit (Figs. 2, 3).

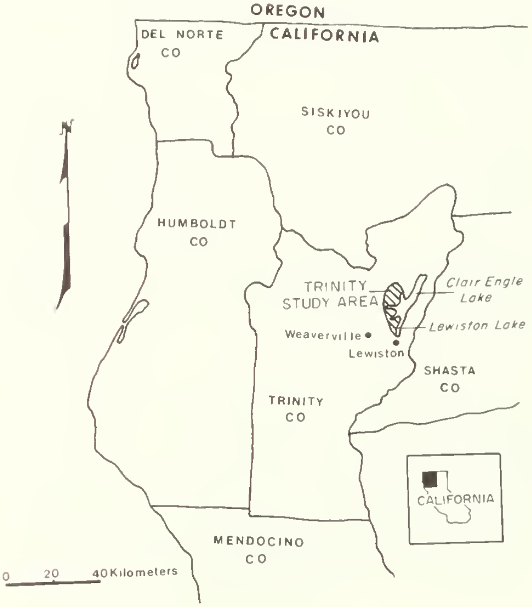

Fig. 1. Map showing location of the study area in Trinity County, northern California.

Topography in the area is generally steep and rugged. Elevations range from 579 m at Lewiston Lake to 2,466 m at Granite Peak. The Stuart Fork Unit has many small streams; the Buckeye-Lewiston Unit has fewer streams and is more arid. The area is characterized by hot, dry summers and cold, wet winters. Mean monthly temperatures in Weaverville, 20 km south of the study area, ranged from 44 C in July to

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Fig. 2. Habitat types on the Stuart Fork Unit of the study area in Trinity County, northern California.

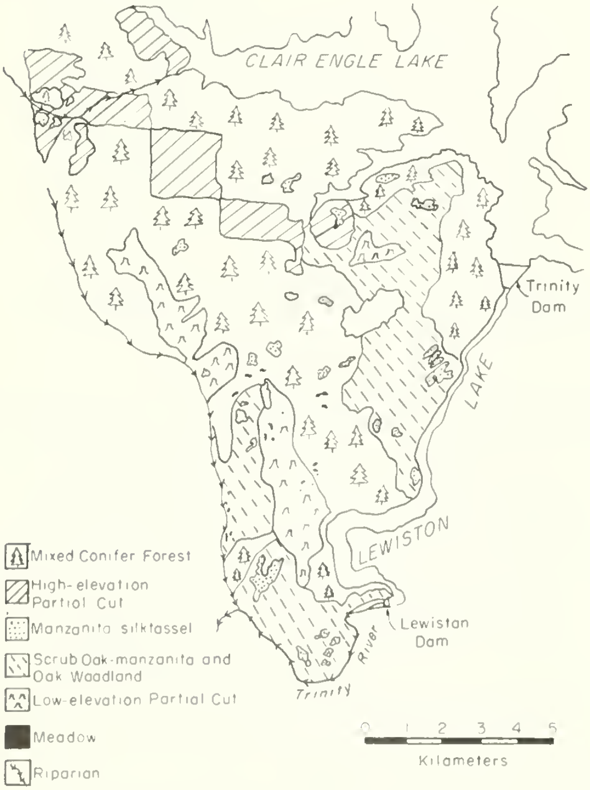

Fig. 3. Habitat types on the Buckeye-Lewiston Unit of the study area in Trinity County, northern California.

−23 C in January. Temperatures at higher elevations were lower.

The Upper Sonoran, the Transition, and the Canadian life zones (Merriam 1898) are represented on the study area. Much of the lower-elevation Buckeye-Lewiston Unit is typified by extensive stands of chaparral and by oak (*Quercus* spp.) woodlands that yield to mixed conifer forests of Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) at middle elevations. The higher elevations are sparsely forested with red fir (*Abies magnifica* var. *shastensis*). Montane chaparral occurs in avalanche zones above 1,676 m (Ferlatte 1970).

METHODS

Types of vegetation on the study area were delineated with the aid of high-altitude, infrared photographs obtained from the National Aeronautics and Space Administration. The relative area occupied by each vegetation type was estimated with a planimeter. Vegetation in 8 of the habitat types discernible on the photographs was sampled using 5 random 30.5-m transects in each type. Each transect had 20 randomly selected 0.09-m^2 quadrats that were used to estimate the percentage of canopy cover of all plants with stems less than 5.1 cm dbh (diameter at breast height). A 0.08-ha circular plot was sampled on each transect to gather data on species composition and density and to estimate the percentage of canopy cover for woody species measuring 5.1 cm or greater dbh.

Seasonal food habits of black bears were determined from scats collected during 1972, 1973, and 1974. Food items present in each scat were recorded and frequencies calculated. Scats collected in 1973 and 1974 were subjected, by month, to a volume analysis for food items.

The selection and use of each habitat type by black bears was estimated from all fresh bear sign (1-3 days old) encountered during each month, May-September 1974. Habitat selection is expressed as the percentage of bear sign found in each of 9 habitat types sampled by month. Habitat use was determined from 69 sets of tracks, 35 radiolocations, 13 sightings, 52 feeding sites, and 106 scats.

If a food item available in only 1 habitat type was identified in a scat found in another habitat type, the scat was counted as use of both habitats. Evidence of bear use was recorded as use of 2 or more habitat types if found on an ecotone or within 30.5 m of adjacent habitat types. This situation commonly occurred in small wet meadows and manzanita patches. If sign was found in a restricted habitat type surrounded by forest, it was recorded as use of that type and of the surrounding forest type.

Frequent travel on the numerous roads and trails in the study area during trapping and radiotracking activities provided a relatively uniform coverage of the area. Statistical analysis of habitat selection by black bears in relation to the amount of area occupied by each habitat type was considered inappropriate because data collection was not of a random or systematic design.

Information on the parameters and social organization of the black bear population was obtained through intensive livetrapping and radiotelemetry. Both techniques, as used during this study' were discussed by Kelleyhouse (1975) and Piekielek and Burton (1975).

RESULTS AND DISCUSSION

Description of Habitats and Their Use by Black Bears

Eleven habitat types were identified on the Trinity study area. Two of the types, red fir forest and montane chaparral, were not included in the study because of their inaccessibility. Ferlatte (1970) has described the vegetation of these 2 types. Red fir forest was mapped as mixed conifer forest because of the difficulty of differentiation (Fig. 2). Vegetation in dry meadows was not sampled because bear use of this habitat type was not detected.

Habitat components suspected of being important to black bears are mentioned in text. The lengthy tables resulting from analyses of vegetation and food habits were presented by Kelleyhouse (1975).

Meadows. — Both dry and wet meadows were found on the study area and were widely distributed although they covered less than 1 percent of the area (Figs. 2, 3). Wet meadows occurred at middle elevations (900 m) in the Stuart Fork Unit and ranged in size from 0.05 to 20.20 ha. Grasses and forbs (*Bromus, Carex, Equisetum, Festuca, Juncus, Poa, Trifolium,* and others) covered 59 percent of the wet meadows sampled.

Fifty-five percent of all bear sign encountered during May and 18 percent encountered during June was found in wet meadows (Fig. 4). Grasses and forbs comprised 52 percent and 48 percent, respectively, of the May 1974 diet and 52 percent and 22 percent of the June 1974 diet. This intensive use of wet meadows as a feeding habitat by black bears in spring is probably the result of the abundant herbaceous forage available in meadows at this time of year. Through intensive trapping and radiotelemetry, an old adult male, an adult female, a 4-year-old male, and a 2-year-old female were all known to use the same 0.8-ha wet meadow during June.

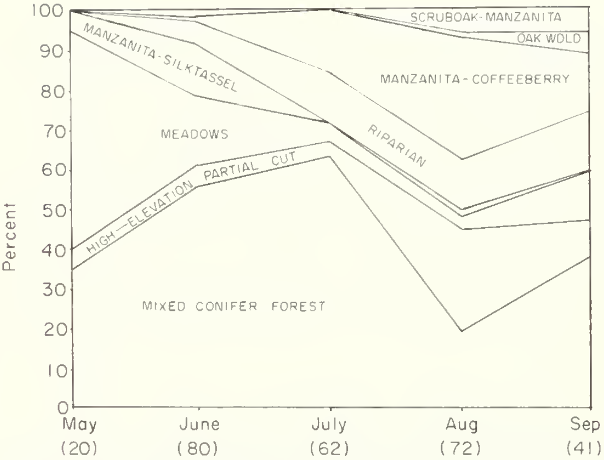

Fig. 4. Proportion of bear sign found in specified habitats on the study area in Trinity County, northern California, 1974. Monthly sample sizes are shown in parentheses.

Use of wet meadows by black bears declined as grasses and forbs desiccated during late June. Reports from Forest service personnel indicated that many bears then moved to higher elevations, apparently in response to later maturation of plants at those altitudes. Mountain meadows provided palatable grasses and forbs well into July.

Some wet meadows at middle elevations contained small ponds that bears used for wallowing. Sign of wallowing accounted for much of the bear use recorded in wet meadows from July through September (Fig. 4).

Because wet meadows are relatively scarce and are obviously favored as a feeding habitat during May and June, they may constitute a seasonally critical habitat for black bears in this area.

Riparian Areas.— Riparian habitat covered less than 1 percent of the study area (Fig. 2). Most of it was found in the Stuart Fork Unit. The lower-elevation Buckeye-Lewiston Unit, with fewer creeks, had fewer riparian areas (Fig. 3). The extent and species compostion of riparian habitat varied with the width of the associated watercourse.

Tree species common to riparian habitat and listed according to their abundance were Douglas-fir, alder (*Alnus* spp.), Pacific dogwood (*Cornus nuttallii*), and Pacific yew (*Taxus brevifolia*). Tree density was 440 trees/ha, and estimated canopy cover was 41 percent.

Riparian areas associated with the larger streams supported a rich understory of creek dogwood *(Cornus sessilis),* California hazel *(Corylus cornuta* var. *californica),* and various species of *Rubus* and willows *(Salix* spp.). Grasses and forbs covered 19 percent of the ground. A run of king salmon *(Oncorhynchus,* *tschawytscha)* congregated at the base of the Lewiston Dam on the Trinity River in late September and early October during each year of study.

Riparian areas were used by black bears as feeding habitat and travel lanes from June through September (Fig. 4). Although grasses and forbs in most middle-elevation wet meadows had desicated by mid-June, herbaceous forage in shaded riparian areas remained palatable and was eaten by bears well into July. Similarly, Tisch (1961) reported that creek bottoms in Montana provided black bears with important herbaceous foods in summer.

Creek dogwood was an important food plant in riparian areas. Creek dogwood berries were taken by black bears during August and September of all years, but were taken in greater quantities during 1973 because of a failure of the manzanita berry crop throughout the area.

Some adult male bears, including 1 radiocollared animal, moved as far as 17.7 km during the last week of September to feed on king salmon spawning below Lewiston Dam. Few scats containing fish were found, however, because the bears bedded away from the river and presumably defecated in that vicinity.

Well-defined bear trails in most riparian areas indicated extensive use of this habitat type as cover while traveling. Black bears may also use streams for thermoregulation during periods of heat stress. On 2 occasions, black bears recovering from the effects of drugging immersed themselves in shaded streams, presumably to reduce body temperature. One recently used muddy bathing hole was found in a small creek outside of the study area when the temperature was approximately 40C.

Mixed Conifer Forest.— Mixed conifer forest covered approximately 30 percent of the study area (Figs. 2, 3.). Tree density on sample plots was 906 trees/ha, and estimated canopy cover was 68 percent. Common tree species listed in order of abundance were Douglas-fir, California black oak *(Quercus kelloggii)*, and ponderosa pine. Golden chinquapin *(Castanopsis chrysophylla)* and Pacific dogwood were the most common species of shrubs in the sparse understory.

Logs and stumps in various stages of decay covered 8 percent of the ground. Ants (Formicidae), other insects, and their larvae living in these logs and stumps were eaten by bears. Leaves, twigs, and acorns from Oregon white oak *(Q. garryana)* and California black oak covered 50 percent of the ground, indicating that acorns were readily available to bears.

Black bears made considerable use of mixed conifer forest during all periods except late August (Fig. 4). Bears used this habitat for traveling, resting, and escape cover during all months and as feeding habitat during July-early August (insects) and October-November (acorns). No evidence of sapwood or cambium feeding was noted such as that reported in western Washington by Poelker and Hartwell (1973).

Most bear sign was encountered near ecotones of mixed conifer forest with wet meadows, manzanita brush fields, and high-elevation partial cuts. McCollum (1973) found concentrations of bear sign near ecotones of mixed conifer forest with other habitat types in southwestern Oregon. All bear beds found in mixed conifer forest were within 30.5 m of a potential seasonal food source that was usually located in a different habitat type such as a meadow or berry patch.

Although no dens were inspected on the study area, nearly all dens found in surrounding areas were in mixed conifer forest. One exception, reported by a logger, was a den located in the base of a Douglas-fir in an older high-elevation partial cut in the Stuart Fork Unit. Bear sign found soon after bears emerged from their dens indicated that most black bears probably denned in mixed conifer forest.

Partial Cuts.— An estimated 40-50 percent of the study area had been logged since 1950, creating a mosaic of seral vegetation types (Piekielek and Burton 1975). Selective logging resulted in 2 types of partial cuts: low-elevation cuts (below 762 m) and, on more mesic sites, high-elevation cuts (above 762 m) (Figs. 2. 3).

Low-elevation partial cuts had 741 trees/ha, and estimated canopy cover was 49 percent. The understory lacked species diversity. No bear use of this habitat type was noted.

Mean tree density in high-elevation partial cuts 3-9 years old was 583 trees/ha; estimated canopy cover was 44 percent. The sparse understory included Pacific dogwood, California hazel, and wild rose (*Rosa* sp.). Logs and stumps covered 18 percent of the ground.

Bear use of high-evelation partial cuts was relatively high only during August, when increased foraging by bears in logs and stumps was noted. August was the only month during which this habitat type received more use than the mixed conifer forest (Fig. 4).

Berry-producing plants and herbaceous plants known to be used by bears were not abundant in partial cuts on the study area, although such species commonly occur on clearcut areas in southwestern Oregon (McCollum 1973). Observed differences in secondary plant succession between the 2 areas are probably caused by environmental factors rather than silvicultural practices. The lack of vegetative food sources for bears after disturbance of timbered sites in the study area may be typical of other arid areas in California. If so, extensive logging in such areas probably has at least a short-term (1-10 years) adverse impact on black bear populations.

High-elevation partial cuts 15-25 years old resembled mixed conifer forest and were used by bears in essentially the same ways. All recently logged areas were avoided by bears. Jonkel and Cowan (1971) also noted that black bears made little use of recently logged areas, whereas bear use of a 10-year-old logged area was essentially the same as that of the surrounding spruce (*Picea* sp.)-fir (*Abies* sp.) forest. McCollum (1973) reported that the incidence of bear sign in clearcuts decreased dramatically beyond 183 m from cover.

Manzanita Brush Types.— Three manzanita brush types covering an estimated 36 percent of the study area and occurring at elevations of 579 m to 1,676 m were identified and mapped. The manzanita-coffeeberry (*Rhamnus californicus*) type, with 348 trees/ha and an estimated canopy cover of 15 percent, provided more cover than either of the other brush types. This habitat was located in the western one-third of the Stuart Fork Unit at elevations of 760 to 1,520 m (Fig. 2). The manzanita-silktassel (*Garrya* sp.) type occurred in small patches in both study units at mid-elevations (Figs. 2, 3). The scrub oak (*Q. dumosa*) - manzanita type was located at elevations below 600 m in the eastern portion of the Buckeye-Lewiston Unit (Fig. 3). Oaks in this habitat type were canyon live oak (*Q. chrysolepis*), scrub oak, and Oregon white oak.

Black bears in the study area depend heavily upon manzanita berries as a staple food during late summer and fall. Manzanita-silktassel habitat was also used during early summer, when black bears were observed to eat unripened manzanita berries (Fig. 4). Manzanita-coffeeberry habitat appeared to be the most frequently used of the manzanita brush types (Fig. 4). The scrub oak-manzanita habitat sustained some bear use as adult males began moving into the lower elevations of the Buckeye-Lewiston Unit during September (Fig. 4). Black bears in many other regions of the West depend upon various species of *Vaccinium* for a late-summer and fall staple food (Jonkel and Cowan 1971, Poelker and Hartwell 1973).

Analysis of scats collected during 1972 and 1974 indicated a high incidence of manzanita berries in summer and fall scats. Manzanita berries were present in 97 percent (1972) and 83 percent (1974) of the August scats and in 96 percent and 57 percent of the September scats. Manzanita berry production was greatly reduced after the extremely low temperatures and light snow pack of the winter of 1972-73. Leaf galls were present on most manzanita plants during the following summer. Manzanita berries occurred in only 33 percent of the scats collected during August 1973; creek dogwood and coffeeberries occurred in 50 and 67 percent of the scats, respectively.

Oak Woodland.— The oak woodland habitat type covered approximately 5 percent of the total study area but was found only in the Buckeye-Lewiston Unit. Because oak woodland and scrub oak-manzanita habitats were found in close association, they were combined on the habitat map (Fig. 3). Oregon white oak, the most abundant tree species, occurred in dense stands of 764 trees/ha. Estimated canopy cover was 33 percent. The understory was sparse, but oak litter covered 63 percent of the ground. Acorns began dropping during early September in 1974. Bear use of oak woodlands increased thereafter (Fig. 4). Use of oak woodlands by bears was highest where fingers of mixed conifer forest extended into the woodlands, thus providing escape cover in close proximity to food. Bears continued to feed in oak woodland habitat until denning.

In summary, black bears in the study area selected wet meadows in May and June shortly after emerging from dens. Bears then moved into riparian areas and high mountain meadows in late June to feed on palatable herbaceous plants. Mixed conifer forest then received its share of use when bears sought insects in decayed logs and stumps. This type was also used as traveling cover throughout the year. High-elevation partial cuts were used by bears for a brief period in August in their quest for insects. Manzanita brush habitats provided the bulk of early-fall staple food until acorns became available in late September in oak woodland and mixed conifer forest. Most bears then presumably denned in mixed conifer forest habitat.

Parameters of the Bear Population and Home Range Use

A total of 70 black bears were captured during the population study. All resident bears and most transient bears using the study area were believed to have been captured (Kelleyhouse 1975). Estimates of population density in the Stuart Fork Unit ranged from 0.8 bear/km^2 in 1972 (Piekielek and Burton 1975) to 0.4 bear/km^2 in 1974 (Kelleyhouse 1975).

The sex ratio of captured bears (43 males, 27 females) differed significantly from an even ratio at the

0.05 level. The preponderance of males may be explained by longer mean movements and larger home ranges than those of females or by a slightly uneven sex ratio. The mean summer home range size for 4 adult males was 10.6 km^2; summer home range size for 6 adult females averaged 3.6 km^2.

The study area was considered a complete ecological unit for black bears because of its large size, altitudinal extremes, and habitat diversity and interspersion. The more mesic Stuart Fork Unit supported high numbers of black bears throughout the year. The Buckeye-Lewiston Unit served primarily as a fall foraging area for adult male bears that moved long distances to feed on seasonally abundant salmon, manzanita berries, and acorns (Piekielek and Burton 1975). Stickley (1961) and Erickson and Petrides (1964) reported similar fall movements by black bears in the East.

Summer home ranges of sows on the study area may actually represent annual home ranges since no sows were killed by hunters or observed outside of their summer ranges. Summer home ranges of adult sows were located at elevations of 760 m to 1,680 in the Stuart Fork Unit. Sows selected home ranges with extreme habitat diversity; all ranges included wet meadows, riparian areas, mixed conifer forest, and at least 1 of the manzanita brush types within a relatively small area. Theoretically, habitat diversity within the home range favors cub survival by reducing the length of foraging expeditions during the cubs' first year of life.

The summer home ranges of adult male bears 4 years old or older were larger than those of sows. Some males had separate fall home ranges connected to their summer ranges by a migratory corridor similar to that described for grizzlies (*Ursus arctos*) by Craighead and Craighead (1972). This arrangement allows males to take advantage of widely spaced sources of seasonal foods (such as king salmon and manzanita berries) and may actually allow more males than females to occupy an area.

Transient subadult bears 1-3 years old made frequent movements in the study area, although there is evidence suggesting that some subadult females may coinhabit their sow's home range through the second year of life. When food is scarce and the population of resident adult bears is relatively dense, intolerance by adults may force subadults to use suboptimal habitat. Skinner (1952), Jonkel (1962), and Erickson (1965) have reported various degrees of intraspecific intolerance among black bears. Two subadult bears were captured repeatedly in seasonally suboptimal habitat types. A 2-year-old male remained near a desiccated meadow for 1 week in late June after adult bears had left the area, and a 3-year-old female remained in an area of mixed conifer forest after resident adults had moved to patches of manzanita-coffeeberry in late August to feed on ripening berries.

Reported fluctuations in black bear numbers can perhaps be explained by differential mortality of subadults. Transient subadults constituted a large but variable portion of the black bear population. They comprised 39 percent of all bears captured during 1973, after the good manzanita berry crop in 1972, but only 22 percent the next year, after the poor berry crop of 1973.

The failure of the manzanita berry crop in 1973 coincided with reduced survival of cubs born in 1973 and was followed by reduced production or early survival of cubs in 1974. No yearling bears were captured or observed on the study area during 1974, suggesting high mortality of cubs born in 1973, and only 1 set of cubs was known to be on the study area during 1974. The manzanita berry crop was estimated to have been highest in 1972, lowest in 1973, and intermediate in 1974. Jonkel and Cowan (1971) reported a similar relationship between huckleberry (*Vaccinium* spp.) crops and black bear reproduction in Montana. Hence, it appears that major food shortages are linked to low cub production or survival and high subadult mortality, resulting in low subadult to adult ratios in black bear populations. Successive failures of manzanita berry crops could therefore decrease population size by affecting only subadult survival.

CONCLUSION

Bray and Barnes (1967) noted that forested habitat is a common denominator in all descriptions of black bear habitat. However, the logging industry is placing ever-increasing demands upon the mixed conifer forests in northern California. Despite the extensive cutting of mixed conifer forest on the study area during the past 20 years, logging continues at an accelerated rate. In this study, recently logged areas were found to be of only limited seasonal value to bears whereas mixed conifer forest habitat was used continually. I therefore believe that the bear population in this area is likely to be adversely affected by large-scale logging operations.

Another habitat type being lost to logging and logging road construction is wet meadow habitat. It is noteworthy that sow home ranges were located in an elevational belt that included all the wet meadows in the study area but were absent in the low-elevation Buckeye-Lewiston Unit where all major habitats except wet meadows were represented. This important habitat type could be protected and its use by bears ensured by leaving a buffer zone of timber around each meadow and by locating new roads and log landings a reasonable distance from meadows.

Construction of new logging roads and continued maintenance of existing roads results in ready access to black bear habitat. Hunting black bears with hounds is a popular sport in northern California, but extensive forest road systems may allow this hunting method to become too efficient. The potential for overharvest is a real problem. Although main forest roads must be maintained for fire control, many of the spur roads and skid trails should be gated or bermed. Bears now have ample escape cover in the region, but true refuge cover is rapidly being lost through expansion of forest road systems.

A recent development near the study area is the conversion of manzanita-silktassel habitat to monotypic ponderosa pine plantations. If this stand conversion proves successful and is later accepted for large-scale operations, the further loss of important habitat will be certain to affect resident bears adversely.

Reducing the harvest of black bears after failures of the manzanita berry crop seems a reasonable way of compensating for the adverse effects of poor berry crops on production and survival of young. Although black bears are difficult to census on an annual basis, berry production can be gauged and bear management made more responsive, particularly in heavily hunted areas.

Successful management of black bears in California requires cooperation between land and wildlife managers in the recognition and conservation of the various habitat types necessary to meet all seasonal needs of black bears. In addition agreements must be reached to protect black bears from overharvest by regulating access to bear habitat.

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THE BROWN BEAR IN POLAND

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Abstract: In early times, the brown bear (*Ursus arctos* L.) was preserved by law for royal hunts and occurred in large numbers in the extensive forests of Poland. From the 16th century on, its destruction became increasingly intensive, and by the end of World War I, only a few bears were left. Full legal protection was given the bear in 1952. Attempts to reintroduce the bear into the Białowieża Primeval Forest were halted by World War II. At present, there is a western population (Tatra Mountains) and an eastern population (western Bieszczady Mountains) in Poland. Their combined numbers are estimated to be about 30, with a density of 0.02-0.33 animals per 1,000 ha. Because of increasing human activities and interference in the bear's range, preservation of the bear populations will soon require the establishment of extensive and less disturbed areas in which the brown bear can live in comparative security.

HISTORICAL REVIEW

The brown bear was considered as big game from early historical times in Poland and was preserved by law for royal hunts. There are records of such hunts in old chronicles: Anonim tzw. Gall, 1112 (third edition, 1968) and Wincenty Kadłubek, living at the end of the 12th and beginning of the 13th century, and Marcin Bielski's chronicle of 1551 (cited after Forelle and Szuszkiewiczowa 1976). Illegal killing of bears was treated as a serious offense as late as the 13th century.

Owners of forest lands, foresters, peasants, and gatherers of wild honey, suffering damage, killed bears despite the fact that legal hunting was reserved for kings and nobles. Some bears were killed by poachers. The bear must once have been a common animal in extensive forests, since early accounts tell us that knights ''wore a bear on their armour, whole skins with stuffed heads and paws set as ornaments in silver or gold'' (Łoziński 1879).

With the passage of time the bear, being intensively hunted and killed, became an increasingly rare species. It was first exterminated in the west and central parts of Poland. In the mid-1800s, it was fairly often encountered in Lithuania and in the south of Galicia but was heavily hunted. The bear was considered a harmful animal, and bear hunts took place without any restraint or limitation. Young bears were caught and handed over to the famed Smorgonska academy and other ''bear schools,'' where inhumane methods (fire and iron) were used to teach them to perform.

Immediately after World War I, there were few brown bears in Poland, although their numbers increased slightly later on. The animals lived mainly in areas of the eastern Carpathians, where their numbers were calculated to be about 200 (Burzyński 1931).

In the 1930s, the number of brown bears in Poland was estimated (overestimated, in some opinions) at 275 animals. They occurred in 3 groups: (1) eastern Carpathians, 256; (2) Polesie region, 15; and (3) Tatra Mountains, 15-20 in the entire region and 4 transients (passing in and out of Poland) (Anonymous 1935a, b; Wodzicki 1935). This level was probably maintained up to the 1940s. Directly after World War II, the number of bears within the new boundaries of Poland was estimated at about 10-14. They persisted only in the Tatra and Bieszczady mountains. In the latter, their numbers during the 1960s were estimated as 25 (Kosiba 1964). Later data show that the number of bears in these regions decreased from 36 in 1970 to 28 in 1974 (Central Statistical Office 1975).

PROTECTION

In view of the diminishing number of bears, the need for their protection was first mentioned in the second half of the 19th century. In 1927, a decree was passed regulating bear hunts, establishing a long closed season, and forbidding the shooting of female bears (Couturier 1954).

In May 1934, the Małopolski Hunting Society formed a Bear Preservation Section that applied for changes in the permitted hunting seasons and methods: forbidding (1) shooting in midwinter, (2) using carrion to attract bears during hunts, and (3) attacking bears in their winter dens. The suggestion was made that shooting should be permitted only in very limited cases (Wodzicki 1935). During this period a plan was formed for reintroducing the bear into the Vilnius region, using animals caught in the Polesie region (Anonymous 1935c).

Not until after World War II was the brown bear in Poland given protection throughout the whole year, and shortly afterwards the bear was included in the list of animals protected by law (Orders of the Ministry of Forestry, dated 22 March 1949 and 3 November 1952, respectively).

REINTRODUCTION ATTEMPTS

The brown bear was exterminated in the second half of the 19th century in the Białowieża Primeval Forest (lat. 59°29′ N to 52°57′ N; long. 23°31′ E to 24°21′E; about 1,250 km^2). In 1937, authorities of the State Forests Administration decided to reintroduce the brown bear into this area.

Two methods of reintroduction were used: (1) releasing young brown bears brought from Byelorussia, and (2) placing in the forest a pregnant female in a cage equipped with a sleeping compartment and bars sufficiently far apart to allow the young bears to leave the cage and grow up under natural conditions. The results of these experiments are summarized in Table 1.

Table 1. Summary of data on reintroductions and numbers of brown bears in the Białowieża Primeval Forest during 1937-47.

Period	Origin of animals	Number and sex of animals	Fate of animals
30 April 1938	Release of young bears (method 1)	4 (2 M+2 F)	1 F killed; 1 F+1 M recaptured, sent to zoo; 1 M remained free.
3 August 1938	Release of young bears (method 1)	3 (1 M+2 F)	1 F recaptured, sent to zoo; remaining 2 disappeared without trace, probably killed.
Summer 1938	Young born in forest, left in freedom (method 2)	2 (1 M+1 F)	Wintered in forest; in spring 1939 occasionally visited place of birth.
1939-44	Adults introduced or released from cages	2	Bears aggressive, caused 2 or 3 human fatalities; shot.
—	Others, probably originating from earlier reintroductions	3	Remained free; probably reproduced.
1945	Free-living	4 (1 M+1 F, ad; 2 juv)	1 juv illegally killed.
1946	Next offspring of adult pair	5	1 small bear illegally killed.
1947	——	1	Tracks only.
1963	Migration from Byelorussia?	1	Tracks only.

The first method proved unsuccessful. Of the 7 young animals released (none was more than 1.5 years old), only 1 male survived. The remainder were soon either killed by poachers or had to be recaptured when they began leaving the forest and came into conflict with the local population — either begging for food or stealing it, and entering buildings. The people themselves behaved thoughtlessly, as they tried to attract the young bears and fed them.

The second method proved more effective. In the summer of 1937, a warden's hut was set up in the Białowieża National Park, and a cage containing a pregnant female bear taken from Poznań Zoo was a distance of about 200 m from the hut. Except for the 2 keepers that supervised and fed the animals and made observations, the bears were allowed no contact with humans.

Two young were born in January 1938 (Table 1), which were wild and avoided humans. At the end of April they began to leave the cage — at first slipping easily between the bars. As the young bears grew larger, the bars were purposely bent apart to permit easy movement between them. At first, the 2 young bears returned to the cage for the night but by autumn they were completely independent. The bent bars of the cage were straightened and the young bears remained free. They appeared only sporadically near the cage in the spring of placed at 1939 (Karpiński 1947, 1949).

During the German occupation, 2 other adult bears were released from cages into the Białowieża Primeval Forest, but they attacked humans, killing 2 or 3 persons and seriously injuring another. These bears were then shot. Directly after World War II, there were probably 4 bears in the Białowieża Forest: an adult male and female with 2 young. Soon after this observation, 1 of the young bears was killed by poachers. The 3 animals were occasionally seen, and offspring were again recorded in 1946; the next illegal shooting of a young bear also occurred that year. In March 1947, the tracks of only a single large bear were found on the remains of snow. The bears had either been killed or had wandered into

Byelorussian territory. The last tracks of a bear in the Białowieza Forest were seen in May 1963 (Table 1).

Although the experiments made by Karpiński (1949) did not result in a permanent population of the brown bear in the Białowieża Primeval Forest, they represented a successful attempt to introduce a large predator into the forests of Central Europe.

CURRENT STATUS OF THE BROWN BEAR IN POLAND

A total of 29 detailed questionnaires were sent out in the autumn of 1976 to all administrative units of the state forests in the Carpathians and their foothills, and 28 replies were received. Twenty units reported the presence of bears, either permanent residents or transients. For the period 1973-76, 17 of these reports were confirmed by visual observations of the animals or their tracks. Brown bears live permanently and reproduce in the area of the western Bieszczady Mountains, the most southeasterly area of the Polish Carpathians (Buchalczyk and Markowski 1979); and in the Tatra Mountains. They also have permanent retreats in the Babia Góra Mountains. The western population (Tatra Mountains and the western part of the Carpathians) connects with the compact range of this species in Czechoslovakia, and the eastern population (Western Bieszczady Mountains) possibly comes into contact with the population living in the Ukraine. The brown bear also occurs, probably only as a migrant, in the Beskid Sądecki Mountains and the Beskid Niski Mountains (Fig. 1).

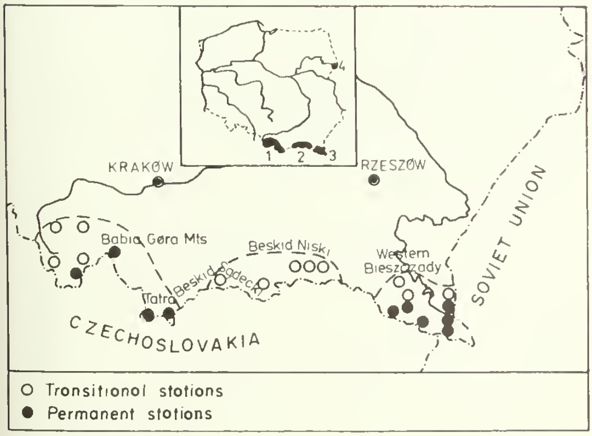

Fig. 1. Distribution of the brown bear in Poland (1976). 1. Western population, including Babia Gora Mountains and Tatra Mountains. 2. Transitional stations of the brown bear, including Beskid Sadecki Mountains and Deskid Niski Mountains. 3. Eastern population, western Bieszczady Mountains. 4. Białowieża Primeval Forest (historical data only).

It has been estimated that about 30 brown bears live within Polish territory (Table 2). This estimate is based on the minimum numbers of bears (not possible maximums) reported in the questionnaires for adjacent areas and takes into account the brown bear's tendency towards lengthy movements and the more extensive and widely separated regions involved. This number is smaller than that recorded for 1970 and indicates a decrease in the numbers of these predators. In the Bieszczady Mountains, the largest retreat, only 5-6 young bears were reported, according to the questionnaire data. Sumiński (1976) states that at present there are 10 brown bears living in the Tatra Mountains and 25 in the Bieszczady Mountains.

Table 2. Current status of the brown bear in Poland, according to data from questionnaires, November 1976. Density is calculated from probable number of animals.

Region	Numerical estimates		Density per 1,000 ha
	Probable	Maximum	
Most westerly part of Polish Carpathians and Babia Góra Mts.	3	5	0.06
Tatra National Park	7	10	0.33
Beskid Sądecki Mts. and Beskid Niski Mts.	2	4	0.02
West Bieszczady Mts.	18	27	0.05-0.17 0.12
Total	30	46	0.09

The density of the brown bear in Poland varies from 0.02 to 0.33 per 1,000 ha. It is highest in the area of Tatra National Park, where the bear occurs over a relatively small area. In general, however, numbers are smaller than in Czechoslovakia.

DISCUSSION

In Central Europe the brown bear occurs in the greatest numbers in Rumania. Owing to state protection and limited shooting, its numbers rose from about 1,000 animals in 1940 to about 3,500 in 1964. Density varies from 0.6 to 1.8 per 1,000 ha (Almašan and Vasiliu 1967).

In Czechoslovakia the bear occurs only in Slovakia, with a density of 0.1-0.9 animals per 1,000 ha, and occupies the 42 larger forested areas with the greatest variety of vegetation of the 64 areas examined. The animals thus already occupy most of the areas currently available for them. At present, their spontaneous decrease in numbers in certain ecosystems clearly points to their ecological requirements, and this guideline may serve as a starting point when defining habitats suitable for their successful reintroduction (Nováková et al. 1969).

In Byelorussia the brown bear occupied extensive areas in the central and northeast parts of the country at the beginning of the present century. During the period 1915-25, there was a considerable decrease in the numbers of this species, representing a decrease in the index of the bear's occurrence in 7 districts of the Byelorussian Republic and its complete disappearance in 3 other districts. According to data from the Nature Conservation Committee on the Byelorussian SSR in 1960, there were 81 bears in Byelorussia, where bears are now a protected species (serzhanin 1961).

The brown bear, if not persecuted, may accustom itself to coexistence with humans and continue to live in large forested areas where some cultivation takes place. Nevertheless, increased tourist traffic and intensified human interference have a deleterious effect upon these animals. A bear driven from its den during winter does not resume its sleep for a long time, and when a mother bear is driven from her den, the young freeze to death (Slobodyan and Gutzulyak 1976).

Apart from known single cases of exceptional tameness and lack of aggressiveness (Onegov 1976, Slobodyan and Gutzulyak 1976), the brown bear is disturbed by heavy tourist traffic (in Poland in the Tatra and Bieszczady Mountains) and by excessive and increasing interference in forests. Therefore, the relatively limited areas of the Polish national parks will not long suffice to sustain brown bears, and, consequently, additional suitable retreats will have to be created for them. Extensive areas with only limited forestry activities would be favorable to continuing settlement by brown bears, as these animals could then establish permanent winter dens there, obtain food, and bring up their young in peace.

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BEAR MANAGEMENT AND SHEEP HUSBANDRY IN NORWAY, WITH A DISCUSSION OF PREDATORY BEHAVIOR SIGNIFICANT FOR EVALUATION OF LIVESTOCK LOSSES

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Abstract: During the 19th century the brown bear (*Ursus arctos*) population in Norway was reduced to remnant level. The population has since been restored and recently seems to be increasing. Concern is present for bear management in connection with sheep predation, as sheep husbandry is important throughout Norway, the stock in 1976 amounting to 1.6 million animals. The management technique now practiced combines selective hunting of troublemakers with monetary compensation for sheep killed.

The number of sheep killed by bears is insignificant compared with the total sheep mortality, and bear predation is important only locally, primarily in areas in Hedmark, Hordaland, and Finnmark counties. Ethical arguments against bears are raised in connection with observations of overkill, and a research program has been initiated to analyze predation patterns in greater detail.

Overkill by bears is not restricted to surplus killing. In most cases, small amounts are consumed from each carcass — nutritionally valuable parts such as breast fat deposits and udders. This behavior may represent extreme food selection under plentiful prey conditions and should be compared with selective grazing among herbivores. The organization of behavior in predatory mammals relevant to livestock losses is discussed.

Several grazing techniques and herding systems have been adapted to the Scandinavian forest and mountain ecosystems and are typical of vast areas covered with moraine deposits and mineral soils. During the Middle Ages, highly differentiated chalet systems were already organized in Norway, keeping and rotating herds of grazing animals under the protection of herdsmen far out in wilderness areas.

Predation by the brown bear and other large carnivores represents a traditional conflict in Norway. Bear and sheep may compete for space and plant biomass in outlying grazing areas, and the bear can become an efficient predator on sheep. Large predators have certainly been influential in the development of the chalet culture in Scandinavia; danger of predation was an important consideration when choosing localities for new chalet farms. Reinton (1955), in studies of the chalet culture in Norway, claimed that many chalet barns were originally built equally as defense against bears and as protection from inclement weather. Disproportionately strong doors and locks were distinctive features of such buildings. The practice of allowing animals to graze at night, periodically common on the European continent, was seldom practiced in Scandinava, due, in part, to the danger of predation (Szabó 1970). Some claim that the earlier herding system in Norway was originally developed for the sole purpose of protecting livestock from predators. Most herding of livestock ceased in Norway when the numbers of predators gradually decreased in the outlying grazing areas.

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PRESENT STATUS OF SHEEP FARMING

Commercial sheep husbandry in Norway has remained small in scale, and even today small herds of sheep are kept mostly by individual farmers. Flocks of sheep are introduced without herdsmen into grazing lands, many of which are topographically rough, and most flocks are tended at rather irregular intervals. Total stock figures show the development of sheep farming in Norway from 1940 to 1976 (Fig. 1). During the war the number was kept low and figures ranges

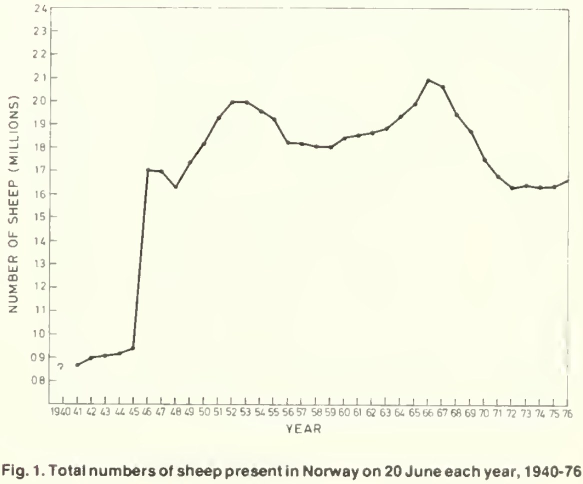

Fig. 1. Total numbers of sheep present in Norway on 20 June each year, 1940-76.

between 0.8 and 1.0 million. Postwar, however, the stock increased to 1.7 million, and since then the number has fluctuated between 1.6 and 2.1 million, with peaks during 1950-55 and 1964-68. In the 1970s, the stock remained at about 1.6 million animals, but is now increasing. The 1976 total was 1,667,488, whereas the 1974 and 1975 figures were 1,632,217 and 1,639,313, respectively, an increase of 2 percent in the latter years.

At present, agricultural experts advocate the economic policy of increasing sheep production in Norway. A prognosis for 1990 predicts 1,993,000 animals. One of the national goals is to reduce the importation of certain meat products and fodder, thus becoming more self-sufficient through better utilization of national resources. There are few ecological or biological arguments against a strategy of self-support, which includes increasing use of local outlying grazing areas above the present level of sheep production.

LOSSES AND COMPENSATIONS

Sheep losses compensated for as bear depredations in Norway during 1966-75 are shown in Table 1. As can be seen, the yearly compensated loss fluctuated between 30 and 240 animals. The losses are presently small in relation to the total sheep stock. Sheep losses are, however, generally restricted to certain small areas, the most important found in Finnmark (Wikan 1970, 1972), Hordaland (Elgmork and Mysterud 1976), and Hedmark (Myrberget 1968; Mysterud 1974, 1975a, 1975b) counties. Some losses also occur in Oppland and Buskerud (Elgmork 1976b), Sør Trøndelag, Nordland, and Troms counties. Economic compensation, which does not represent actual market value, is awarded for sheep that can be documented as killed by bears. Fig. 2 gives some examples of calculated prices per sheep for ewes killed in Hedmark county in recent years.

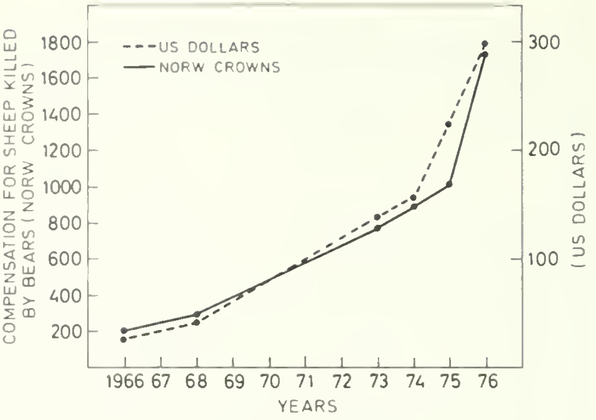

Fig. 2. Economic compensation awarded per sheep for ewes killed by brown bears in Hedmark County, 1966-76. Amounts given are in Norwegian crowns (solid line). U.S. dollar equivalents (stippled line) are based on current exchange values.

One way to influence sheep producers in a positive direction has thus been to adequately compensate their economic losses. A future strategy could be to increase this compensation to profit level.

STATUS OF THE BEAR POPULATIONS

From an original population consisting of several thousand animals, the brown bear was relentlessly shot in Norway during the 18th and 19th centuries and reduced to a remnant level. The approximate annual kill around 1850 averaged 225 individuals. Hunting statistics indicate a steady population decline from 1850 to 1925 throughout the country (Myrberget 1969). By the beginning of the 20th century, the population had been

Table 1. Numbers of sheep compensated for as being killed by bears, by county, in Norway, 1966-75.

Year	Counties									Total
	Hedmark	Oppland	Buskerud	Hordaland	Sør-Trøndelag	Nord-Trøndelag	Nordland	Troms	Finnmark	
1966	39	4	4	0	190	0	0	0	0	237
1967	12	5	0	0	0	0	0	0	78	95
1968	40	6	0	0	0	0	0	0	122	168
1969	0	0	17	0	0	0	0	0	58	75
1970	0	6	3	0	0	0	0	0	26	35
1971	0	0	18	0	0	0	0	0	51	69
1972	0	0	19	0	32	0	0	0	0	51
1973	63	0	21	0	0	0	0	3	0	87
1974	32	0	0	31	0	0	117	0	0	180
1975	48	5	0	69	0	13	0	0	87	222
Total	234	26	82	100	222	13	117	3	422	1,219

greatly reduced, and between 1920 and 1930 it was at a minimum. In about 1940, Olstad (1945) believed that resident populations were present only in the Vassfaret area in Oppland and Buskerud counties (Elgmork 1976a) and in South-Varanger in Finnmark. However, recent investigations have shown that remnant populations have also survived in other areas (Mysterud 1977). Myrberget (1969) estimated the population at 25-50 animals in 1969, but it must now be roughly estimated at more than 100 individuals. Decreasing trends have changed during the latter half of the 20th century, and the populations now seem to have entered a period of increase. The total number of bears killed has remained at a stable level since 1940; the distribution of the kill by counties is shown in Table 2. Since 1970, 11 bears have been removed from the populations. Methods of removal include legal hunting (3), shooting of stock-killers (4), self-defense killing (1), and poaching (3).

Table 2. Hunting statistics for brown bears in Norway, 1940-76. (Based partly on Myberget 1969.)

Years	Counties										Total
	Hedmark	Oppland	Buskerud	Telemark	Sogn og Fjordane	Sør-Trøndelag	Nord-Trøndelag	Nordland	Troms	Finnmark	
1940-49	2	1	4	1	1	0	2	4	0	1	16
1950-59	4	0	1	0	1	0	2	10	0	5	23
1960-69	5	0	0	0	0	1	1	3	0	11	21
1970-76	2	0	0	0	0	0	1	0	2	6	11
Total	13	1	5	1	2	1	6	17	2	23	71

PROTECTION AND MANAGEMENT OF BEARS

Since 1940, measures to protect the brown bear have been as follows: During 1940-41, the species was protected during the denning period from 1 November to 15 May. During World War II, 1942-45, bears were given total protection. After the war, the protection was removed except for the period 1 November-15 May. In 1966, this protection was extended to 15 June in Troms and Finnmark counties, primarily to prevent hunting with snowscooters (Myrberget 1969). On 28 May 1971, the bear was given total protection in Oppland and Buskerud counties, but not until 11 May 1973 was the species given total protection throughout the country. It is legal, however, to kill bears attacking humans and livestock, regardless of protection laws.

A significant political pressure for removal of bears stills emanates from interests connected with sheep and reindeer (*Rangifer tarandus*) husbandry. The federal wildlife administration is attempting to use selective removal to solve the problem of stock-killers. The technique now being tested includes shooting only troublemakers through ordinary hunting — careful removal of predatory bears at the time and place of the problem, preferably only the individual actually involved. The removal of troublemakers is undertaken by small groups of hunters from the local areas who are paid for their efforts by the federal government. The personnel of each hunting group is selected by the local game management unit and approved by the wildlife administration. The hunters are not professionals, but hunt only when stock-killers appear in their area.

In 1968, 1969, and 1970, permits to remove stock-killers during the protected period prior to 15 June were given to Sør-Varanger municipality, Finnmark County, and 1 bear was shot in 1968. During 1973, total protection was enacted and the first permit to remove a stock-killing bear was issued in Trysil, Hedmark County, where a subadult male was shot (Mysterud 1975b). In 1975, Trysil municipality was given a new permit, but no bear was killed. In 1976, 11 permits to remove 8 different bears were issued in 8 municipalities in Hedmark (8), Sør-Trøndelag (2), and Finnmark (1) counties. Seventeen hunting groups were formed, 2 in municipalities which did not receive permits. One subadult male was shot in Trysil municipality by the collective efforts of the 15 hunting groups that were in operation. Thus, only 3 bears have been removed by authorized hunters during the period 1968-76; this low efficiency has led to a discussion on different bear-hunting techniques. Removal of specific killers is considered the most selective and efficient means of contending with the predator problem (Cain et al. 1972), and it will be important to develop an efficient strategy for future removal of troublemakers. In spite of the acknowledged hazards to livestock, opinion polls, even from counties with the greatest losses of sheep, show that a majority are in favor of preserving a bear population.

SHEEP-KILLING PATTERNS OBSERVED IN BEARS

Much more data are needed from detailed studies of which individual bears develop into stock-killers before we can evaluate the long-term consequences of their removal from the population. Hedmark County, where the bear population has long been notorious for killing sheep and where some damage to sheep flocks is more or less constant (Mysterud 1975a), has been selected for studies, and data on sheep-killing bears have been collected since 1968 (Mysterud 1974, 1975b, unpublished data). The investigations so far have shown that sheep predation incidents in the area can be roughly grouped into 3 categories:

(1) Sheep killed by adult male bears and used as a regular food source by the male and/or associated family group resident on or near sheep grazing pastures.
(2) Sheep killed, often in numbers, by subadult males that have established home ranges on the grazing areas. Such individuals may develop into habitual sheep-killers and troublemakers.
(3) Occasional sheep killed by straggling or transient bears, most often of little significant to the total kill.

Field observation of predation patterns in the study area has shown that the usual pattern of bear predation is that 1 or a few sheep are killed at a time and are either consumed or cached for future consumption. However, situations can arise in the outlying grazing areas where a number of sheep are killed within a relatively limited time and space. In 1 case from Hedmark, 26 of a herd of 28 sheep were killed during 1 night. Other overkill incidents occurred in 1973 and 1976 (Mysterud 1975b, unpublished data). The number of sheep struck down by the predator, in some cases clearly exceeding the immediate or short-term need for prey biomass, and multiple kills and unconsumed carcasses seem to be reported in almost every study of predator losses (Rowley 1970, Henne 1975, Dorrance and Roy 1976, Nesse et al. 1976). Little seems to be known about the biological significance of such killing patterns. This observed phenomenon will therefore be explored and explained in a theoretical discussion of the general organization of mammalian predatory behavior.

SURPLUS KILLING

One well-known type of overkill reported among mammalian predators is surplus killing of prey (Kruuk 1972, Curio 1976). Surplus killing is defined as the behavior of a predator that kills without either itself, its young, or members of its social unit attempting to consume the prey, although they have free access to the carcass and the prey is among their potential food species (Kruuk 1972).

Surplus killing occurs primarily in closed, artificial conditions, for instance when a fox (*Vulpes* sp.) gets into a henhouse or mink *(Mustela vison)* into a hatchery pond. Such events are sometimes described as killing "orgies," a phenomenon exceptionally detrimental to domestic livestock if they have no means of escape (Fox 1971, Nesse et al. 1976). Young and Goldman (1946) mention a case where a puma (*Felis concolor*) entered a sheep pen and, in the course of 1 night, killed 192 sheep. Blocking of escape routes by fences may be an important factor in explaining surplus killing, but it also occurs in unfenced natural ecosystems. The phenomenon applies to mammalian predators in general; under conditions where normal antipredator reactions of the prey are blocked, surplus killing seems to be released. Among bears, several examples of surplus killing have been described for the polar bear (*Ursus maritimus*). Even Nansen (1924) called attention to the fact that polar bears killed far more young seals than they consumed (Lønø 1970). Perry (1966) mentioned 1 case in which a polar bear killed 21 narwhals (*Monedon monoceros*) enclosed by ice in a small pond, and Freeman (1973) reported multiple kills of beluga *(Delphinapterus leveas)* by a solitary bear.

During field investigations into high densities of small rodents, large numbers of lemmings (*Lemmus lemmus*) and other small mammals such as shrews are often bitten to death but left uneaten (Mysterud unpublished data). One attempted explanation of this has been that lemmings, for example, contain substances that make them less coveted as prey (Hagen 1952, Andersson 1976). However, under other conditions, large quantities of lemmings are consumed by the same predator.

During certain winter conditions, prey species may tramp through snowpack while a predator walks upon it. Surface structure of snowpack seems to be extremely important in some predator-prey relationships; and on certain types of crusts, examples are known where brown bears have killed a number of moose (*Alces alces*) (Hellgren 1967, Wikan 1970). However, the carcasses were not left completely uneaten; the predation therefore represents killing pattern no. 2 discussed below.

The caribou-hunting behavior of American Indians and Eskimoes, summarized by Kelsall (1968), may also be explained as surplus killing. During certain incidents, when natives are faced with large numbers of caribou and have plentiful ammunition, they frequently seem to go berserk and fire blindly into the animals until ammunition or caribou are gone (Kelsall 1968:221).

Surplus killing has been assumed to occur only in extremely rare cases (Curio 1976). This is probably a correct assumption when comparing the surplus-kill percentage with the usual consumption killing. When it does occur, however, it may be of quantitative importance to the group or population affected. Dorrance and Roy (1976) have, during their investigations on sheep losses to predators in Alberta, Canada, reported that the probability of predation was lower in confined flocks — those kept in pens or sheds throughout the year — than in free-ranging flocks. But when predation did occur in confined flocks, it was particularly severe. As a result, predation losses were highest in confined flocks and lowest in range flocks. Conclusions concerning the ecological significance of this behavior should therefore not be drawn until field investigations provide information on the frequency of this form of killing.

EXTREME FOOD-SELECTION KILLING

Overkill phenomena other than true surplus killing, where no part of the animal would be eaten (Kruuk 1972), have been observed. Sheep carcasses investigated in most overkill incidents in Hedmark are not without small eating marks (Mysterud unpublished data). In such cases, the breast of the animal is opened in a stereotyped way, and breast fat deposits and/or parts of the udder are removed (Fig. 3). These incidents may represent extreme food selection as defined by Stenseth and Hansson (1977): a selection of small but nutritionally valuable parts of the animal. Such killing is also part of human hunting behavior, exemplified by the killing of caribou by northern Indians for removal of tongues (Kelsall 1968). High sheep density may well represent an ecological situation where individual bears develop optimal eating habits — "grazing" on sheep udders and breast fat deposits. This preference constitutes a combination of high-energy fat storage and udder tissue rich in proteins, minerals, vitamins, etc., and represents a nutritionally balanced intake. If this "organ grazing" constitutes extreme food selection, whole carcasses should not be considered as units when a predator's eating behavior is considered. This eating pattern may be better compared with selective grazing among herbivores that remove specific parts of plants. Field studies of a variety of species show that herbivores usually select plant items so that the net gain of metabolizable energy is maximized, as shown by Stenseth at al. (1977) for the field vole (*Microtus agrestis*). The breadth of the food niche of field voles has been shown to vary with the density and quality of all available food items. With the more extreme organ selection and smaller amount consumed per sheep, a larger number of animals must be killed to meet a bear's food requirements.

Fig. 3. A ewe killed by a raiding bear in Hedmark, southern Norway, 1976, showing the consumption marks typical of extreme food selection on sheep. The bear has cut the hide, exposed the breast, and consumed the fat deposit together with small amounts of udder. Instead of eating more from this carcass, other nearby ewes were killed and the selective eating pattern repeated.

It is not the purpose of this paper to present a detailed model of this behavior, but it is not difficult to theoretically describe such biological phenomena by simple, continuous functions, presented here in 3 steps.

When disregarding certain factors, the average amount consumed from each carcass may be described as a function of sheep population density. The number of animals killed per unit time (z) multiplied by the amount, measured in weight (v), consumed from each carcass satisfied the food requirement of the bear. If this requirement is a rough constant, K, and the prey animals can be regarded as "homogeneous food," then $zv = K$. Hence, $v = \frac{K}{z}$, which expresses a hyperbola. Obviously the homogeneity assumption is an oversimplification, but one might reasonably present the function $v(z)$, shown in Fig. 4.

The number of animals killed per unit time (z) may be assumed to be an increasing function of the sheep population density (x). Such a functional response curve, modified from Holling (1959), is denoted by $z(x)$, and it can have 1 of several forms. In Fig. 5, an arbitrary illustration of such a function is shown. If we

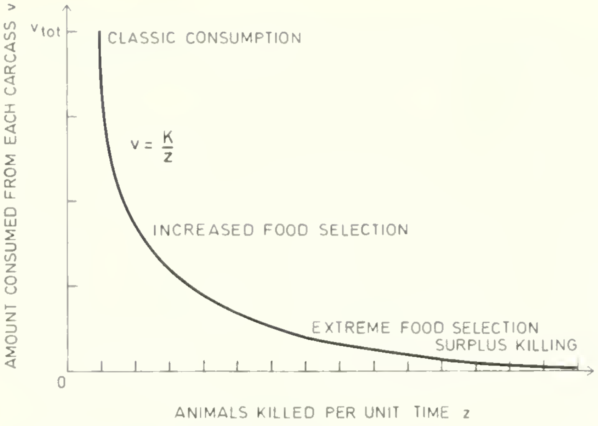

Fig. 4. One basic relationship in predation incidents on sheep is the amount eaten from each carcass (v) as a function of the number of animals killed per unit time (z). The function runs from classic consumption, where 1 animal is killed and completely consumed $(z = 1, v = v_{tot})$, to surplus killing, where many animals are killed which are not consumed $(z \rightarrow \infty, v = 0)$. Between these values, increased selection of prey parts develops with increasing z, a phenomenon denoted as extreme food selection $(z \rightarrow \infty, v \rightarrow 0)$.

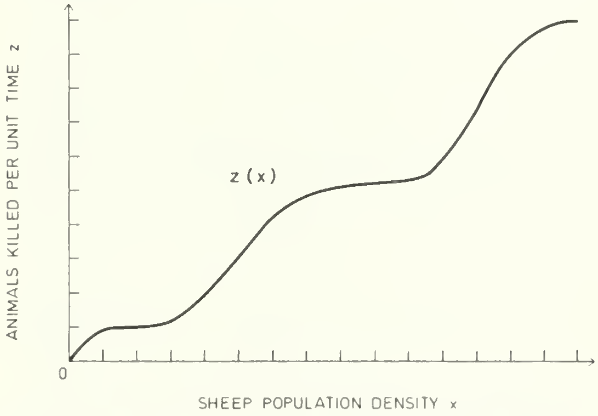

Fig. 5. Functional response curve $z(x)$ for bear-killed sheep, where x denotes sheep population density and z is the number of animals killed per unit time. The function $z(x)$ can have several forms; an arbitrary example is given here.

combine the curves in Figs. 4 and 5, we see that the weight or precentage consumed from each carcass becomes a decreasing function of x (Fig. 6). The higher population density (x) means more animals killed per unit time (z) and a smaller amount (v) eaten from each carcass. This function, denoted by $v(z(x))$, can have several forms, of course; only 1 example is illustrated in Fig. 6. It must be pointed out that the $z(v)$ functions actually depend on several other factors, not included as arguments in the function. Of special interest is the relative ease with which a bear can capture a sheep. This factor perhaps stem from some sort of optimization between the energy required to eat and digest most or all of an animal, compared to the energy expended in capturing an animal. On pastures with high sheep density, bear search, hunt, chase, and capture efforts are, of course, all minimized.

Let us explore in some detail the succession of elements organized as part of the predatory behavior sequence relevant to an understanding of this last statement.

THE PREDATORY BEHAVIOR SEQUENCE

Restricted definitions of the concept of predation in

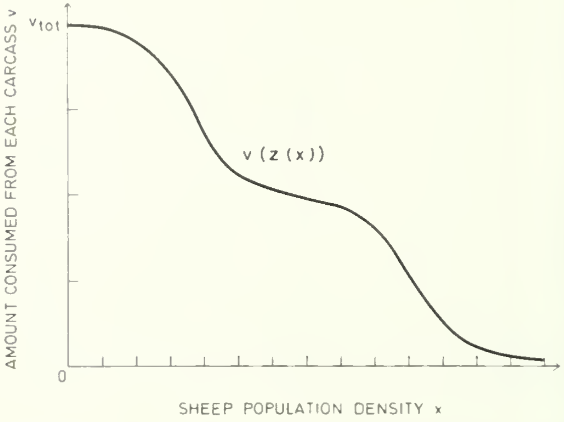

Fig. 6. Amount eaten from each carcass (v) as a function of sheep population density (x). The function is expressed as $v(z(x))$, where z is the number of animals killed per unit time (cfr. Figs. 4, 5). The function $v(z(x))$ can have several forms; only 1 example is given here.

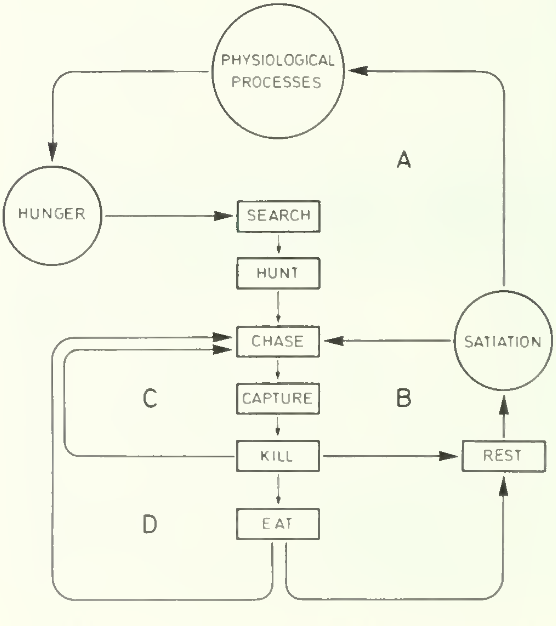

Fig. 7. Organization of specific behavioral patterns associated with predation by large mammals. Loop A describes classic killing-and-consumption predation, B and C surplus killing, and D extreme food-selection killing. All patterns have been observed in areas where brown bears prey on sheep.

most textbooks generally include the killing and eating of animals (Hassel 1976), but Curio (1976) has argued that "eating" should be avoided. Curio (1976:1) defined predation as "a process by which an animal spends some effort to locate a live prey and, in addition, spends another effort to mutilate or kill it." For our purpose it is advantageous to further break down the definition. In the simplified model presented in Fig. 7, separate behavioral elements, each assumed to have its specific threshold motivation, have been identified in the organization of predatory behavior. All of the observed patterns of predation associated with large carnivores can be explained by this model.

Classic killing-and-consumption predation follows the sequence shown in loop A of Fig. 7. *Hunger* provokes *search* for prey, and the *hunt* is then initiated. The predator may locate fresh scent trails (olfactory stimulus), or may hear (auditory stimulus) or sight (visual stimulus) the prey. Different strategies have been developed for approaching or surprising the prey. In certain species, the location of prey culminates in the predator *chasing* the prey in the attempt to capture it. Specific behavior patterns have been developed in all species to *capture, kill,* and *eat* the prey. *Rest* is usually induced or associated with a period of *satiation,* and after assimilation of the food, hunger is again induced. *Search* → *hunt* → *capture* → *kill* → *eat* is thus an idealized and simplified behavior sequence, almost dogmatically described for most mammalian predators. However, Kruuk (1972) has observed in the African wild dog *(Lycaon pictus)* that both satiated and resting animals can be stimulated to hunt anew by the sudden appearance of prey near them. A chase will then release the components *capture* and *kill,* but not necessarily *eat* (Fig. 7, loop B). Thus, chasing seems to be motivated differently from killing and eating (Kruuk 1972). Fox (1971) suggested that the prey-killing response of canids has a very high satiation level and that prey-killing can therefore continue beyond the nutritional needs of an individual simply because the prey is available and vulnerable. However, another study of sheep-killing by coyotes *(Canis latrans)* under captive conditions showed that food deprivation had no descernible effect on the killing behavior but did influence feeding activity on kills. The observations directly suggested that hunger is not always the primary motivation for predatory behavior (Connolly et al. 1976).

During surplus killing incidents, it seems that environmental conditions can release behavior sequences of the type *chase* → *capture* → *kill* → *chase* → *capture* → *kill* → *chase* → . . . (Fig. 7, loop C). In fenced areas and other enclosures, the release of such a sequence may be explained simply by blockage of the normal flight reaction of the prey. The predator becomes linked up in a continual C-loop: As one animal is killed, a new stimulus to chase is immediately received. The stimulation to stop hunting is difficult to isolate (Grant 1972).

Extreme food selection might similarly be described by the sequence *chase* → *capture* → *kill* → *eat* → *chase* → *capture* → . . ., with only small, nutritionally valuable parts eaten after each kill (Fig. 7, loop D).

That one or several behaviors can be smoothly linked together is a matter of efficient adaptation in different species when thresholds are low. Even the *capture* behavior in the model is sometimes observed separately from *killing,* for instance when polar bears play and throw young seals in the air (Perry 1966) or young cats capture mice and play with them without killing them. In some cases, extreme organ selection has been observed on sheep which have not actually been killed (Mysterud unpublished data). The survival of such animals may be explained as shock-bite recoveries (Mysterud 1975b), general shock recoveries, incomplete killing due to human disturbance, incomplete killing behavior by young animals, or eating performed without killing. From purely biological arguments, it is not unlikely that, under certain circumstances, handling of prey animals becomes so easy that a behavioral sequence following a modified D-loop, *chase* → *capture* → *eat* → *chase* . . . (Fig. 7), could develop where there is a net gain of energy by omitting killing. There is also the possibility that prey-killing may have evolved as part of the eating process and that specific killing bites or methods are lacking. Henne (1975) has reported 2 instances in which coyotes fed on sheep before they died, and the same has been observed with coyote predation on mule deer *(Odocoileus hemionus)* (Cahalane 1947) and elk *(Cervus canadensis)* (Robinson 1952). A restricted concept of predation could be used synonymously with killing behavior defined, for instance, as the removal of live prey animals from populations. But even this definition will not be specific, as killing is also an element of intraspecific competition (Curio 1976).

DIFFERENTIAL RATE IN MAMMALIAN PREDATION

The predatory strategies of mammals may be organized so that removal of prey animals can be described at different rates, dependent on environmental factors relating to escape behavior, etc. Consequently, mammalian predator pressures may be far more efficient than supposed from estimates of whole carcass consumption, and the speed at which prey animals are eliminated may be maximized under various circumstances. Naturally this may be of significance in both artificial and natural situations where the population of prey animals is excessive and the number of predators too few to control prey populations through eating procedures. In most situations, stability of prey populations can probably be maintained in part through the pressure exerted by maintaining classic consumption killing. The most important effect of the mechanism of differential rate operating through extreme food-selection and surplus killing may be in systems where a large surplus of cyclic animals regularly must be killed off, which is usually the case in large areas of the northern hemisphere. This mechanism is also important for any population that undergoes irregular fluctuations.

In the construction of models describing predator-prey relationships, differential predation rates of these types will complicate the description of predation efficiency due to erroneous estimates of prey removal drawn from energy arguments, which are most often based on consumption of the whole prey animal. That is, when calculating the needed prey number based on energy and nutritional demand per individual predator and multiplying by the estimated size of the predator population, there is strong evidence that prey removal might be underestimated. From investigations of bears and sheep in Hedmark, it is already clear that such simple evaluations cannot be used in connection with sheep-bear relationships.

WHAT ARE THE FUTURE RESEARCH NEEDS?

In regard to predation and livestock, the only conclusion one can draw from literature is that much more research is needed (Jobman 1972). This discussion proposes that predatory behavior as a strong selective force and control mechanism for surplus population numbers might be more biologically significant than tissue-eating and the associated transfer of matter and energy in ecosystems emphasized in energetic contexts (Cringan and Harris 1972). Predation pressure exerted by large carnivores may be of prime importance in development of role play, space use, and social evolution, in both prey and predator species, expressed by Edmunds (1974:14) as an "armed race" between predator and prey, both of which constantly develop new behavioral patterns involving both gene pools. Prey removal rates in husbandry — differential livestock loss sizes — are an important field of study in evaluation of these evolutionary consequences.

For livestock production it is basic to realize (1) that evolutionary behavioral equilibria in open systems exist before the introduction of flocks of animals whose behavior or social structure is not adapted to the prevailing ecosystem. Sheep and domestic reindeer, the 2 most important rangeland species in Norway, often graze in socially unstructured aggregates and periodically graze within fenced areas, making them highly vulnerable. (2) The majority of domestic animal species have greatly reduced locomotive capacity compared with wild animals. Production of sheep is today guided by commercial aims such as quantity and quality of wool and meat, and natural defense and/or escape mechanisms have been generally bred out in exchange for increased productivity or increased ease of managing the animals (Howard 1974, Klebenow and McAdoo 1976). More detailed knowledge of predator behavior should bring parameters of prey behavior patterns, social structure, locomotor capacity, etc., within the scope of livestock research to minimize losses.

Ecosystem management which aims at maintaining predator and livestock populations within the same space, therefore, needs a knowledge of predator-prey relationships for development of good predator management programs and estimation of optimal livestock densities and tolerable loss sizes. However, an understanding of the predator behavior sequence and livestock removal rates ought to be regarded as of utmost importance, whether we are to introduce more sheep into the habitat of a small bear population or into the habitat of an increasing bear population. At present, these 2 alternatives seem to be the only realistic choices in Norway.

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STATUS OF THE BROWN BEAR IN THE PYRENEES

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Abstract: The population size of the Pyrenean brown bear (*Ursus arctos* L.) has declined from about 200 animals to 20 or even less during the past 40 years. Distribution covered the Pyrenean slopes from the Atlantic to the Mediterranean Sea but is now restricted to an area of about 800 km^2 in the western French Pyrenees. This area includes a national park, which, however, covers only a small portion of the bear's habitat. Thus, the bear is living largely outside the reserve. Forest exploitation and other human activities within the bear's range have been minimal until recently, so the species was able to withstand man's impact. However, a developmental program begun in 1976 will severely deteriorate the mountain landscape and, if allowed to continue, will bring the Pyrenean brown bear to extinction.

As land in central and western Europe has long been heavily utilized and densely populated by man, predators quite early became serious competitors with man. This situation led to almost complete extinction of the larger carnivore species by hunting. Relict populations retreated to remote areas. The more these areas are developed, particularly for tourist activities, the more management problems arise for big game animals. Even if a species has complete legal protection, if often suffers severely from human disturbance and habitat destruction.

The Pyrenean brown bear is a striking example of the problems of predator management in Europe. An extremely limited relict population has retreated to a very restricted range in the western French Pyrenees. Even there, in a rather remote region, the bears are suffering more and more from human interference, particularly from developmental programs. This case study may cast some light on the management needs for larger carnivores in central Europe. However, our knowledge of the Pyrenean brown bears is still fragmentary, and this population will have to be studied much more intensively. Results of such study will also serve management planning for other relict populations of this species in Europe.

FORMER AND PRESENT DISTRIBUTION

In central and western Europe the brown bear has nearly been exterminated. Only 4 relict populations have been able to survive. One of these is in the Cantabrian Mountains of northwestern Spain. The population was believed to comprise 70-100 animals some 15 years ago (Notario 1964). Accurate data have not been obtained recently, but numbers will certainly have decreased markedly since then — if former figures were correct. It is possible that the population may have been overestimated, however.

Until 1930, at least, this Cantabrian population was linked with the Pyrenean bear (Röben 1974), whose distribution is now very restricted (Fig. 1) and may comprise about 20 animals or even less. The population has apparently declined by about 50 since Curry-Lindahl's (1972) report, or the figures cited were too high.

Two relict populations reside in Italy. One, in the Alps (Dolomites) west of Trento (studied by Krott 1962), is unlikely to survive, as it comprises only 6-14 animals (Barigozzi and Barrai 1972). A recent very comprehensive survey by Roth (1976, 1978), however, indicates a stable population of about 10 bears. The second is still a viable population of ostensibly 70-100 bears (Zunino and Herrero 1972) in the Abruzzo Mountains of central Italy near Rome. Despite legal protection, this population is under rather heavy pressure from human activities. Nevertheless, this brown bear population seems to be the most numerous in western Europe.

The Pyrenean brown bear population, formerly occupying most of the Pyrenean chain, was estimated as 150-200 animals (Bourdelle 1937) on the French (northern) slopes and later as 70 animals by Couturier (1954), the distribution still comprising about three-fourths of the Pyrenees, the most easterly region excepted. Today, this brown bear population has dwindled to a few animals in the Basses-Pyrénées district.

PRESENT POPULATION STATUS

Though I am unable at present to prove this figure, the number of Pyrenean brown bears may well have dropped below 20, although offspring have been observed regularly. The principal threat to the species is increasing disturbance caused by intensified forest exploitation and road construction on lower mountain slopes. These activities were unimportant until 1976, when a new wave of development seriously accelerated habitat destruction, particularly in the Aspe Valley. Thus, the national park's buffer zone will be so seriously altered that the bears will have to retreat to higher altitudes, where habitat is far below optimum for this species. The low reproductive rate will then be unable to

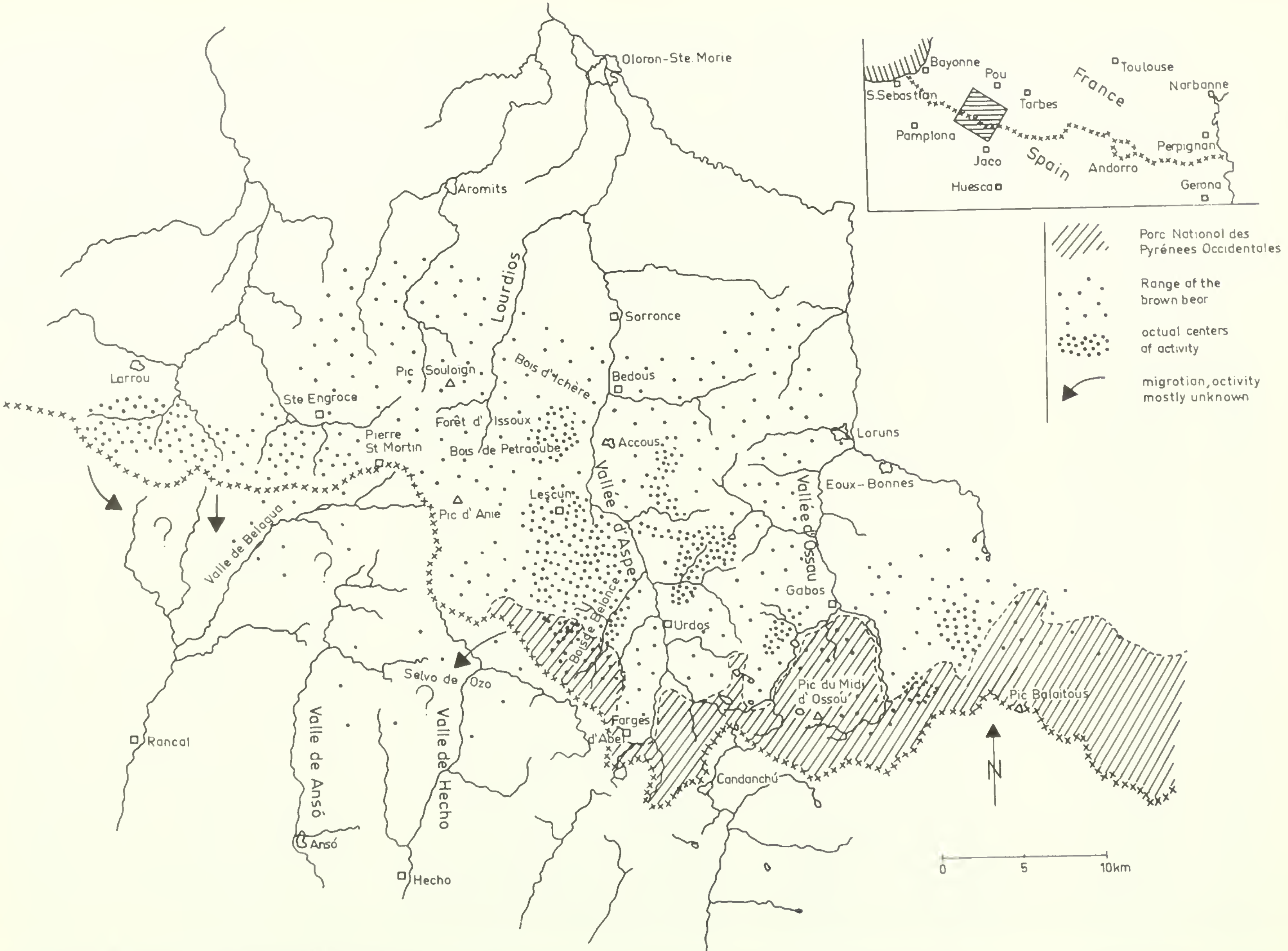

Fig. 1. Present range of the brown bear in the western Pyrenees.

counter further losses by poisoning, which, although infrequent, occurs every year. Finally, it is obvious that the gene pool of the Pyrenean bear is dangerously limited.

HABITAT REQUIREMENTS

Most of the Pyrenean bear's range consists of rather steep slopes covered with meadows or forest. Characteristic trees are beech (*Fagus sylvatica*) and fir (*Abies alba*) and, to a lesser extent, oaks (*Quercus* spp.) and other broad-leaved trees as well as isolated pockets of pine (*Pinus silvestris*). Forest utilization until recently has been negligible, mainly because of the inaccessibility of forested areas and low rental values.

Pyrenean brown bears have become almost nocturnal because of steady human interference. It is mainly the female bears with cubs that are reported active in the daytime (J. Cédet and J.-P. Izans, personal communication). Winter denning usually takes place from November to March, depending somewhat on weather conditions, but bears have been observed outside their dens during periods of mild weather in January. After emergence, the bears occupy relatively limited home ranges at low and medium altitudes until about June or July, when shepherds bring their livestock up into the mountains. The bears then move to higher elevations, and home ranges begin to enlarge. During summer, when shepherds are moving higher into the mountains, the bears seek still higher elevations to avoid disturbance. Finally, towards autumn, bears range over a wide area. To what extent this range includes the southern slopes on the Spanish side of the Pyrenees is largely unknown but appears to be of little importance (Vericad 1970, personal communication 1976).

Though a thorough food habits analysis has not been conducted, one can conclude from the data available (Couturier 1954; Röben, unpublished observations) that the Pyrenean bear is largely herbivorous, possibly not from choice but because animal food is scarce. Big game animals are in short supply — as almost everywhere in France on land not privately owned — because of a hunting system that, during the hunting season, allows anyone who purchases a hunting license to shoot (with some restrictions) anywhere and anything he desires. Thus in the surroundings of the Pyrenean National Park, red deer (*Cervus elaphus*) are extremely rare, and roe deer (*Capreolus capreolus*) not abundant. This fact is very important for the bear, since winter-killed deer (e.g., by avalanches or starvation) could be a staple food item in early spring. Because carrion is absent, the bears are obliged to live mainly on buds, leaves, roots, and bulbs during spring. In summer and autumn, berries are an important food source, particularly the blueberry (*Vaccinium myrtillus*), which as a plentiful fruit for several weeks constitutes almost the entire diet of the bear. As berries ripen at different periods, depending on altitude, the bear profits by migrating gradually from lower to higher elevations.

MANAGEMENT PROBLEMS

Because of man's extremely high population density in western and central Europe, all national parks are established in high-altitude areas where human intrusion is limited by hostile climate. Several threatened species whose habitats should be protected by the creation of parks do not profit greatly from this protection since they are hardly able to survive there. The activity range of the Pyrenean bears is mostly outside the national park's boundaries; only parts of the park can be used by bears (Fig. 1). Though totally protected by law everywhere in France, bears are being disturbed by human activity outside the national park. Thus, a true bear reserve does not exist in Europe.

In early summer, bears start to prey upon livestock, which is then readily available on the mountain meadows (Fig. 2). Their prey is almost exclusively sheep, rarely goats, and occasionally cattle; only once during the past 10 years was a horse reported killed by a bear. Livestock depredations attributed to bears by the shepherds are examined by game wardens and, if verified, compensation is paid by the national park (since 1968) for every lost animal. From 1958 to 1967, amends were made by the Counseil Supérieur de la Chasse (Chimits 1973). Compensation has certainly prevented more intense poaching of bears. The costs of compensation may be about 20,000 to 65,000 French francs ($4,400 to $14,300) per annum. Numbers of depredations have decreased steadily during the past few years (Fig. 3), which may also indicate a further reduction in the bear population.

MANAGEMENT RECOMMENDATIONS

In order to assure the survival of the Pyrenean brown bears, several strict measures must be considered throughout the bears' range:

(1) Road construction in large portions of the Pyrenean bear's habitat is incompatible with preservation of this relict population and must be curtailed.

(2) Forest exploitation must be restricted and should be abandoned wherever possible. The construction of new forest roads, particularly in hitherto undisturbed areas, must not be allowed.

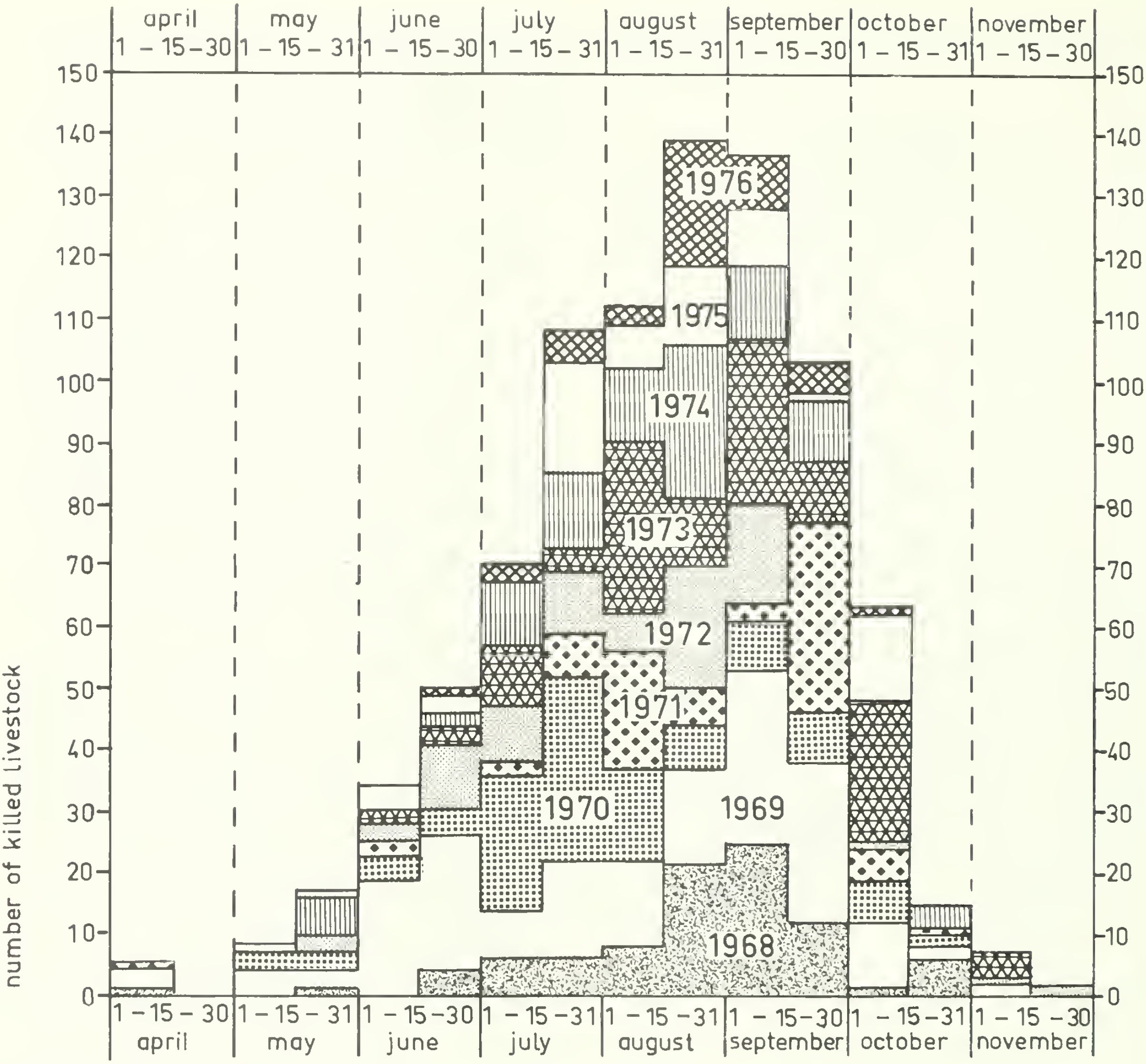

Fig. 2. Number of livestock depredations by Pyrenean brown bears, by month, 1968-76.

(3) Hunting should be prohibited or at least strictly limited everywhere in the brown bear's range. This measure is not only to protect bears from hunting pressure (which occurs even if the bear itself is unhunted) but also to protect and to permit better management of prey species of the bear so that these species can regain normal population densities.

(4) Supplementary feeding with carrion should be undertaken until food conditions have improved for the bear. Feeding sites should be established in inaccessible places for supply by helicopter.

(5) Licenses for the construction of houses outside villages must not be given. Rebuilding of abandoned cottages and farms as weekend homes should be prohibited. The more cottages abandoned, particularly in remote areas, the better for bear preservation.

(6) Pasturelands should no longer be subsidized as in the past. The constantly repeated statement that livestock grazing is necessary to preserve mountain landscape is untrue and objectively wrong. Pasturing could be favored throughout the Pyrenees but it need not be done in the very refuge of the Pyrenean bear.

(7) In particular, grazing activities in woodland habitat should be prohibited. Several forests have been severely affected by cattle, even inside the national park.

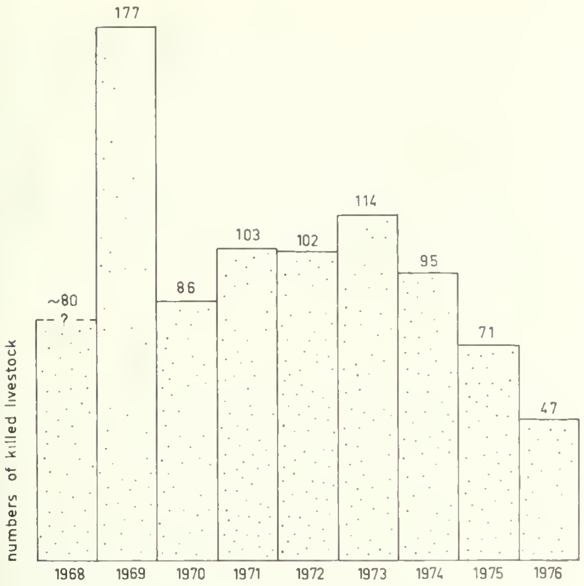

Fig. 3. Number of livestock depredations by Pyrenean brown bears, 1968-76.

(8) Burning of meadows and brush, which is done extensively every spring, should be prohibited within the bear's range.

(9) Compliance with all regulations for the protection of bears must be strictly enforced throughout the area.

(10) In general, the Pyrenean people are very conscious of the need to preserve the bears. However, educational programs should be developed and implemented in areas where these concepts are still poorly understood.

LOOKING FORWARD

Only 2 years ago, the status of the Pyrenean brown bear did not yet seem too unfavorable. However, since then the situation has changed drastically. A recent campaign of development has begun that is rapidly altering forest and pastureland in a largely senseless manner. This situation is not uncommon in Europe, where similar programs are not uncommonly carried out in remote, relatively undisturbed areas for the sake of "progress." In the special case dealt with here, this disastrous imprudence, however, does not only affect a hitherto intact landscape but also the ultimate relict population of the Pyrenean brown bear, which cannot long endure this impact. Any additional disturbance may cause the final vanishing of this bear population, which is already living under minimal conditions. If deterioration of the bear's habitat continues at the present rate, the Pyrenean brown bear will be extinct within the next decade.

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DEFECATION RATES OF CAPTIVE BROWN BEARS[1]

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Abstract: The number of scats dropped by captive European brown bears (*Ursus arctos*) was recorded in all months of the year, 1971-73. An overall total of 3,634 scats was recorded in 1,094 bear-days. Clear seasonal differences were found, with low values of about 2 scats per bear-day from November through June and higher values in the remaining months, and with a distinct peak in August of 7.19 scats per bear-day for adults. Extremes observed ranged from 0 to 11 scats per bear-day. Preliminary data indicate at least a 28 percent higher defecation rate for cubs. Significant ($P < 0.01$) differences were found among individual bears kept under identical conditions. Possible application of these findings to estimation of bear densities or bear use in the wild is discussed.

While studying the last autochthonous brown bears of the Alps (province of Trento, also called Trentino, northern Italy), we were forced by the secretive habits of the animals and the dense cover to use indirect methods to arrive at least at an informed guess of population size and distribution. Since the species apparently does not select special locations for defecation (although exceptions have been noted by Tratz 1963:47f and Ustinov 1974), and because finding droppings depends much less on ground conditions than finding tracks, scats are the best indicators of bear presence. This study was made in the hope that information about defecation rates would enable us to draw direct conclusions from numbers of scat finds.

Pelton (1972) used scat counts to monitor distribution of black bears (*Ursus americanus*), and he cites Spencer (1955) as having used scats to estimate black bear density. In a less quantitative way, scats were used by Lentfer et al. (1969:29) as indicators of relative bear use of various habitats. I am aware neither of others having systematically used scats to document the presence of bears nor of any literature dealing with bear defecation rates, except for a single observation made by Zunino (1971).

Special thanks are given to E. Hänni, Sr., who made most of the daily scat counts.

METHODS AND MATERIALS

Scats were counted daily by zoo keepers cleaning the stables and runs of the captive bears. Since it was often not possible to determine the defecation rates of individual bears, only part of the data could be used in some analyses. All counts were made during 1971-73 and involved 26 different bears (8 adult males, 9 adult females, and 9 cubs). Small proportions of the counts were made in the zoo of Basel (1 male, 3 femals, 1 cub; total of 38 bear-days, all in September) and in a small private zoo near Gossau, Switzerland (3 males; 99 bear-days, September and October). In both places, feeding by the public is prohibited.

Most of the data (from 4 males, 6 females, 8 cubs; 957 bear-days, all months except October) originated from the bear pit of Bern, where the public is encouraged to feed the bears; carrots, feed cubes, and dried figs are sold for this purpose. This bear pit consists of 3 semicircular outdoor compartments and 9 unheated indoor stables. The 2 larger compartments each have a maximum linear dimension of about 23 m and a surface area of roughly 300 m^2; the smaller compartment, about 15 m and 150 m^2.

The adults are kept in pairs (sometimes 1 male with 2 females) except when the females are in late pregnancy or have their cubs (November-December until spring). Being, as a rule, separated from their offspring by mid-May, the females usually breed every year. Each pair normally is kept in an outdoor compartment in the morning or afternoon and in an indoor stable the other half day and the night. The females, usually pregnant, generally remain voluntarily in the stables all winter (mid-November, or December, until April).

On days when visitors are few, additional food is offered so that the animals feed practically *ad libitum* throughout the year. The main diet consists of carrots and supplementary items such as artificial feed cubes (containing fish flour, meat flour, and cereals), dried figs, and old bread and apples. The diet changes little throughout the year.

RESULTS

Defecation rates observed ranged from 0 (or 0.13 for longer periods: 1 female in December had 2 scats in 15 days) to 11 scats per bear-day (10 or 11 scats a day counted 4 times for a male and 8 times for a female in 24 calendar days in August). The overall average was 3.3 (3,634 scats in 1,094 bear-days). This last figure, however, is of little significance, since seasonal varia-

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[1] This paper was prepared with support from the Swiss National Science Foundation (Grant No. 3.566-0.75).

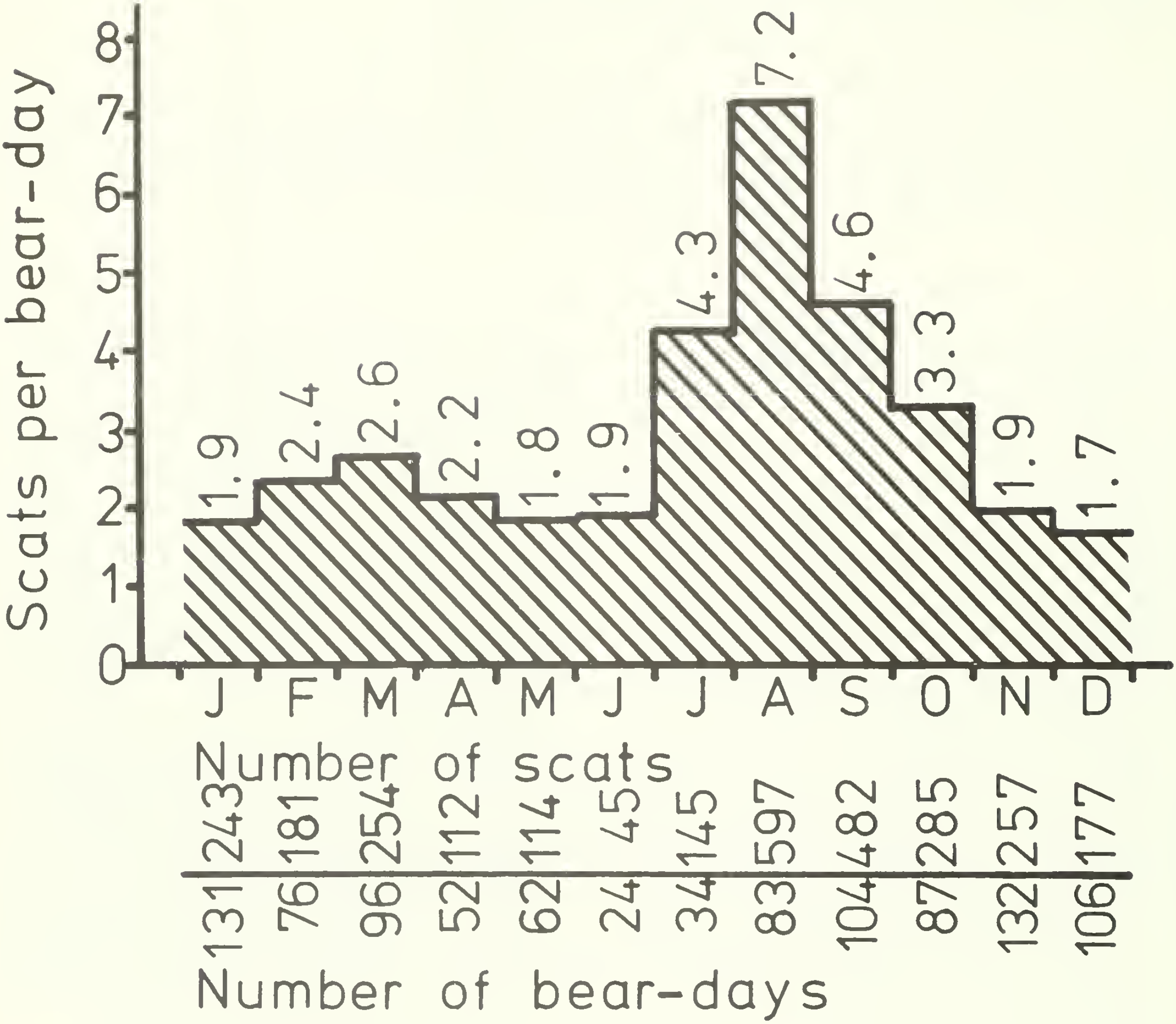

Fig. 1. Seasonal variation of the defecation rate. Counts made for 8 adult males and 8 adult females in 3 different years (1971-73) were combined.

tions were large (Fig. 1). Although the bears eat practically *ad libitum* throughout the year, some doubt arose as to possible influences of visitor frequencies on the defecation rates through intensity of feeding. Figures from the Swiss Federal Bureau of Statistics show that the greatest numbers of tourist-nights and tourist arrivals in Bern occur in August, the time when bear defecation rates are highest. The breakdown of data according to the day of the week (Table 1) shows highest defecation rates on Mondays ("weekend effect" with some time lag; footnote a, Table 1). But this weekly pattern differed seasonally, with no consistent peak in August-November (no data from October), whereas the weekly maximum was usually on Sunday or Monday during January-May. We suspect that the visiting public to some extent stimulates the bears to eat more food than they would otherwise consume, even with unlimited food available.

But increased tourism can explain only a small part of the August peak in defecation rates. The July-August increase in defecation rates amounted to 69 percent (Fig. 1), which is 4.6 times (95 percent confidence interval, 2.8-7.4) as great as the increase in tourist-nights and 3.9 times (2.3-6.3) as great as the increase in tourist arrivals (statistics summed over the years 1971-73 when scats were counted). The difference between the increase in defecation rates and the increase in tourism is highly significant ($P < 0.01$; test

Table 1. Defecation rate of bears of the pit of Bern as a function of the day of the week. Combined data from 18 bears (4 adult males, 6 adult females, and 8 cubs) and from all months except June, July and October (data lacking because year was inadvertently omitted from 2 record sheets).

Day of week	Number of scats[a]	Number of bear-days	Defecation rate
Monday	393	105	3.74
Tuesday	266	89	2.99
Wednesday	231	75	3.08
Thursday	363	106	3.42
Friday	380	108	3.52
Saturday	196	70	2.80
Sunday	202	65	3.11

[a] For technical reasons the afternoon scats of those bears that had to spend the afternoon indoors were recorded as being of the following day.

and confidence limits arbitrarily taking Poisson limits for numbers of scats, tourist-nights, and tourist arrivals, and using procedures given in Roth 1976). The seasonal variations in defecation rates appear to be largely caused by annual physiological cycles still functioning in captive bears living out-of-doors much of the time.

The few counts available from cubs indicate that they have a higher defecation rate than adults. In 11 calendar days in late August and early September, 8 cubs had a rate of 6.9 (608 scats/88 bear-days). In the same period, 7 adults had a rate of 5.4 (415/77, cubs 28 percent higher). Data from the zoo of Basel point to an even larger difference. There, a group of 3 adults produced 92 scats in 21 bear-days in September, a defecation rate of 4.4. A sow-cub group in the same days achieved a rate of 7.6, which is 74 percent higher (107 scats/14 bear-days). This difference is significant ($P < 0.05$, sign test).

Because the bears in Bern are usually kept in pairs, we have few data to clarify differences of defecation rates between the sexes, but from spring through fall, these differences do not seem to be important (Table 2). In winter, however, the pregnant females show a much clearer tendency than males to enter winter dormancy and often refuse food and water for up to 1 month, also after giving birth to cubs (E. Hänni, personal communication). Accordingly, their defecation rate approaches zero (Table 2: Jan. 1973). Also, the temporary decrease in the rate of defecation from April to June (Fig. 1) may be attributable to males and not to females (Table 2). The males show little appetite during the rut (May-June) (E. Hänni, personal communication).

Compared with seasonal variations, small but statistically significant differences among defecation rates of individual bears were found. In August-September 1971, for a group of 5 adults (2 males, 3 females), a defecation rate of 5.0 was determined (302 scats/60 bear-days), whereas for a pair the rate was 6.0 (145/24) over the same days (higher rate for 10 of 12 calendar days, difference significant, $P < 0.05$, sign test). Again, in November, the same pair had a higher value of 2.1 (50/24) than the group of 5 with 1.8 (110/60, difference significant, $P < 0.05$). The figures for single adults (Table 2) substantiate the hypothesis that there are individual differences in defecation rates. Male 1 showed consistently low rates. From January to March, defecation rates of all 4 males increased, but the order from low to high remained M1-M4-M3-M2 in all 3 months. Data for M4 are imcomplete but conform to the pattern. Even small differences seem to be relatively consistent.

Table 2. Comparison of defecation rates (scats/bear-day) of individual adult bears. Number of bear-days is equal to number of calendar days of counting. Figures in parentheses are numbers of scats counted.

Month	Number of bear-days	Bear number						Statistical significance of difference[a]
		Male 1	Male 2	Male 3	Male 4	Female 1	Female 2	
Jan. '72	15	1.1 (16)	2.8 (42)	2.6 (39)	-	-	-	M1 — each of the others**
February	19	1.3 (25)	3.1 (58)	2.8 (54)	2.3 (44)	-	-	M1 — each of the others** M2 — M4**; M3 — M4*
March	24	1.7 (41)	3.2 (76)	3.0 (73)	2.7 (64)	-	-	M1 — each of the others**
April	15	2.2 (33)	-	-	-	1.9 (28)	-	-
May	31	1.5 (46)	-	-	-	2.2 (68)	-	**
June	12	1.3 (15)	-	-	-	-	2.5 (30)	**
July	17	3.5 (60)	-	-	-	-	5.0 (85)	**
August	24	8.0 (192)	-	-	-	8.8 (210)	-	*
September	6	5.2 (31)	-	-	-	5.7 (34)	-	-
November	11	1.9 (21)	-	-	-	2.5 (27)	-	*
December	26	1.5 (39)	-	-	-	1.0 (26)	-	-
Jan. '73	23	1.4 (32)	-	-	-	0.3 (7)	-	**

[a] Sign test, comparing numbers of scats of each day, *$P<0.05$. **$P<0.01$.

APPLICATION OF FINDINGS TO ESTIMATION OF DENSITY AND USE

The well-known method of estimating population density from numbers of scats or pellet groups can be expressed in the following equation:

$$D \text{ (animals/km}^2\text{)} = \frac{s \text{ (scats)}}{t \text{ (days) } a \text{ (km}^2\text{) } d \text{ (scats/animal-day)}}$$

where dimensions are shown in parentheses, and D = density, s = number of scats found, t = time interval in which scats were deposited by the animals, a = area searched for scats, and d = average defecation rate. If we multiply the density by the factor 365, we get the use expressed in animal-days per year and unit area, which shows that *use* is simply another, finer, measure of density.

This method as it is used to estimate densities of ungulates, where the sample area a is cleared of old pellets and newly deposited pellet groups are counted after a period t (Neff 1968), would in most cases not yield enough data for bears, which occur at much lower densities and have low defecation rates. We must therefore modify the procedure in such a way that all scats found can be used. Thus, for t we use the average time for scats to decompose, for which we have a rough and preliminary estimate of 18 days (Fig. 2); and for a we multiply the length of a sample route by the effective strip-width, for which we have a preliminary value of about 3.5 m (Fig. 3). Seasonal variations in defecation rates force us either to make all counts in the field during the same month or to make adjustments by calculation. Using observations collected by interviewing local residents, we obtained a peak of frequency of scat finds in October for the wild bears in the Trentino region (Roth and Huber 1972). These figures were corrected for a hunter bias (hunting season unduly increases the fall peak) and were then standardized by placing the average of the 2 peak months (September and October) equal to unity. We get the following values, which can be interpreted as relative probabilities (expected frequencies) of finding bear scats in the Trentino (January to December): 0, 0, 0, 0.1, 0.4, 0.2, 0.3, 0.4, 0.9, 1.1, 0.3, 0. The numbers of kilometers walked each month in 1969 were multiplied by the factor for the corresponding month, giving the number of September-October km equivalents. Summing over the whole year of 1969 yields 164 September-October km equivalents (real km = 397), which, through multiplication by the $3.5 \bullet 10^{-3}$ km of effective strip-width, results in an estimate of a = 0.57 km² September-October equivalents (real a searched = 1.4 km²).

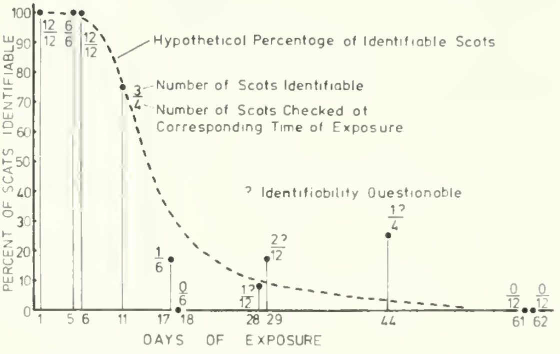

Fig. 2. Identifiability of weather-exposed bear scats as a function of the time of exposure. The decomposition of 3 series of a total of 28 scats was observed. Graphical integration of *plausible* smooth curves yielded the following values for the average time required for scats to decompose to unidentifiability: lower limit = 13 days; upper limit = 22 days; medium value = about 18 days.

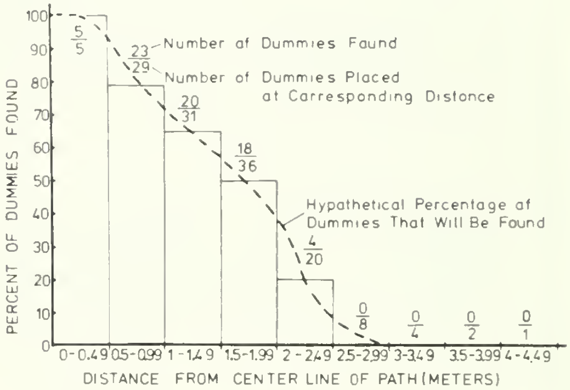

Fig. 3. Rate of success of finding bear scat dummies as a function of the perpendicular distance from center line of path. The dummies were 11 black-painted round pieces of wood, 6.5-15.5 cm long and 3.0-4.5 cm in diameter, used in 14 trials for a total of 136 placements. The test path was walked with field-average attention after dummies were roughly placed (pacing) by another person using 3 random numbers (location along route, distance from path, and left-right of path according to uneven-even). The exact distances from the center line of the path were measured after the trial. Graphical integration of a *plausible* smooth curve yielded a half-width of a hypothetical strip within which all dummies would be found and which would produce the same number of finds (at same dummy density) of 1.585 m (strip-width = 3.17m). Some measurements in the field when scats were found indicated somewhat higher values, which put our rough estimate of strip-width at 3.5m.

Analogous to the standardizing procedure used to calculate a, we take for the defecation rate d the average of the 2 months with highest values (August and September, Fig. 1; captivity could have easily shifted the annual cycle 1 month), which is 5.9 scats per bear-day. In 1969 I made 12 scat finds along the 397 km walked. Not included in these figures are the finds and the routes walked while purposely searching specific areas selected on the basis of recent bear or bear-sign observations made by other persons. Also, to avoid undue variance (which ideally should not exceed that of a Poisson distribution), only the *first* observation of a *clump* in space and time was considered. According to the bear density in the Trentino, a clump was defined as any 2 or more scat finds that were less than 1 km apart *and* were made within a month's time. So we have s = 12 scats, t = 18 days, a = 0.57 km^2 September-October equivalents (real km^2 = 1.4), and d = 5.9 scats/bear day. We calculate a density of about 20 bears per 100 km^2 (rough 95 percent confidence interval: 11-36). Using the real a of 1.4 km^2 and the average defecation rate for April-November of 3.4 scats/bear-day, we get a density estimate of 14 bears per 100 km^2. These density figures are much higher than estimates based on direct counts using sightings, tracks, etc., and on comparing frequencies of observations from the Trentino with those of other areas, which give seemingly more reasonable values of 2-4 bears per 100 km^2.

One of the reasons for the too-high estimate of bear density could be a considerably higher defecation rate of wild bears. Zunino (1971) observed a wild bear feeding on berries in the Abruzzo mountains of central Italy during 1 day (24 hours?) and counted 15 defecations. Also, some of our data from Yugoslavia indicate a higher defecation rate by wild bears. It is hoped that more direct measurements of defecation rates of free-roaming animals will become available through the use of radiotelemetry.

In summary, we are still very far from having a satisfactory method of estimating bear densities by counting scats. But the defecation data presented here may give some insight into possible correlations (month, age, sex) and variabilities (individuals) that are likely to be found — probably to an even larger extent in wild bear populations — on the way to this goal.

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THE BROWN BEAR IN SWEDEN — DISTRIBUTION, ABUNDANCE, AND MANAGEMENT

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Abstract: Between 1913 and 1942, the brown bear (*Ursus arctos*) was totally protected on state land in Sweden. The resultant increase in the population allowed a shooting season to be established in 1943 in 2 areas, in central and northern Sweden. Official shooting statistics show that the annual harvest of bears decreased sharply after 1971 even though the population was believed to be increasing. To resolve the status of the brown bear, a nationwide survey embodying questionnaires and some field work was carried out in 1975-76. Reports from Lapp villages, local affiliates of the Swedish Sportsmen's Association, large lumber companies, and the Swedish Forest Service were used to determine the nationwide distribution of the species and to estimate the maximum and minimum numbers of bears for each area that reported. Survey results indicate that the present brown bear population numbers 400-600 individuals widely but very unevenly distributed in northern and central Sweden, with marked concentrations in the northern parts of Jämtland and in wooded and low mountain areas in central Norrbotten. As a result of the survey, it is suggested that the open season be abolished and that a license system be established for better adjustment of the harvest to the true distribution of the species.

The brown bear was originally found throughout Sweden but by the end of the 19th century, it had been exterminated from the southern portion of the country. Some suspected that the brown bear was also decreasing farther north, and in the 1880s it was suggested in Parliament that the bounty for shooting brown bears should no longer be paid by the government. Bounties were discontinued in 1893, but brown bear populations apparently continued to decline. To halt the decline, the government put the brown bear under protection on state land in 1913 (Lönnberg 1929). The population then increased to the point that it was considered necessary to reintroduce hunting. Open seasons have been held since 1943, with brown bears being hunted in September and/or October in 2 areas in central and northern Sweden. Juveniles and females with juveniles are protected year-round.

Official statistics suggest that some 20-30 brown bears have been shot annually since 1943. The smallest number, 9 bears, was harvested in 1949; the highest, 41, in 1966. There is no obvious trend except that during the last 6 years, the figures show a pronounced decrease. Bears shot in 1971 numbered 20, followed in the next 5 years by 15, 12, 11, 8, and 7. There is no equivalent decrease anywhere else in the series. This decline runs counter to public opinion, which holds that the populations is increasing. To resolve this question, a survey of the population was carried out in 1975-76.

Methods and Materials

A basic premise was that the survey should comprise the entire Swedish population of brown bears. Because it would be impossible to make a field survey, a questionnaire with some very limited field investigations was utilized.

The questionnaire was based on the assumption that people who engaged in outdoor activities had some idea of the brown bear distribution and abundance in their particular areas. Questionnaires were therefore distributed to the Lapp villages, to local organizations of the Swedish Sportsmen's Association, and to the forest districts of the largest forestry companies, including the Swedish Forest Service. A map was attached to each questionnaire.

The questionnaires were distributed in April and May 1975. First and second reminders to those who had not answered were sent out in July and September/October, respectively. Information about the survey was published in some newspapers and periodicals and was presented on local radio and television programs.

Questionnaires were sent to 876 sportsmen, and first-time responses were received from 167 (19 percent). After the 2 reminders, responses totaled 449 and 607 (51 and 69 percent), respectively. Response rates for the 53 Lapp villages were 13, 21, and 35 (25, 40, and 66 percent). The response rate for the forestry companies was more difficult to establish because some companies distributed the material to their own forest districts, which then delivered the reports. Other companies gathered information centrally and submitted a single report. A total of 752 reports were received, which means that about two-thirds of those consulted responded.

Field work covered areas where reports were either contradictory or entirely lacking. This work was carried out by helicopter during 6 days in early May of 1975 and 1976, when the ground was still covered with snow but when it was reasonably certain that most bears had left their dens.

Work on the reports started with the transformation of all information to a system for computer treatment. However, it soon became obvious that this method was too simplified and would lose many details given in the reports. The method was abandoned and the material was treated manually. Distribution of the brown bear was determined by county, partly because the county is an important administrative unit. Below county level, a geographic subdivision was chosen, primarily conforming to the main river valleys, which are often boundaries, for example, of Lapp villages.

All reports from a given area were compared with reference to information about distribution and abundance of brown bears. For each area a minimum and a maximum estimate was made of the total number of bears. Discrepancies between individual reports were evaluated according to the reliability of the informant and the extent of agreement among informants. This procedure resulted in a narrative description of each area, with discussion as far as the details permitted. This description was transferred to maps, 1 for each county and another for the entire area of distribution.

RESULTS AND DISCUSSION

Brown bears are distributed over a large but not continuous area in central and northern Sweden (Fig. 1). The distribution is very uneven. Marked concentrations are found in the northern parts of the county of Jämtland and in central parts of the county of Norrbotten. The area includes the upper part of the coniferous zone and the lower part of the alpine zone. Movements towards higher elevations are common in summertime. Early in the summer, bear distribution is supposed to be influenced by movements of migrating domestic reindeer (*Rangifer tarandus*) herds and especially by the calving grounds. Later in summer and in autumn, rich crops of berries (mainly *Empetrum* spp.) apparently attract bears. Extensive movements are also known to occur in the conifer forest, in 1 case even as far as out to the archipelago of the Gulf of Bothnia. Such movements usually occur in early spring and are assumed to be related to lack of adequate food within the normal range (Haglund 1968).

The survey material was used to interpret the present status of the brown bear population. Total numbers of brown bears are estimated to be between 400 and 600. This estimate represents an increase from the figure of 370 bears in a survey from 1966 (Haglund 1968). The results agree with the general opinion of those who returned questionnaires; of 297 reports from areas with brown bears, 159 mentioned an increasing population and 29 reported decreasing numbers.

During the past decade, development of the bear population has not been uniform. In the county of Norrbotten — where hunting is allowed in 1 area — the population seems to be increasing at such a rate that it has doubled in about 25 years. In the county of Västerbotten — where no hunting is allowed — the population is obviously decreasing. The population in the mid-1970s is about one-third the size it was at the beginning of the 1940s. There are also areas where the reports indicate a fairly stable population.

There are discrepancies between the distribution of brown bears and the areas where hunting is allowed (Fig. 1). This situation creates problems of different kinds. For example, some Lapp villages have applied for specific licenses to shoot brown bears because of excessive damage to reindeer farming, whereas in areas where brown bears are only occasional visitors, a 2-month season limits their chances of reestablishment. To overcome these disadvantages, it was recently suggested that the open season be abolished. A well-designed license system should then make it possible to adjust the harvest to the true distribution of the population.

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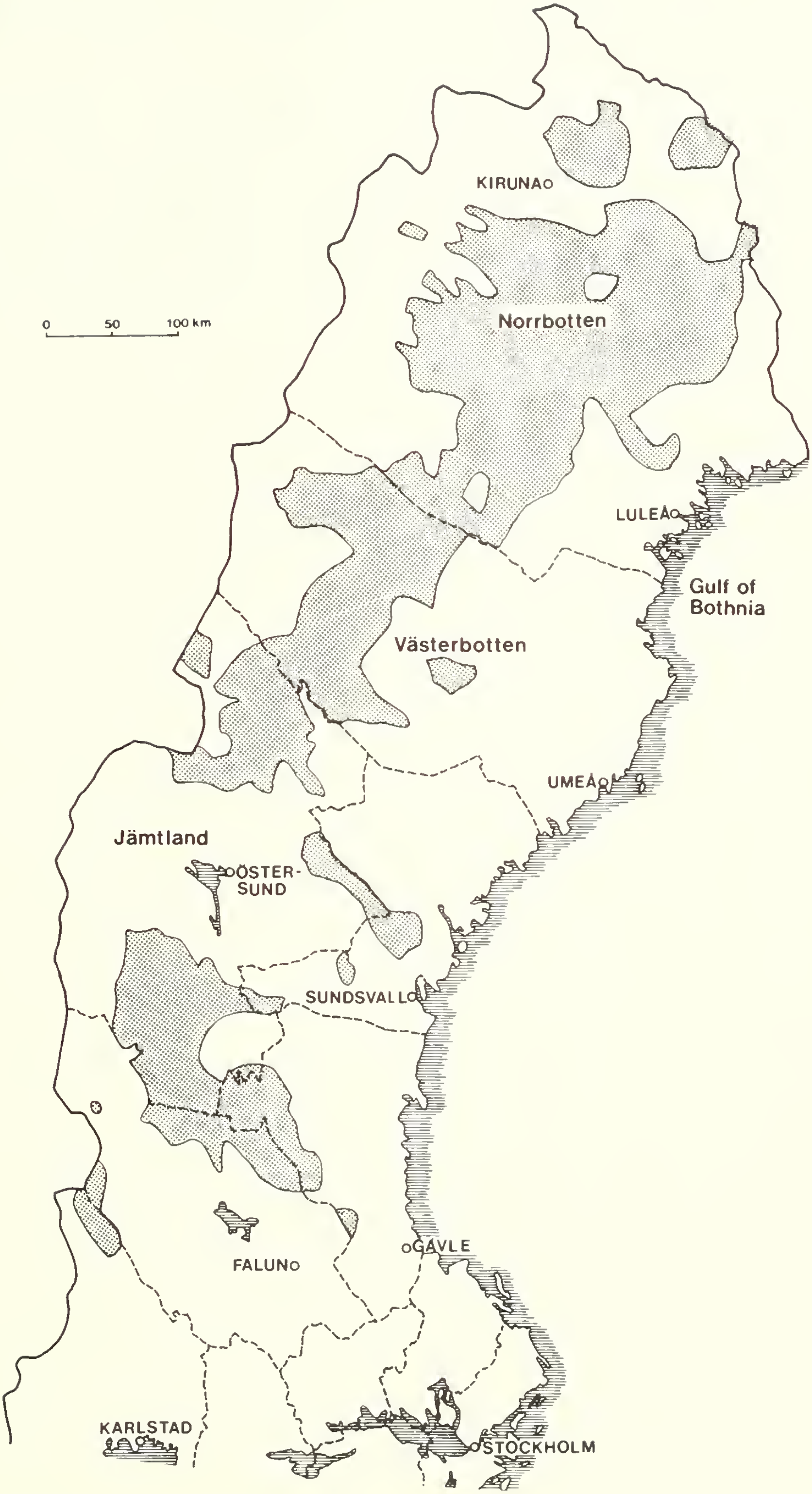

Fig. 1. Distribution of the brown bear in Sweden, 1975-76.

ON THE DISTRIBUTION OF THE BROWN BEAR IN BULGARIA

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Abstract: Fossils of the brown bear (*Ursus arctos* L.) and the cave bear (*U. spelaeus* Blum.) from Bulgaria indicate that during the Diluvium the brown bear was rarer than the cave bear. About the end of the Diluvium and the beginning of the Aluvium, the cave bear became extinct and the brown bear spread through Bulgaria.

According to Ruskov (1959), there were 450 brown bears in the mountains of Bulgaria in 1959. The low number of bears was because hunting laws dating from 1897 considered it a harmful animal; this law was repealed in 1941. Another reason for the low number is increasing economic development in the mountains. The number of brown bears is now satisfactory (about 520 individuals); hunting is forbidden and the species will not become extinct.

Craniological and dentographic data from 7 crania (3 males and 4 females) of brown bears from the mountains of Rila and Pirin indicate that the condylobasal lengths are within the limits of 18 individuals of *Ursus arctos arctos* from the European part of the USSR (Ognev 1931). Precise subspecific determination of Bulgarian brown bears will be possible when more crania are available.

ECOLOGY OF THE BROWN BEAR IN THE ENISEI TAIGA

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Abstract: The brown bear (*Ursus arctos*) is very important in the USSR from a practical point of view: It is a source of valuable hunting trophies; the meat is nourishing; the high-calorie fat has medicinal properties; the bile is in high demand in medicine; and by consuming the carcasses of dead animals, the bear performs a sanitary function in nature.

Our research on the ecology of the brown bear was conducted in 1967-76, in a 35,000-km^2 area in the middle of the Siberian taiga, where the Podkamennaya Tunguska discharges its waters into the Enisei River. We gathered 72 skulls of animals of different sex and age, took measurements and weights of 38 animals, analyzed the stomach contents of 29 animals, and determined the ages of 62 specimens by tooth cementum layers.

This paper describes the measurements and life history of the brown bear, including four annual feeding periods which may be differentiated. Bears in the Siberian taiga appear to have a selective impact on the moose population. Cases of bear cannibalism are known. Bears very seldom attack people.

BROWN BEAR MANAGEMENT IN SOUTHEASTERN ALASKA

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Abstract: Brown bears *(Ursus arctos)* inhabit the mainland of southeast Alaska and the islands north of Frederick Sound. Greatest numbers occur in Alaska Game Management Unit 4, the ABC (Admiralty, Baranof, and Chichagof) islands, where about 70 percent of the southeastern harvest is taken. Average sport harvests increased from 51 bears per year (1949-56) to 60 per year (1962-72) to 141 in 1975. Other pertinent harvest statistics have remained fairly consistent since 1949: average skin size (length plus width), 4.1m; average skull size (length plus width), 54.6 cm. Based on dental annuli, ages of males have averaged 8.1 years since 1968. The highest mean annual age was 9.4 years in 1976. The goal of management is to maintain a high-quality hunting experience, which an annual harvest rate of 60-80 animals per year will do much to provide. Harvest statistics gathered over the past 30 years will provide guidelines to insure that management plans are biologically sound. Current regulations that should limit the harvest to desired levels are a $25 tag fee for resident hunters and a limit on the number of guides who can operate in Unit 4. If these fail, time-space zoning, further restrictions on guides, or ultimately permit-only hunting will be necessary. Transfer of nearly 151,760 ha to private land through the Alaska Native Claims Settlement Act and continuing large-scale clearcut logging further cloud the management issue, but with prudent management policies, high-quality and reasonably high-quantity brown bear sport hunting should be possible for many years to come.

Alaska Game Management Unit (GMU) 4 consists of Admiralty, Baranof, and Chichagof islands, known as the ABC islands, as well as smaller adjacent islands. The majority of southeastern Alaska's brown bears are found on these islands, and our greatest body of data pertains to this part of southeastern Alaska.

This work was financed in part through Federal Aid to Wildlife Restoration, Alaska Project W-17-R. The Boone and Crockett Club provided for the author's transportation to the Fourth International Bear Conference in Kalispell. Sincere thanks are due D. E. McKnight, R. E. Pegau, and L. M. Bergdoll of the Alaska Department of Fish and Game for their assistance in preparing this paper.

THE AREA

The ABC islands are the northernmost islands of the Alexander Archipelago (Fig. 1). Admiralty and Baranof islands each have an area of about 2,575 km^2 and Chichagof has about 3,540 km^2. They are separated from the remainder of the archipelago by Frederick Sound. All are characterized by rugged topography, with some peaks rising to 900-1,200 m only 1-2 km from salt water. The shoreline, some 3,700 km in extent, is very irregular and has many long, narrow fjord-like bays. These bays are characterized by steep, forested hillsides and are fed by numerous anadromous fish streams draining heavily timbered U-shaped canyons. Most of the bays are bordered by narrow strips of grass-sedge vegetation that spread out to form large deltas at the heads of the bays. Extensive, dense stands of a Sitka spruce (*Picea sitchensis*)-western hemlock (*Tsuga heterophylla*) consociation, which is the dominant vegetative type, reach to an elevation of about 600 m. Muskegs and subalpine and alpine vegetation occur above that elevation.

Brown bears have apparently occupied the ABC islands since recession of the last Ice Age some 10,000 years ago (Klein 1965). They are the only large carnivore on the islands. Wolves *(Canis lupus)*, wolverines (*Gulo gulo*), and black bears (*Ursus americanus*) — but no brown bears — are present on the Alaskan islands of the Alexander Archipelago south of Frederick Sound. All four of these species coexist on the adjacent mainland (Klein 1965).

Brown bears appear well adapted to the habitats available on the ABC islands and at the appropriate times of year make use of most habitat types. Bears emerge from their winter dens, which are located at or above timberline, in April and May and descend to the beaches, where newly emerging grasses, sedges, and forbs provide the bulk of their diet. Some scavenging of animal remains, i.e., winter-killed deer (*Odocoileus hemionus sitkensis*) and marine mammal carcasses, occurs. Bears remain near the beaches until early summer when berries begin to ripen and anadromous fish begin to appear in the streams. They feed on fish and berries until the fish runs begin to diminish in September and October. At that time, they move to higher elevations where they remain for a short period, feeding on berries and other vegetation until the onset of winter makes that food supply unavailable. They enter their winter dens usually in October and November.

With primary food sources consisting of anadromous salmonids and vegetation associated with early stages of postglacial succession, and a lack of competition from other mammalian species, brown bears probably became relatively abundant fairly soon after they colonized the ABC islands.

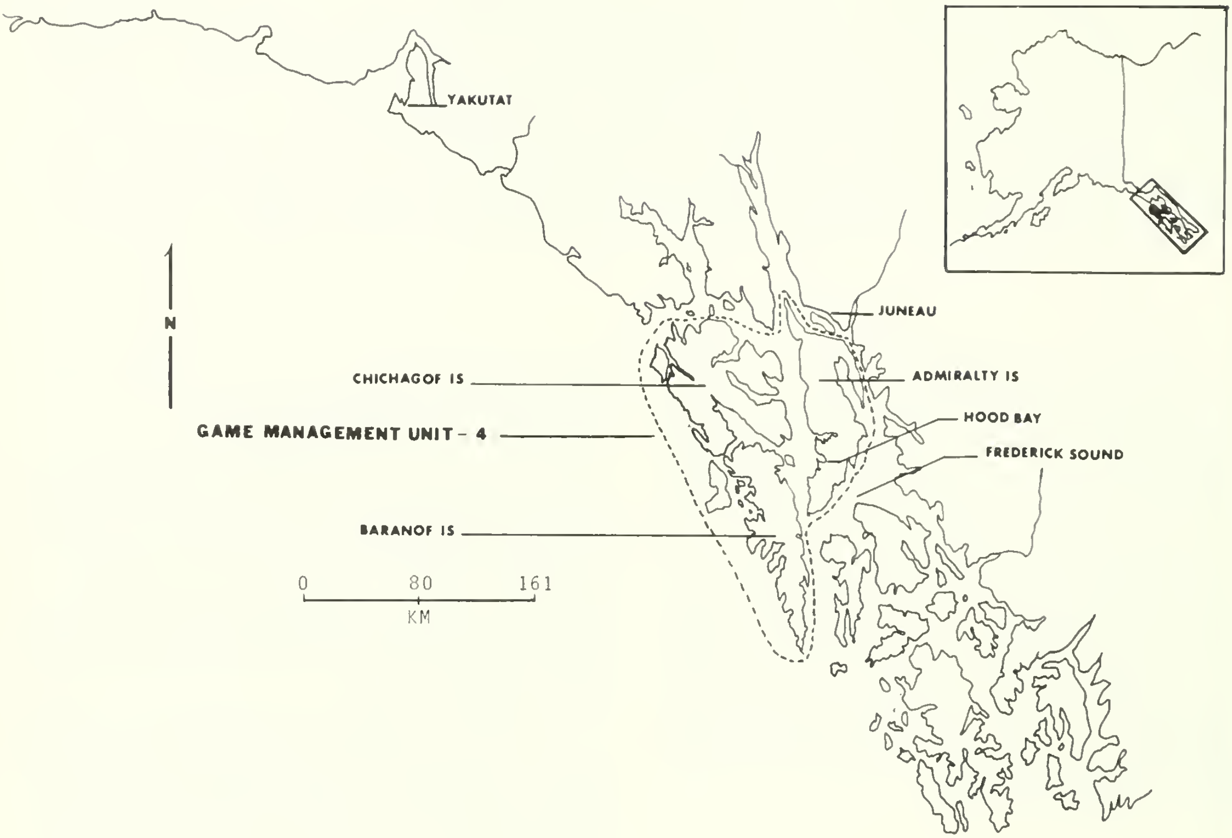

Fig. 1. Southeast Alaska.

POPULATION LEVELS

Much has been written on the abundance of bears on the ABC islands since Holzworth's (1930) account of his photographic expeditions there in the late 1920's. The first attempt to enumerate bears was made by Dufresne and Williams (1932) in a cooperative study between the U.S. Forest Service and the Alaska Game Commission. That study covered Admiralty Island only and was based on track counts made while bears were concentrated along fish streams during the sumsummer. They estimated that 900 bears inhabited Admiralty Island. Estimates based on track counts also indicated 940 bears for Chichagof Island in 1938 (Holbrook 1938) and 445 bears for Baranof-Kruzof islands in 1939 (Holbrook 1939) — a total of 2,285 bears for the ABC islands.

Klein (1958) tested the track count technique on Admiralty Island and found it unreliable except for local situations. Expanding his Admiralty Island data, he estimated the population on the ABC islands as 1,800 bears in 1958.

A U.S. Forest Service study from 1960 through 1966 (Perensovich 1966), using aerial censuses and track counts, made no population estimates but concluded that there were no data to suggest declines in population during the period of that study. Perensovich's study was aimed primarily at measuring the impact of logging on bears. A similar study was continued by the Alaska Department of Fish and Game until 1968 (Lentfer et al. 1969). At that time, it was concluded that although the aerial census technique was not satisfactory for population estimation, the data collected did indicate no appreciable changes in population densities.

More recently, a population study conducted at Hood Bay on Admiralty Island from 1971 to 1975 (Wood 1976) estimated a population of 72-105 bears from ratios obtained through observations of tagged to untagged bears. Previous estimates for Hood Bay were 49 by Dufresne and Williams (1932) and 20 by Klein (1958). Although past studies varied considerably in technique, technology, and objectives, all indicated that bears were abundant and none suggested population declines.

In addition to data on bear population densities and status, studies have provided information on the reproductive biology of brown bears in GMU 4. Klein (1958), from 555 bear observations, found that cubs-of-the-year composed 9.7 percent of the population and yearlings and older cubs represented 11.9 percent. Litter sizes were 2.2 for cubs-of-the-year and 1.9 for yearlings and older cubs. Perensovich (1966), in a sample of 190 bears, found litter size in cubs-of-the-year to be 2.1 and in older cubs to be 1.6.

Johnson (1974, 1976, 1977) reported litter size of cubs-of-the-year to be 1.75 and of yearling and older cubs, 2.0. Cubs of all ages represented 22.6 percent of the 31 individual bears seen in 1973, 31 percent of the 32 individual bears seen in 1974, and 24 percent of the 21 individual bears seen in 1975. No cubs-of-the-year were seen in 1974. All observations were made in May and June in Hood Bay on Admiralty Island. These data indicate that cub production and survival in southeastern Alaska have been quite consistent, at least since 1958. They are similar to data from other coastal parts of Alaska (Klein 1958, Lentfer et al. 1969, Glenn et al. 1976).

Sightings and recoveries from tagged bears (Wood 1976 and unpublished records of the Alaska Department of Fish and Game) indicate that there is only limited interchange of bears between adjacent bays on Admiralty Island. Among 10 recoveries of 44 bears tagged in Hood Bay, 1 was taken from Pybus Bay, 7.3 km distance, and 1 from Chiak Bay, 4.8 km distant; the remainder were taken in Hood Bay.

HUNTING/MANAGEMENT

For many years, both hunters and nonhunters have been highly interested in the bears on the ABC islands. As the timber industry developed in southeastern Alaska, action to afford habitat protection for bears also developed. The principal early proponent for protection of bears was the New York Zoological Society, with J. M. Holzworth its spokesman (Senate hearings, 1932). Admiralty and Chichagof islands received the most attention. The philosophies of the two factions are summarized and fairly well represented in a management plan for Admiralty Island published jointly by the Alaska Game Commission and the U.S. Forest Service (Heintzleman and Terhune 1934). Portions of that plan, which were adopted and incorporated in Alaska game regulations, do not differ greatly from present philosophies of the Alaska Department of Fish and Game, e.g., the plan suggested holding the annual kill from Admiralty Island at 35 animals, which is similar to our current recommendation. Developmental interests, however, generally have not complied with another objective of the plan: "Other resources will be so managed as not to cause a diminution of the number of these animals." Although no cutting of timber was recommended in areas of heavy bear concentrations, some fairly extensive clearcutting has occurred on the southern portion of the island. A long-term logging contract, first signed in 1966 but since canceled, was also not in accord with the intent of the plan.

Brown bear hunting on the ABC islands can be divided into three rather distinct periods — before 1925, 1925-59, and 1960 to the present. Regulations governing bear hunting during these periods are summarized in Table 1. Before 1925, there were few regulations governing the taking of bears in Alaska. Although harvest records are scanty, the ABC islands were well known for their bear-hunting potential. A. Hasselborg, a homesteader who lived on Admiralty Island for many years, reportedly killed more than 300 bears and sold over 200 of them to museums (Holzworth 1930). Until 1925, brown bears could be taken as furbearers. The only known record of the possible magnitude of use of bears for fur is a report in the U.S. Senate hearings of 1932 that the Native people of the village of Angoon on Admiralty Island annually sold 25-50 bear skins. The hearings also noted that fox farmers frequently killed bears for fox food.

In 1925, a fairly comprehensive set of regulations was adopted and applied with little alteration until Alaska achieved statehood in 1959. These regulations ended commercial hunting, established an annual bag limit of 3 bears, and provided a closed season during the summer months. Guides were required for nonresident hunters. Harvest records for the early years after 1925 are poor at best. Reconstruction of information presented at the Senate hearings in 1932 suggests that the ABC islands sustained an annual kill of about 30

Table 1. Historic brown bear hunting regulations, ABC islands, Alaska.

Year	Bag limit	Season	Guide required for nonresidents	Remarks
Before 1925	No limit	Year-round	No	
1925	3	Year-round	Yes	Sale of hides illegal after 1925
1926-29	3	1 Sep-20 June	Yes	
1930-32	No limit	Year-round		Alaska residents only
	2	1 Sep-20 June	Yes	Nonresidents
1933-34	2	1 Sep-20 June	Yes	
1935-44	1 (Admiralty only) 2 (remainder of area)	1 Sep-20 June	Yes	Thayer Lake and Pack Creek closed areas established in 1935 or 1936
1945-55	2 (Admiralty exception removed)	1 Sep-20 June	Yes	Mandatory guide reporting system initiated
1956	2	1 Sep-30 June	Yes	
1957	2	1 Sep-30 June	No	Game Management Unit system established
1958	1	1 Sep-30 June	No	Mandatory guide reporting system eliminated
1959	1	1 Sep-30 June	No	Cubs and sows with cubs protected hereafter
1960-63	1	1 Sep-30 June	Yes	
1964-66	1	1 Sep-30 June	No	
1967	1	1 Sep-20 June	Yes	
1968-present	1 bear every 4 regulatory years	1 Sep-10 June	Yes	Minor changes in season openings and closures

bears during the period 1927-31. Nonresident hunters took about 80 percent of that harvest.

A memorandum from the U.S Forest Service to the U.S. Fish and Wildlife Service (Heintzleman 1948) indicated that 256 bears were taken on Admiralty Island in the period 1933-40. Resident hunters took 56 percent and nonresidents, 44 percent of the average annual kill of 32 bears. No mention was made of how the data were gathered; however, during that time, persons purchasing an Alaska hunting license were required to report their previous year's bag.

From 1945 through 1956, the U.S. Fish and Wildlife Service required registered guides to submit detailed reports for all guided hunts involving nonresident bear hunters. Although accurate kill data were kept for guided hunts, no records of the harvest from unguided hunts have been located. Data obtained from the mandatory guide reporting system, which are often fragmentary, included sex, date of kill, location of kill, hide size (nose to tail length plus width between tips of forepaws of skins laid out flat), and skull size (greatest length plus greatest width.) Males composed about 64 percent of the reported kill. Admiralty, Baranof, and Chichagof islands contributed 67, 15, and 18 percent, respectively, of the kill. Skin size of all bears averaged 4.7 m, and skulls measured 59.9 cm. The annual kill was about 51 bears for the period 1949-56 (Table 2). For the first 4 years of the mandatory guides reporting period (1945-48), the reported kill averaged only 9 bears per year, presumably because the guiding industry was still hampered by wartime restrictions.

From 1956 through 1960, apparently no harvest records were kept. With statehood in 1959, the Alaska Department of Fish and Game was created. Current regulations, which have been relatively unchanged since then, provide for a closed season during the summer when pelts are of little trophy value; prohibit the taking of cubs or sows accompanied by cubs (cubs being bears 1 or 2 years of age); prohibit the use of helicopters or rotorcraft in any manner; limit the take to 1 bear every 4 regulatory years; require registered guides for all nonresident hunters; require that all bears be presented to representatives of the Department of Fish and Game for sealing; prohibit hunting the same day hunters are airborne; and prohibit barter or sale of bear skins. The sealing program originally required that only skins be presented. That provision was amended in 1967 to require that skulls as well as skins be sealed and was further amended in 1968 to require that a tooth be collected for aging. These requirements have yielded a large volume of data upon which to base management decisions.

Data derived from the sealing program (Table 3) included sex, date and location of kill, skin size, age

Table 2. Historic brown bear harvest data, ABC islands, Alaska.

Year	Admiralty	Baranof	Chichagof	Total
1933	40 (52)[a]			
1934	25 (48)			
1935	26 (61)			
1936	30 (44)			
1937	31 (46)			
1938	33 (64)			
1939	29 (18)			
1940	32 (36)			
1941-44		— No data —		
1945[b]	3	1	0	4
1946	9	1	5	15
1947	6	0	0	6
1948	6	3	3	12
1949	41	9	6	56
1950	56	11	1	68
1951	36	13	18	67
1952	36	5	8	49
1953	38	9	5	52
1954	31	4	13	48
1955	20	3	19	42
1956	18	4	2	24
1957-60		— No data —		
1961	22	4	13	39
1962	25	3	16	44
1963	15	7	4	26
1964	33	5	17	55
1965	34	14	18	66
1966	47	12	17	76
1967	36	11	22	69
1968	29	3	16	48
1969	30	8	27	65
1970	40	11	21	72
1971	29	12	28	79
1972	29	13	35	77
1973	45	8	46	99
1974	44	4	38	86
1975	51	14	40	105
1976	71	21	49	141

[a] Percent resident kill in parentheses.
[b] Nonresident kill only, 1945-56.

based on cementum annuli, and total sport kill. They show that the harvest averaged 70 percent males, 71 percent of which were taken in spring and 53 percent by nonresident hunters. The average bear had a skin size of 4.1 m, a 54.6-cm skull, and was 8 years of age (males only). Total kill averaged 60 per year, 1961-72, but increased to 99 in 1973, 105 in 1975, and 141 in 1976. Admiralty, Baranof, and Chichagof islands contributed 51, 15, and 34 percent respectively, of that kill. There has been an upward trend in the percentage of the kill from Chichagof Island and a corresponding downward trend from Admiralty and Baranof islands. However, pertinent harvest statistics except total kill have remained remarkably consistent. In fact, the mean age of males increased to 9.4 years in 1976. On a statewide basis, the ABC islands account for approximately 11 percent of the annual harvest of brown and grizzly bears.

Data provided by the guide reporting system used by the U.S. Fish and Wildlife Service before statehood and data derived from the current sealing program are not always comparable. Hide sizes reported by guides were typically green, unsalted skins; measurements taken under the sealing program are typically of salted skins. A bear skin normally shrinks about 50-60 cm after salting. Therefore, the 4.7-m average green skin taken during 1945-58 compares favorably with the 4.1-m average salted skin since 1961. Also, under present conditions, bears taken by nonresident guided hunters average slightly larger than those taken by resident hunters. If the sizes of resident hunters' bears could be averaged in with the data for 1949-56, even greater similarity might be shown. The average skull size of 59.9 cm under the guide reporting system is also probably high; guides, especially in the presence of the successful hunter, frequently intensify their efforts to make the trophy appear larger. Under the sealing program, skull measurements are normally taken with calipers.

HUNTING TRADITIONS

Brown bear hunting in southeast Alaska, particularly during the spring season, has traditionally been an aesthetically pleasing experience. The optimum springtime hunting period of 20 May — 10 June, which coincides with high bear availability and pelt primeness, is a pleasant time of year. Over 70 percent of the spring harvest and 50 percent of the yearly harvest is taken during this period. Male blue grouse (*Dendragapus obscurus*) are displaying, filling the bays with their pulsating "hoots." Fishing can be good, clam digging is excellent, a variety of crabs can be gathered, and in the evenings deer are often seen in large numbers on the beaches. Marine mammals such as seals *(Phoca vitulina)*, sea lions *(Eumetopias jubata)*, whales, and porpoises can be observed. Migrating waterfowl and other birds are plentiful. It is not uncommon to see upwards of 50 different bears on a 10-day hunt. All of these experiences can combine to make a memorable hunt. Obviously, hunting success rates are high. Guides and resident hunters traditionally seek solitude from other hunting parties. Transportation is mostly by boat, with hunting forays made by skiff from a large boat. The larger boats provide roving base camps, which guard against hunter crowding through their mobility and enable the guides to survey a great deal of country. Aircraft are infrequently employed.

Table 3. Brown bear sport harvest, Game Management Unit 4, 1961-75.

Calendar year	Total kill	Percent kill in spring	Percent males	Percent nonresident kill	Mean hide size, male[a] (m)	Mean skull size, male[a] (cm)	Mean cemuntum lines[b]	
							Male	Female
1961	39	72	80	59	4.6			
1962	44	73	66	66	4.5			
1963	26	67	74	56	4.4			
1964	55	72	67	44	4.3			
1965	76	65	63	67	4.2			
1966	76	65	63	67	4.0			
1967	69	66	69	48	4.0	57.7		
1968	48	72	76	36	3.9	56.3	8.0 (10)	
1969	65	67	77	52	4.2	57.7	7.1 (32)	
1970	72	85	73	55	4.2	55.9	7.8 (40)	
1971	79	78	64	52	4.3	57.7	8.3 (44)	8.1 (15)
1972	77	66	75	53	4.4	57.2	8.8 (55)	6.4 (17)
1973	99	72	68	40	4.2	54.9	7.7 (63)	8.5 (32)
1974	86	74	73	51	4.2	56.4	7.6 (57)	7.7 (21)
1975	105	72	69	57	4.3	56.4	8.1 (66)	6.4 (29)
1976	141	79	64	60	4.3	56.9	9.4 (90)	8.6 (50)
Mean		71	70	53	4.2	56.6	8.1	7.6

[a] Length plus width.
[b] Tooth sample size in parentheses

An annual exploitation rate of 60-80 bears produced the harvest data parameters outlined above (and in Tables 2 and 3). Biologically, that rate of exploitation appears to have had little impact on the population, as witnessed by the consistency of the data over the years, and also ensures minimal hunter interaction in the field and little or no competition for hunting space or for bears. With harvest levels greater than 60-80 per year, as in the past 4 years, aesthetic hunting conditions are eroded through hunter interaction and competition for space and bears.

MANAGEMENT GOALS

The management goal of the Alaska Department of Fish and Game in GMU 4 is to provide bear hunters with high-quality hunting experiences. A management plan to meet that goal has been drafted and will soon be presented for public review. The plan was based upon hunting tradition and harvest characteristics over the past 30 years. It outlines two basic options available to achieve the management goal: (1) limit the kill to the pre-1972 harvest rate of 60-80 bears per year through a permit hunt; or (2) design a time and space zoning procedure to mininize hunter interaction. It might be possible under the second option to exceed the annual kill of 60-80 bears. Under either option, adherence to the harvest parameters cited above ensures biologically sound management practices.

Until full implementation of the management plan, we are faced with the problem of increasing harvests and decreased quality of hunting experience. If overharvest becomes critical, we can reduce hunting through emergency season closures. Beginning in 1977, a tag costing $25 will be required of all resident brown bear hunters, the first time a resident tag for general hunting has been issued in Alaska. Although initiated to provide needed revenue, the tag is expected to reduce the number of bear kills incidental to other hunting activities of resident hunters. Also, in February 1977, the Alaska Guide Licensing and Control Board set a limit on the number of guides (19) who can contract for hunts in GMU 4. Should that limitation fail to reduce the nonresident kill, the Guide Board also has the authority to assign restricted or exclusive guiding areas to individual guides. The latter measure is less acceptable because it eliminates the opportunity to move about and hunt different areas, which was an appealing aspect of the earlier type of hunting.

MANAGEMENT PROBLEMS

In addition to increased hunting pressure, bear management in southeastern Alaska faces other problems. Transfer of nearly 151,760 ha of land to Native groups under the 1972 Alaska Native Claims Settlement Act (PL 94-2004, 85 Stat. 688) is now under way. The Native lands will be subject to the usual problems associated with the management of a public resource on private property. Because of conflicts, litigation, and trade-offs, it will be many years before these transfers are fully implemented. Some Native groups made selections that would enable them to continue their subsistence way of life, which should favor bear management. Other groups are primarily interested in exploiting the timber resource, which will undoubtedly adversely affect bear management. Also, a special land classification for Admiralty Island is again being discussed.

Development of an extensive logging industry has perhaps had the greatest impact on bear management in southeast Alaska. All lands under administrative jurisdiction of the U.S. Forest Service on Baranof Island and most of Chichagof Island are included in a 1956 50-year timber sale to the Alaska Lumber and Pulp Company, a Sitka-based, Japanese-owned firm. That sale committed most of the merchantable timber (28,173,696 m^3) to logging. At present, approximately 18,211 ha have been logged. Admiralty Island was included in a similar sale; but litigation by environmental groups, notably the Sierra Club, brought about a mutual cancellation of that contract by the U.S. Forest Service and the company involved. Admiralty Island is now subject to independent timber sales.

Logging in southeast Alaska is generally done by clearcutting; unfortunately, the effects of clearcut logging on bear populations and bear hunting are poorly understood. Perensovich (1966) reported that the effects were slight but felt his study was too brief to be conclusive. One known impact, which is primarily a management problem but at the same time contributes significantly to the kill, is the rather large number of bears destroyed in logging and support camps. This kill may approach 10 percent of the reported legal kill. Many of these kills seem avoidable, and we are continually working on this problem. Regulations should be developed to place responsibility on the logging industry or the appropriate governmental agency to minimize bear-human confrontations at campsites. Camps and refuse sites are usually chosen at the convenience of operators.

Oil development on the Outer Continental Shelf and tankers transporting oil from the trans-Alaska pipeline will perhaps not affect bears directly, although a large-scale spill could be ruinous to spring feeding areas. The additional growth in the human population, brought about by oil-related activities, will put more hunters in the field and further compound other problems.

Perhaps the most pressing problem is implementation of a long-range management plan. If the trend toward increased harvests and decreased quality of hunting experiences is allowed to continue, precedents will be established that will be hard to reconcile. Overall, notwithstanding these problems, brown bear management in GMU 4 faces a promising future. Increased demands for the bear resource and for its habitat make it obvious that the idealistic management characteristic of the pre-1972 period will no longer be possible, but adoption of the proposed management plan should assure a continuation of high-quality hunting experiences. Because that plan is based on an exploitation rate that is not expected to alter bear numbers significantly, bear numbers should be adequate for nonconsumptive uses as well.

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REVIEW OF OIL AND GAS EXPLOITATION IMPACTS ON GRIZZLY BEARS

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Abstract: In Montana, the study of grizzly bears (*Ursus arctos*) and their habitat in areas proposed for oil and gas exploitation is in the beginning stages, with few base-line data available for predevelopment guidelines. A review of literature on grizzly bears indicates that exploration and development will be generally detrimental to the bears. Construction of roads into previously unroaded areas and increased use of the land by people appear to have the greatest impacts. Problems of man-bear confrontations in the Alaska pipeline experience include nonresidents' difficulties coping with resident wildlife species, illegal shooting of animals, attraction of animals to garbage at field camps, and harassment from aircraft and other motorized vehicles. Conflicts with grizzly bears prior to development of oil and gas must be determined in order to assess the effects of resource exploitation, including the cumulative influence of various land uses. Habitat essential for the survival of the grizzly bear must be identified and protected. If development occurs in areas of occupied grizzly bear habitat before adequate management data for grizzly bears are available, it should proceed cautiously, thus preventing irreversible damage to the habitat and the bear populations. If full development, is unavoidable, restrictions should be placed on road-building, exploration, wells, fuel production, and associated activities, especially at times when grizzly bears make heavy use of a locality.

Occupied grizzly bear habitat in northwestern Montana faces exploitation of oil and natural gas resources. Few research data are available on grizzly bears to guide management decisions.

Pending oil and natural gas leases on federal land and on occupied grizzle bear habitat in northwestern Montana are shown in Fig. 1. Historically, little development of oil and gas reserves had occurred in the mountains of the region. Some drilling, later abandoned, was done in the early 1900s in what is now Glacier National Park. Starting in the 1950s, large oil and gas fields were developed in the vicinity of the overthrust disturbed belt near Pincher Creek, Alberta. In Montana, widespread seismograph studies and some exploratory drilling have been carried out since the 1950s. At least three "shut-in" natural gas wells are known to exist within occupied grizzly bear habitat northwest of Great Falls, Montana.

Extreme interest has been shown recently in the overthrust belt because of major finds in Utah and Wyoming and because of large producing fields in similar geological formations in Alberta. Leases have been applied for in occupied grizzly bear habitat on much of the federal land outside and some within classified wilderness. Lease applications have been made for over 404,858 ha of federally controlled land and on

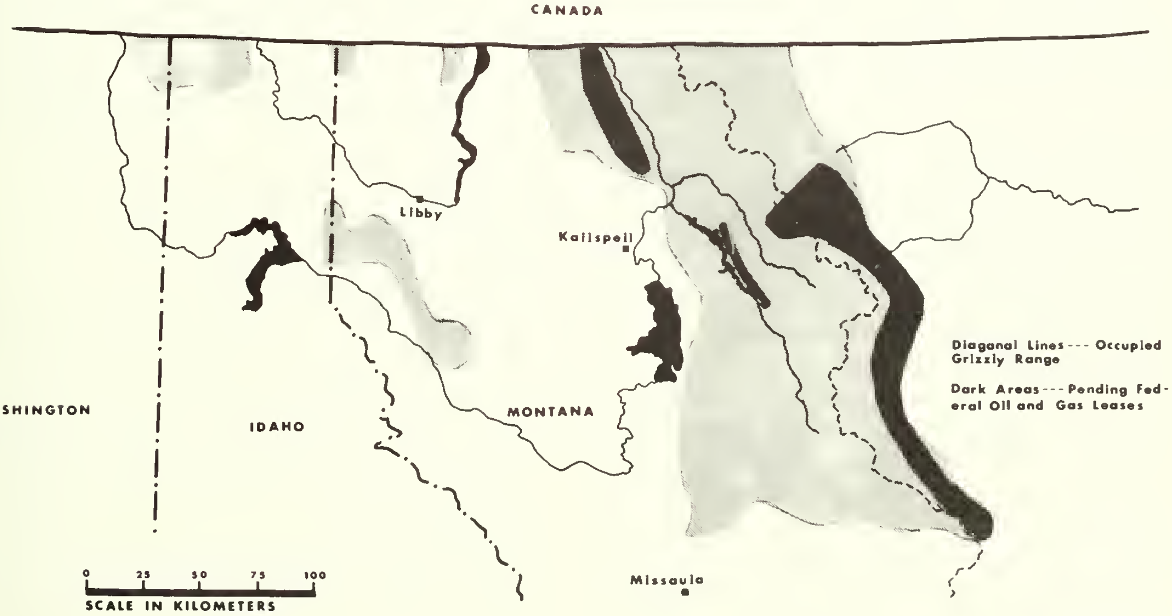

Fig. 1. Occupied grizzly bear habitat and pending federal oil and gas leases in northwestern Montana.

thousands of hectares of land with federal subsurface rights. The total area of private, Indian reservation, and state lands leased within occupied grizzly bear habitat is generally unknown, but most of the private land and some of the state lands appear to have been leased. The lease applications are a constantly growing phenomenon. Exploratory wells were drilled in 1976 and others were under way in 1977 on private, state, and Blackfeet Indian Reservation lands in the vicinity of the disturbed belt of the Lewis Overthrust (*Montana Oil Journal* 1976).

In the United States, oil and gas leasing is conducted under the Mineral Leasing Act of 25 February 1920. The Bureau of Land Management (BLM) within the Department of Interior (USDI) is responsible for issuing leases in all areas where mineral rights have been retained by the federal government. When BLM issues a lease, it grants to the lessee the right to explore for, drill for, extract, and market all of the oil and gas in the leased lands. The lease also grants, for a 10-year period, the right to construct and maintain improvements necessary for the production of oil or gas, so long as oil or gas are produced in profitable quantities. A lease on which actual drilling operations are ongoing at the time of normal termination will be extended for 2 years or as long as oil or gas is produced in paying quantities. Use of land in national forests may continue for as long as 50 years if a producing field is discovered (U.S. Forest Service 1976).

A review of literature on grizzly bears shows a number of impacts related to exploration, development, and production of oil and gas.

Road Development

Hinman (1974) noted that north of the Brooks Range in Alaska, grizzly bears are most commonly found in the bottoms of river valleys, particularly in spring. Man's developmental activities also utilize the river valleys on the North Slope. Rivers provide the transportation corridors, campsites, and sources of gravel for road and other construction. The result is a magnification of the effect of man's presence by concentrating it in some of the most vulnerable and essential grizzly habitat. Singer (1976) documented the importance of river bottoms to grizzly bears on the western edge of Glacier National Park, Montana, during spring and fall.

Barrett and Bruns (1972), in making a subjective analysis of the oil and gas operations in the Pincher Creek region, said that road development appears to have the most significant impact. Many hectares of habitat have been completely denied to native flora and fauna as a result of all-weather road construction, well sites, pipeline heater and pump buildings, railroads, and processing plants. Additional stress is placed on wildlife as a result of incidental human disturbance and heavy hunting pressure along roads and open slopes. Ditches, heavy traffic, and deep snowdrifts resulting from all-weather roads may hinder daily and seasonal movement of wildlife. The overall effect of industrial activity on big game species in the Pincher Creek area has been detrimental, as particularly evidenced by a pronounced decline in the number of grizzlies.

Stuart (1974) wrote that game departments in the northern Great Plains have been aware that accelerated prospecting and development of new oil fields during the past 2 decades has had an adverse impact on big game populations in the areas of activity. The adverse effects are due to increased poaching activities by exploration, drilling, and operating crews and the building and maintenance of roads in areas heretofore inaccessible to vehicle travel.

The USDI (1975) noted that for initial exploratory work, minimum alterations are made in roadway systems. After decisions are made to drill in a given area, an improved road system is required for the transportation of heavy loads. Once production has been established, newly constructed roads are normally upgraded. The report continued (p. 8-17), "Land use and recreation activities may also be disrupted. Scenic views and vistas, wilderness qualities, and physical features are altered, at times permanently. Population density, employment, and cultural lifestyles would undergo long-term changes which affect access, utility networks, waste disposal, and creation of additional corridors."

The Influence of Survey, Development, and Production personnel

Hinman (1974) said that during the preconstruction phase of the Alaska pipeline, one of the chief impacts upon wildlife was animal-people confrontations. Although policies ban the feeding of wild animals and the improper disposal of garbage — which attracts animals — infractions of these directives continue because of problems in enforcement. In some camps, the deliberate feeding of wild animals, particularly for the purpose of photography, is widespread even though officially banned. A fine of $1,000 imposed by Alaska for feeding carnivores in an 8-km strip on either side of the 1,290-km pipeline has been ineffectual (Henning 1976).

Disturbance and Bear Behavior

Quimby (1974), working in the Canning River drainage of Alaska, found that approximately 70 percent of the grizzly bears observed reacted strongly to aircraft disturbance. Helicopters caused the greatest disturbance. Marked animals, previously captured through the use of aircraft, tended to have the strongest reaction. By the time they were sighted from aircraft, 32 percent of the grizzly bears were already fleeing, several at a distance of 0.8 km and 1 bear at approximately 1.6 km. Grizzly bears appeared to be more sensitive to aircraft disturbance than caribou (*Rangifer tarandus*) or moose (*Alces alces*). Hinman (1974) mentioned that it is extremely difficult to enforce any aircraft restrictions against harassment of bears.

Disturbance of bears in or near dens may have a severe impact. Quimby (1974) found that helicopters could disturb grizzly bears sufficiently to cause them to abandon their dens on the Canning River in Alaska. In a "Statement on Proposed Beaufort Sea Nearshore Petroleum Leasing" (1975, unpublished), Lentfer pointed out, "We do not know how much disturbance bears denning in the wild will tolerate. We know that bears in zoos produce cubs successfully only if completely shielded from noise and visual disturbance for the normal denning period and for an additional several months following parturition." Knight et al. (1976) reported the possible disturbance of a denning grizzly bear in the Yellowstone ecosystem. The radio-marked bear abandoned its den after snowmobile activity nearby.

Research information is generally lacking on how disturbance may affect grizzly bear behavior in the Montana locations proposed for oil and gas leasing. Jonkel (1970) said that under natural conditions the behavior of bears seems recessive or defensive rather than aggressive, and only when hunted or when in close association with man through peculiar circumstances do they become dangerous. Wright (1909) observed that the grizzly was wary and, among other peculiarities, liked seclusion. He noted that grizzly bears would change routine instantly if intruded upon, and if molested to any extent would leave regular feeding grounds. Wright spent 25 years closely observing grizzly bears in Montana and nearby areas.

Geist (1971) said that human disturbances can cause severe alterations in the behavior of animal species, with repercussions on the physiology, population dynamics, and ecology of the animals.

Free-living ungulates, if hunted, stalked, and repeatedly frightened, will flee. This response is likely to continue for a long time even if all hunting stops (Batchelor 1968).

According to Geist (1971), investigations conducted by agriculturists and experimental psychologists as well as evidence gained in reindeer husbandry and ungulate control in New Zealand give little cause for complacency. The evidence suggests that we should be much better informed on the direct and indirect effects of hunting, tourism, mineral exploration, construction, and harassment by light aircraft.

Geist (1971:417) continued: "For every stimulus the animal appears to attain an appropriate response, which reduces 'indecision'. If something unfamiliar appears, the animal experiences an alarm reaction, and prepares itself physiologically for flight. If severe disturbance follows, it forms an extremely strong aversion toward this object or situation. It (1) becomes excited if the unpleasant object or any evidence associated with it is sensed, and remains excited even after the object disappears; (2) avoids the locality where the disturbance was experienced; and (3) generalizes to all similar objects and localities and avoids them or becomes disturbed upon sensing them."

Pearson (1975) stated that grizzly bear range in the Yukon Territory can support a density of approximately 1 grizzly per 27 km^2. Populations exist in these densities over a considerable part of the Yukon wherever man has had only limited access. The large areas in south-central Yukon, where human activity has been concentrated since the turn of the century, probably supports a population of about one-half the above density.

The Yukon Territory has an area of 536,466 km^2. Its resident human population is about 20,000; of this number, about 13,000 dwell in Whitehorse (*The Milepost* 1975). Montana has 380,927 km^2 and about 700,000 human residents. Kalispell, Montana, centered adjacent to Montana's grizzly range, has 11,300 people in the corporate city limits and 20,500 residents in the city zone, a population comparable to that of the Yukon.

Spin-off Activities Resulting from Oil and Gas Development

Weeden (1971) stated that the present or foreseeable direct effects of petroleum development on animals, vegetation, soil, and water, though important, are insignificant when compared with the eventual secondary effects resulting from economic and population growth stimulated by petroleum extraction. Hinman (1974:161) said, "Perhaps the most profound effect of the Alyeska Pipeline and oil development in the North in general will be the degree to which this development acts as a catalyst for further development."

MONTANA SITUATION

Logging

In Montana, studies to determine the conflicts between logging and grizzly bears have just begun (Jonkel 1976). Definite answers will not be available for some time. Portions of occupied grizzly bear habitat have been uneconomical to log in the past because the timber extracted would not pay for the road-building. If access roads are built by energy companies, the additional impacts of logging are also likely to occur.

Recreationists

Although limited information is available on the total numbers of recreationists using grizzly bear habitat, their total effect on the welfare of the bear is unknown at this time. Roads developed for oil and gas exploitation would probably increase the number of motorized recreationists. Many of the roads in bear habitat east of the Continental Divide are the result of past seismographic operations. Some of the roads have been closed by land administrators and many others have been closed through deterioration. Relatively few kilometers of the existing roads are suitable for four-wheel-drive vehicles or all-terrain vehicles. Many of the ranchers within occupied grizzly bear habitat on the Rocky Mountain Front have closed their lands to trespass during hunting seasons to all but horseback or foot travel. This closure has resulted from the many acts of motorized vandalism that occurred in the past.

Subdivisions

Subdivision on private land has boomed in Montana in recent years. Scenic mountain foothills and river bottomlands are highly susceptible to development if access roads are built nearby. Most counties do not yet have land-planning programs that protect critical wildlife habitat from subdivision. In the localities where major subdivisions are occurring, 93 percent of the subdivisions are not even exposed to public review (*Great Falls Tribune* 1977).

Grizzly bears and subdivision development appear incompatible. For example, in 1976, 1 grizzly bear was credited with breaking into 30 cabins on the North Fork of the Flathead River. East of the Continental Divide on the Teton River, over 50 recent observations of grizzly bears have occurred around a site that has been proposed for development of a large subdivision. It can be predicted that if much roadless federal land adjacent to private land is leased for oil and gas development, increased conflicts between grizzly bears and subdivision residents and workers will occur to the detriment of the grizzly bear.

Domestic Livestock

Domestic livestock and grizzly bears have conflicted in the past (Murie 1948, Hubbard and Harris 1960). People generally think of the conflict in terms of grizzly bears eating or killing domestic livestock. Little information has been collected on how domestic livestock may compete with the bear (Border Grizzly Technical Committee 1975). Mealey (1975) described grizzly bear grazing and food habits in Yellowstone National Park. Plant species that appear to be very important in the diet of the grizzly bear are listed as highly palatable, decreaser species that are attractive to livestock, according to federal range management handbooks. East Front livestock may therefore compete with grizzly bears for food, particularly in mesic sites such as creek bottoms (Schallenberger 1976). Time-space conflicts have been reported between cattle and elk (Lonner 1974). The elk moved from their preferred grazing areas when cattle utilized the range. Similar reports have been made for moose (Schladweiler 1974) and bighorn sheep (*Ovis canadensis*) (Irvine 1969). Whether grizzly bears have adverse time-space relationships with cattle is unknown. More intensive research is needed to document livestock-grizzly bear relationships before oil and gas impacts are added to existing pressures in localities used by both domestic livestock and grizzly bears.

Forest Fires

Forest disclimax created by fire represents important habitat for the grizzly bear (Jonkel and Cowan 1971, Martinka 1972, Schallenberger 1974). Fire suppression policies of this century have had an effect on the grizzly bear, but the magnitude is unknown. Berries, russet buffaloberry (*Shepherdia canadensis*) and huckleberry (*Vaccinium* spp.) among others, are important to grizzly bears in late summer and fall in Montana. These food species apparently thrive in old burns. Wet, quaking aspen (*Populus tremuloides*) habitat types (described by Lynch 1955) near Glacier National Park appear to produce plant species eagerly sought by grizzly bears. Vogl (1969) reported that aspen reproduction is helped by wildfire. More information is needed on the relationships of fire and grizzly bears. If oil and gas exploitation occurs on forested lands, it seems highly unlikely that natural fire or even prescribed fire will play much of a role in the foreseeable future in locations associated with expensive industrial development structures.

Wild Ungulates.

Cole (1972) reported that 58 percent of the feeding activities of grizzly bears during the March-May period in Yellowstone National Park was related to feeding or preying on ungulates. Craighead and Craighead (1972) also confirmed that animals weakened by severe winters and carcasses of winter-killed animals formed a considerable portion of the diet of Yellowstone grizzly bears in early spring. This factor may be critical wherever grizzly bears of northwestern Montana are as dependent upon large wild ungulates as those of Yellowstone National Park. Adverse effects of oil and gas exploitation upon wild ungulate populations could thus prove detrimental to grizzly bears. Also, the lack of wild ungulates could cause increased conflict with domestic livestock, which would result in further harm to the bears. More spring surveys are needed to determine existing relationships between ungulates and bears.

DISCUSSION

Available information indicates that impacts of oil and gas exploitation should be considered primarily detrimental for grizzly bears in northwestern Montana. The greatest impacts appear to result from construction of roads into previously unroaded areas and from increased numbers of people. Past experience indicates that it is very difficult to prevent man-bear confrontations. Recurring confrontations ultimately reduce grizzly bear habitat and populations. If this loss is to cease, new ways to control industrial activities must evolve. Before oil and natural gas leasing proceeds on East Front public lands, we should determine how much wilderness habitat and how many grizzly bears are going to be lost or affected at levels detrimental to the bear populations because of the *cumulative* impacts of developmental projects.

Hasty exploration and development of oil and natural gas resources could seriously reduce or eliminate grizzly bear habitat and populations. If careful research evaluation of the oil and natural gas situation indicates that grizzly habitat must be exploited, then development of these resources can be conducted under carefully controlled conditions.

The mineral leasing law of 1920 should perhaps be changed so that exploration leases can be granted on public lands, if necessary, without the present automatic provisions for development and production. If exploration shows that reserves are available, then the public could decide whether development and production impacts would outweigh other social costs. Exploration data on public lands should be made available to the public so that the land is not subjected to repeated exploratory activity by the various companies.

The foregoing discussion offers solutions for grizzly bear management. However, development may proceed in some regions of occupied grizzly bear habitat before adequate management data are available on the grizzly bear. If exploitation of oil and natural gas is unavoidable, adverse impacts could be minimized if pilot projects were established adjacent to existing roads, with exploration, development, and production greatly restricted during times when grizzly bears make heavy seasonal use of those areas. Restrictions on spin-off developments would also help to minimize the impacts and measure the effects of oil and gas operations on grizzly bears.

Finally, the long-term cost of protecting unique mountain wildland and resident species such as grizzly bears should be considered in the cost of exploiting oil and natural gas resources. Man must expect to give a little if he is to continue to have grizzly bears in presently occupied habitat.

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RESPONSES OF GRIZZLY BEARS TO HYDROCARBON EXPLORATION ON RICHARDS ISLAND, NORTHWEST TERRITORIES, CANADA

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Abstract: Observations on numbers, distribution, locations of dens, and responses of grizzly bears (*Ursus arctos* L.) to industrial disturbances were noted on Richards Island, Northwest Territories, Canada, during 1972-75. During this period, 13-23 bears occupied the 2,460-km² study area. Bear responses to hydrocarbon exploration and related activities were observed 23 times, and 35 dens were located. Bears were distributed evenly over the study area during summer but avoided camps by 1 km or more. Density was comparable to that of other arctic mountain and coastal bear populations, and no decline was apparent. Effects of industrial activities included slight loss of habitat, disturbance of denning areas resulting in abandonment of dens, and relocation of problem bears. It is predicted that proposed natural gas production facilities will not be compatible with continued survival of grizzly bears in Richards Island.

Grizzly bears have so long been abundant in the Mackenzie Delta region that one of the Eskimo place-names is Aklavik, or "Bear Country" (Porsild 1945). Richards Island in particular has been the location of numerous reported sightings (Clarke 1944, Porsild 1945, Macpherson 1965, Nolan et al. 1973). Although generally protected east of the Mackenzie River, grizzly bears are hunted within the Reindeer Grazing Reserve, which includes Richards Island (Northwest Territories 1971). Yet arctic grizzly bears are slow to mature and reproduce (Curatolo and More 1975) and they probably cannot stand increased pressures on their populations (Macpherson 1965). The spread of modern culture has caused grave concern for the grizzly's continued survival, both in areas of the western Canadian Arctic (Macpherson 1965) and on the North Slope of Alaska (Bee and Hall 1956). The threat of hydrocarbon exploration to grizzly bears has been recognized since 1956 (Bee and Hall 1956, Barry 1959). Since then, bears have been studied by Quimby (1974), Slaney (1974), Pearson (1975), Pearson and Nagy (1976), and others in this general region in order to predict the impact of proposed industrial development.

Oil companies have explored Richards Island since the mid-1960s. Oil and natural gas have been found and construction of production facilities may begin soon.

Grizzly bear studies by F. F. Slaney and Co. Ltd. during 1072-75 were part of a broader environmental program to determine indices of mammal density and to identify and describe important habitats near areas of possible future facilities for natural gas production on Richards Island. Results were reported by Slaney (1974, 1975) and by Harding (1976). The purpose of the present paper is to discuss results from the above studies in the context of bear observations and den site locations in relation to existing gas exploration facilities and to present new observations on grizzly responses to hydrocarbon exploration collected by the senior author during the course of these studies.

The studies were supported by Imperial Oil Ltd., Gulf Oil Canada Ltd., Shell Canada Ltd., and Canadian Arctic Gas Study Ltd., who gave permission for the publication of data.

STUDY AREA

Richards Island, a part of the Mackenzie Delta, has an arctic climate and biota influenced by the Mackenzie River, with attendant warmer weather and seasonal flooding of lowlands (Gill 1972). Its southern apex 69°00′ N, 134°40′ W coincides with the northern tree limit. Vegetation is typical of arctic coastal tundra. Because the area is a complex interface between arctic and subarctic climates, forest and tundra biomes, lowland and upland terrain, and freshwater and marine ecosystems, it supports an abundance and a wide variety of wildlife (Harding 1974). Topography includes deltaic floodplains and Pleistocene uplands (Mackay 1963) ranging in elevation up to 70 m above sea level.

Hydrocarbon exploration facilities in the area include 3 base camps, drilling rigs (each with associated camp and airstrip), a communication tower with generating plant, gravel (borrow) pits, and a network of winter roads. These facilities and associated aircraft flight corridors are distributed over approximately half the study area and are concentrated in the southwest portion of the island.

Facilities proposed for the study area include wharf sites, more gravel mining sites, 2 natural gas processing plants, an elevated pipeline gathering system radiating from each plant (Slaney 1974), a 122-cm buried gas trunk line, and all-weather roads to Tuktoyaktuk and Inuvik (Foothills Pipe Lines Ltd. 1975, Pearson and Nagy 1976).

During 1972 and 1973, a miminum of 13 and 23 grizzly bears, respectively, occupied the 2,460-km² study area (Slaney 1974). During 1974 and 1975, 14 bears (including 3 sow-cub groups) and 16 bears (including 4 sow-cub groups), respectively, denned on the island (Harding 1976).

Because there was no apparent seasonal movement to or from denning areas, the numbers of bears denning in the study area were considered representative of the population densities. These densities of 1 bear per 176 km^2 and 154 km^2 are similar to those reported by Curatolo and More (1975) of 1 bear per 119-228 km^2 in arctic mountains, and 1 per 200 km^2 by Pearson and Nagy (1976) on the arctic coast. Of the 35 dens located, 28 (80 percent) were within general areas of hydrocarbon exploration activity as indicated by flight corridors (Slaney 1974, 1975).

METHODS

During May-September, 1972 and 1973, observations were collected opportunistically during the course of other studies. These observations covered the study area but concentrated on known bear denning areas and areas of proposed hydrocarbon development.

During 1974-75, aircraft, snowmobiles, and snowshoes were used to track bears after their emergence from winter dens, and in areas of industrial activity. The Canadian Wildlife Service began a capture-marking program in 1974 on the study area. Radiocollars and color-coded markings facilitated the monitoring of individual bear movements. Reactions of bears to Cessna 185 and 337 and Bell 206 aircraft approaches at various altitudes and horizontal distances were recorded during the den surveys of 1973, 1974, and 1975. Industrial personnel were interviewed with respect to bear-man encounters.

RESULTS AND DISCUSSION

Den Disturbance

At least 2 denning bears were disturbed by hydrocarbon-related operations during the study. In January 1973, a seismic vehicle was driven over an active den, causing the bear to abandon it. The bear left the area and was observed several times before it was shot by an Eskimo trapper during March or April. Again, In November 1973, a denning bear was disturbed during gravel mining operations. The bear fled the area and its den was destroyed. Although these 2 denning bears were disturbed, others wintered successfully in dens 1.6-6.4 km from active camps. Their movements after emergence are discussed below.

Industry-related Movements

Of 17 instances where bear movements were followed in detail within 7.2 km of camps, 16 of the bear groups did not venture closer than 1.0 km to the camps. Tracks measured during the summer of 1973 indicated that on at least 8 occasions, bears foraged or traveled within 2.6-7.4 km of industry camps without being seen and without entering the camps. A good example occurred in July 1973 when tracks of a large single bear were located and followed along a beach towards a drilling rig. The tracks indicated that as the bear came in sight of a drilling rig 1.4 km away, it turned and then bypassed the rig, keeping approximately the same distance from it. On a ninth occasion, tracks of 1 bear were found adjacent to an active gravel pit, although the bear had not been noticed by shift workers.

In April 1974, 3 bear dens were located within 4.8 km south of a borrow pit and the associated camp. Upon abandoning their dens, 2 single bears and a sow-cub group traveled generally northward toward the camp, bypassing it by 1.2, 1.0, and 2.0 km, respectively. An adult male spent several days foraging 3.0 km from a drilling rig that was audible to the investigator at that distance but was not visible because of a low, intervening hill. Similarly, another adult male foraged for several days approximately 7.2 km from a staging camp. The camp was visible to the investigator at that distance. Tracks indicated that these male bears finally left the vicinity of the camps without venturing closer.

In 1975, a single bear vacated a den 1.6 km from a gravel excavation camp and bypassed the camp by approximately 1.0 km. Similarly, a single adult and a sow-cub group, which denned 3.2 and 6.4 km, respectively, from a staging camp, did not approach the camp.

Only twice did bears persist in remaining near camps. In July 1974, a subadult female grizzly was seen repeatedly near a camp's sewage lagoon. At the request of camp administrators, Canadian Wildlife Service personnel tranquilized and relocated the bear. In 1975, personnel of the same camp again requested the removal of a bear that had been observed for several days among the buildings. Later, however, the bear left of its own accord. Bears entered camps briefly on 4 other occasions. Each of 3 different industry staging camps were approached once by single bears during summer 1973. In May 1974, a single bear entered a drilling rig camp. In all of these instances, camp personnel chased the bear away, twice assisted with, respectively, a light truck and a forklift.

These observations showed that although bears did not avoid general areas of industrial activity, they appeared to avoid drilling and staging camps by distances of at least 1 km. Whether bears consciously avoided those areas or their travel routes bypassed the camps for other reasons could not be ascertained. However, during 4 years of study, a minimum of 13-23 bears coexisted with industrial activity on the island. Presumably, most had an opportunity to enter camps. Since only 6 such instances were recorded, it must be assumed that most bears actively avoid industrial camps.

Disposal methods have usually been adequate to prevent bear attraction to garbage. The bears that did enter camps fled quickly from crowds of people or from motorized vehicles. In the 2 instances mentioned previously where bears persisted in remaining near a camp, area personnel requested that the bears be relocated.

Responses to Aircraft

Grizzly bears were observed from aircraft by the senior author 53 times during 1972-75. Because industrial operators have used fixed-wing and helicopter aircraft intensively in the area for years, bears had had prior experience with them. The value of these data was primarily in the indication of wide variability and unpredictability in responses. Of 36 bear responses to fixed-wing aircraft, 22 (61 percent) were overt (running or hiding), indicating aversion and some degree of energy expenditure. Most (15, or 88 percent) of the 17 bear responses to helicopters were overt. Bears that had been tranquilized and captured usually tried to avoid subsequent approaching aircraft by hiding or fleeing, suggesting learned avoidance behavior. Such learned avoidance could occur, and probably has, in relation to camps as well as to aircraft.

CONCLUSIONS

We have no evidence to suggest that the current numbers and distribution of grizzly bears are being affected by hydrocarbon exploration or associated activities, but neither can we show that the population has not been affected. The fact that observed densities are within the range of those of other arctic mountain and arctic coastal bear populations indicates at least that grizzlies on Richards Island have not as yet been decimated by industrial activity. Individual bears are, however, being affected through (1) slight loss of habitat due to avoidance of drilling and staging camps; (2) disturbance of bears during dormancy, causing abandonment of dens; and (3) relocation of problem bears frequenting camps.

The implications of these findings with respect to proposed gas production facilities are serious. Although pre-impact data are unavailable, the population has apparently stabilized in relation to existing facilities. The addition of proposed facilities and the intensity of related activities will undoubtedly cause bears to withdraw or be removed from industrialized areas. The construction of proposed all-weather roads will make the area more accessible to hunters from Tuktoyaktuk and Inuvik, further threatening the population. For these reasons we feel that the cumulative impact of the proposed hydrocarbon development facilities will be that of reducing the current grizzly bear population on Richards Island to the point where continued existence of the population will depend on immigration from adjacent areas.

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THE NATURAL FOOD HABITS OF GRIZZLY BEARS IN YELLOWSTONE NATIONAL PARK, 1973-74[1]

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Abstract: The natural food habits of grizzly bears (*Ursus arctos horribilis* Ord) in Yellowstone National Park were investigated in 1973-74 to identify the grizzly's energy sources and trophic level(s), nutrient use, and distribution. Food consumption was determined by scat analysis and field observations. Food quality and digestibility were estimated by chemical analysis. Grizzlies were distributed in 3 distinctive feeding economies: *valley/plateau*, a grass/rodent economy where grizzlies were intensive diggers; *mountain*, primarily a grass/springbeauty/root economy where grizzlies were casual diggers; and *lake*, primarily a fish/grass economy where grizzlies were fishers. The economies occured in areas with fertile soils; distribution of bears within each was related to the occurrence of succulent plants. The feeding cycle in the valley/plateau and mountain economies followed plant phenology. Grizzlies fed primarily on meat before green-up and on succulent herbs afterwards; meat, corms, berries, and nuts became important during the postgrowing season. Succulent grasses and sedges with an importance value percentage of 78.5 were the most important food items consumed. Protein from animal tissue was more digestible than protein from plant tissue. Storage fats were more digestible than structural fats. Food energy and digestibility were directly related. Five principle nutrient materials (listed with their percentage digestibilities) contributed to total energy intake: protein from succulent herbs, 42.8; protein and fat from animal material, 78.1; fat and protein from pine nuts, 73.6; starch, 78.8; and sugar from berries and fruits, digestibility undetermined. Protein from succulent herbs, with a nutritive value percentage of 77.3, was the grizzlies' primary energy source. Because succulent, preflowering herbs had higher protein levels than dry, mature herbs, grizzly use of succulent herbs guaranteed them the highest source of herbaceous protein. Low protein digestibility of succulent herbs was compenstated for by high intake. Grizzlies were digestively flexible and maximized use of protein from plant and animal sources. They were adapted to the most constant and abundant sources of protein: succulent herbs and animal material from open, fertile grasslands. Competition among grizzlies for animal food during the pregrowing season may be regulatory for the grizzly population. The grizzly population level can be partially accounted for by the grizzlies' status as secondary consumers during pregreen-up periods and primary consumers during the growing and postgrowing seasons. The essential environmental requirement was the availability of fertile grasslands and herblands interspersed with cover and capable of maintaining artiodactyls, rodents, and abundant nutritious herbs as sources of food.

Extensive grizzly bear (Rausch 1963) use of unnatural foods (garbage and camp groceries) in Yellowstone National Park occured from the early days of the park until closure of the Trout Creek and West Yellowstone open-pit garbage dumps in 1971 (Skinner 1925, Cole 1976). After these primary sources of unnatural foods were removed, most grizzlies resumed use of natural foods (Cole 1974).

This report on grizzly bear use of natural foods is based on research conducted in 1973 and 1974 as part of the Interagency Grizzly Bear Team Study. The overall objectives were to develop hypotheses about the grizzly's natural energy sources and tropic level(s), the quality and quantity of nutrient use, and grizzly distribution.

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STUDY AREA

The study area included all of Yellowstone National Park, which occupies about 8,900 km^2 in the states of Wyoming, Montana, and Idaho. The geology of the park was described by Keefer (1972) and Eaton et al. (1975), the climate by Lowery (1959), and the vegetation zones by Despain (1973b). Soil types in the park were described by Washington (1917), Despain (1973a), and Stermitz et al. (1974).

Interactions among the park's geologic events, climate, soils, and vegetation resulted in 3 apparent physiographic/vegetative units (Fig. 1). These units are as follows: (1) the mountainous unit with the spruce-fir (*Picea engelmanii-Abies lasiocarpa*) and alpine-tundra zones and herblands and grasslands covering fertile andesitic soil; (2) the valley and plateau units with grasslands and the Douglas-fir (*Pseudotsuga menziesii*) zone covering fertile, transported soils; and (3) the plateau unit with lodgepole pine (*Pinus contorta*) covering infertile rhyolitic soils.

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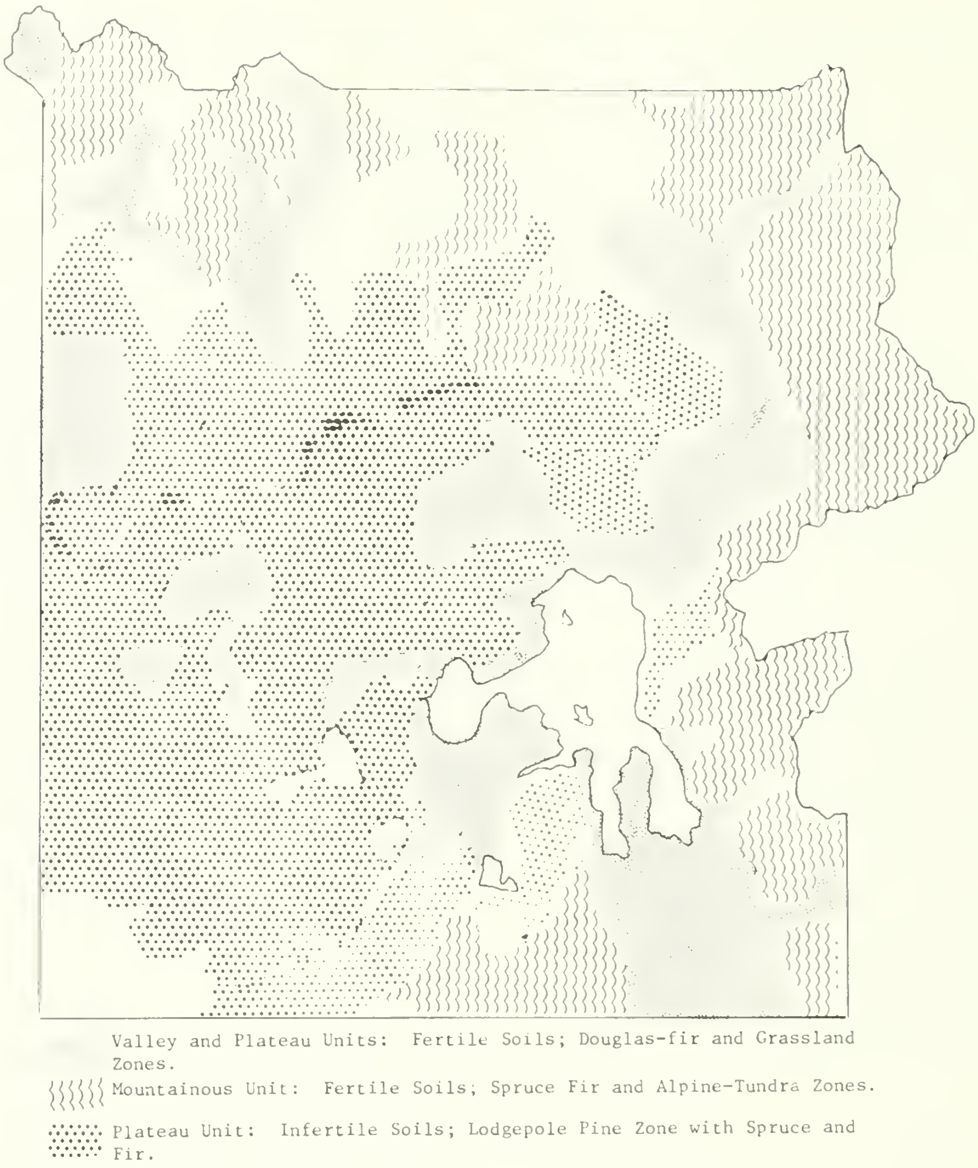

Fig. 1. Map showing 3 generalized physiographic/vegetative units in Yellowstone National Park.

METHODS

Quantitative Analysis: Scat Collection, Preparation, and Analysis

Collections of scats and visual obeservations of feeding that were made during 557 man-days in the field were used to determine the quantitative importance of food items used by grizzly bears. In 1973, this activity was parkwide, excluding the Absaroka Range. In 1974, activity was concentrated in major use areas identified in 1973.

Size distinguished grizzly scats from black bear scats; those with diameters 5 cm or greater were normally considered grizzly scats (Murie 1954). Several field observations verified the validity of this criterion. Other evidence considered in identifying grizzly scats consisted of associated track sign and feeding activity sign, visual observation of bears, and the general nature of the location. Scats with diameters less than 5 cm were assumed to be those of small or immature grizzlies only if there was some evidence of grizzly use of the location.

Every grizzly scat located singly was collected. When groups of 10-25 scats were located, one-half the total in each group was collected. When groups of more than 25 scats were located, one-third the total in each was collected. All scats were individually identified according to location, altitude, vegetative surroundings, and age estimated to the nearest month by characteristics of the site (Mealey 1975). Scats were air-dried for storage; those that were extremely moist or infested with insect eggs or larvae were oven-dried at low heat to kill organisms that could change the nature of scat contents.

Analysis of scat contents was conducted in the field and in the laboratory. Scat contents were more identifiable when fresh in the field, and plant remains were easily compared with nearby specimens. Materials analyzed in the field were taken to the laboratory for further study.

Analysis of bear scats in the laboratory followed the techniques of Tisch (1961), Russell (1971), and Sumner and Craighead (1973). Basic steps involved (1) rehydration of fecal material to render it pliable and to restore its original form, (2) separation of material into homogeneous groups by use of screens (No. 10 and No. 20 mesh), (3) identification of contents, and (4) recording of identified materials.

Identification to species, through macroscopic and microscopic examination, was usually successful for all plants except grass and sedge. Animal materials were identified with the aid of reference collections of bones and hair and textual references (Spence 1963, Hoffman and Pattie 1968).

The occurence and volume of each identified food item were recorded as each scat was analyzed. Visual estimates of volume were recorded under 1 of 4 categories: trace-25 percent, 25-50 percent, 50-75 percent, and 75-100 percent. Estimation of scat composition by volume undervalued the use of some foods as indicated by proximate analysis techniques that established differential digestibility of food items.

Data were grouped in a number of categories including 3 that related grizzly food use and plant phenology: pregrowing season, 1 April-1 June; growing season, 1 June-1 September; and postgrowing season, 1 September-15 November. These periods reflect plant growth conditions in Yellowstone Park (D. G. Despain, personal communication, 1974).

Food items were ranked according to importance value (Sumner and Craighead 1973) calculated as:

$$\text{Importance value} = \frac{\text{Percent frequency of occurrence} \times \text{Percent of diet volume}}{100}$$

where percent frequency of occurrence equals the total number of times a specific food item appeared in scats of the sample group, divided by the total number of scats in the sample; and percent of diet volume equals the total percentage volume of an item occurring in scats of the sample group, divided by the total number of scats in the sample.

Importance value was chosen as the indicator of food item importance because it establishes relative equilibrium between items that occurred frequently but in low volume percentages.

Percents composition per item and importance value percents were calculated. Percentage composition per item suggests a degree of selection for particular foods; values were derived by dividing the total percent volume of an item by the total number of scats containing that food item. Importance value percentages were derived by adding the importance values in the group and dividing individual values in the group by the sum.

Qualitative Analysis: Food Quality, Digestibility, and Nutritive Value

Identities, energy values, and apparent digestibilities of the principal nutrient materials of the most important grizzly foods were determined, as were seasonal nutritive values.

Standard proximate analysis procedure detailed by Crampton and Harris (1969) was used in estimating the quality and apparent digestibility of food items. Food items containing starch were also evaluated by a special starch analysis method (Banks et al. 1970). Food quality is defined in terms of the amounts of protein, fat, and carbohydrate present in a food item and the caloric values of the item. Apparent digestibility is an estimate of nutrient utilization and digestive efficiency. Digestibility was estimated by calculating the percentage of nutrient intake not present in food item residues in scats.

Determinations of food quality and apparent digestibility were subject to a minimum of 4 sources of possible error: (1) analytic procedures could not account for all material completely assimilated; (2) in proximate analysis, nitrogen-free extract values are determined by difference; (3) feces probably contained protein and fat from nondietary origin (Crampton and Harris 1969); and (4) sampling error.

Food items and scats containing residues of the same items were collected at the feeding sites. Scat and food item samples were paired and submitted for analysis. Analytical methods for proximate analysis followed the Association of Official Agricultural Chemists handbook (Horowitz 1975), and the analyses were performed by the Analytical Chemistry Laboratory of Montana State University.

The digestibilities of 4 principal grizzly nutrient materials were estimated by averaging the values for individual food items.

Seasonal nutritive values were calculated from data on seasonal food use in 1974. Nutrient importance values were determined by a method similar to that used for the determination of food item importance values.

A nutritive value index (NVI) of the principal nutrients was calculated to estimate each nutrient's contribution toward the grizzly's energy intake. The index was calculated according to the formula:

$$\text{NVI} = \frac{\begin{matrix}\text{Nutrient intake percent}\\ \text{(Percent importance value)}\end{matrix} \times \begin{matrix}\text{Digestibility}\\ \text{percent}\end{matrix}}{100}$$

Nutritive value indices were converted to percentages to facilitate comparisons.

RESULTS

Distribution

Grizzly distribution in the park was influenced by unique processes of interaction between bears and their foods. In 1973, 3 such processes were hypothesized and each identified as an economy. These were the *valley/plateau*, *mountain*, and *lake* economies. The basis for initially distinguishing these economies was the simultaneous occurence of scats in each. After further study in 1974, each economy seemed to represent a mix of physiographic and biotic conditions resulting in a characteristic pattern of interactions between grizzlies and food items that allowed the bears to maximize food use. Each economy appeared to represent a center of concentrated grizzly feeding activity determined by locations of scats collected in 1973 and 1974. Areas of high grizzly density determined by aerial surveys were coincident (Knight 1974, 1975).

Feeding economies were centered on areas with fertile soils (Fig. 1). Little feeding activity was apparent on infertile soils. Highest grizzly densities, excluding the lake economy, were reported on the rich grasslands of Hayden and Pelican valleys (Knight 1975), although use of these areas was not as evident in 1975 as in 1973-74 (Knight 1976).

Valley/Plateau Economy

Major epicenters of the valley/plateau economy were Hayden, Pelican, and Lamar valleys, and Cougar Creek Flat. Fertile, transported soils support an abundant grassland biota that provided most of the food used in the economy. The valleys and flat were largely surrounded by plateaus with infertile soils and lodgepole pine forests. The plateau component provided cover and occasional food.

Comparing grizzly foods of the valley/plateau economy between years indicated that the diets in 1973 and 1974 were similar. Grasses and sedges were the most important items both years. The importance of white clover (*Trifolium repens*) and elk thistle (*Cirsium foliosum*) differed between years because an area with scats containing primarily the remains of these items was sampled in 1973 but not in 1974. For the 2-year period, grasses and sedges constituted 82 percent of diet importance.

The general feeding cycle appeared to follow plant phenology. During the pregrowing season, grizzlies were primarily meat eaters, congregating on ruminant wintering areas and taking the animal material available. Cole (1972) has detailed this activity. Corms, roots, and grass were eaten before and during early green-up. During the growing season, grasses, sedges, forbs, and rodents were the primary foods. Succulent vegetation in open areas near cover was perferred; its availability, linked with that of rodents, influenced distribution of grizzlies. Most plants were succulent at that time and bears were widely distributed.

During the postgrowing season, succulent grasses and forbs remained important foods. Since these foods were associated only with moist sites, feeding was limited to such sites and bears were narrowly distributed. Seasonal foods in the lodgepole pine forests became available as grasses, sedges, and forbs in the valleys desiccated; whitebark pine (*Pinus albicaulis*) nuts, and berries were taken along with mushrooms (*Russula* sp.) and the rhizomes of smilacina (*Smilacina* sp.). Predation on male, breeding elk (*Cervus canadenis nelsoni*) may also have occurred. Extensive use was made of melica (*Melica spectabilis*) corms in Pelican and Lamar valleys.

Intensive digging was the characteristic feeding activity of grizzlies in the valley/plateau economy, especially during the growing season. Pocket gophers (*Thomomys talpoides*) and voles (*Microtus* sp.) apparently motivated this activity. Locally concentrated excavations ranged in volume from a few hundred cubic centimeters to nearly a hundred cubic meters. Most were from 1 to 5 m^3 in volume. Large numbers of scats were often found at digging sites. Average residues in scat contents were 90 percent grasses and forbs and 10 percent rodents. Grizzlies apparently pursued rodents but often settled for grasses, forbs, and a small amount of meat. Bears were observed locating, digging out, and eating roots, corms, bulbs, and young gophers. The small but consistent degree of success in catching rodents probably held the bears in the feeding pattern. Intensive digging activity and associated evidence of grazing usually occurred in locations where xeric sites were interspersed with mesic or hydric sites. The excavations occurred on the xeric sites and grazing occurred on the adjacent mesic or hydric sites.

White clover was used extensively where it was abundant and associated with other foods. As many as 50 scats containing only white clover residues were found in individual white clover patches.

Possession of a bull elk carcass during the postgrowing season, after herbs had dried, did not preclude a grizzly's other foraging activities. Most scats collected near its meat cache contained residues of plants and elk.

Mountain Economy

The Gallatin and Washburn ranges were major centers of the mountain economy. Their fertile andesitic and sedimentary soils supported abundant vegetation in mountain meadows, herblands, parklands, and on ridgetops.

The most important food items consumed in the mountain economy in 1973 and 1974 were identical and were similarly ranked. For the 2-year period, springbeauty (*Claytonia lanceolata*) ranked first in food consumption importance, grasses and sedges ranked second, the roots of Umbelliferae ranked third and whitebark pine nuts ranked fourth.

Again, the general feeding cycle followed plant phenology. There were elk and moose (*Alces alces shirasi*) wintering areas in the economy, and use of ruminant material probably occurred during the pregrowing season although this period was not sampled. During the growing season, springbeauty, grasses, and sedges were the most important foods. Springbeauty was taken primarily in ridgetop herblands; grasses and sedges were taken in meadows and parklands. Feeding activities and distribution of bears in relation to these foods were influenced by plant succulence. Feeding began in snow-free locations and followed snowmelt and green-up to the highest elevations by late June and August. After desiccation of plants on the highest ridgetops in late August, feeding occurred at lower elevations where plants remained green. Such sites were stream bottoms, springs, and herblands associated with persistent snowbanks. During the early postgrowing season, feeding activities continued to be influenced primarily by succulent vegetation on moist sites. Pine nuts and gooseberries (*Ribes setosum*) appeared to be incidental foods. In October, after the desiccation of most herbs, feeding activity was concentrated on ridges at elevations of about 2,740 m where pine nuts, Umbelliferae roots, and springbeauty corms were taken exclusively.

Foraging patterns of the early postgrowing season in the mountain and valley/plateau economies were similar in that grizzlies concentrated on moist sites with succulent herbs and used seasonal foods incidentally. Foraging in the late postgrowing season was different in the 2 economies because grizzlies in the mountain economy ate pine nuts, roots, and corms on high ridges, whereas in the valley/plateau economy grizzlies fed on grasses, forbs, pine nuts, mushroons, rhizomes, and ruminants in the lodgepole pine forest.

Casual digging for springbeauty corms and biscuitroot (*Lomatium cous*) roots was the characteristic feeding activity of grizzlies in the mountain economy. The resulting excavations were usually shallow, a few cubic centimeters in volume.

Eating of whitebark pine nuts occurred in 2 ways. Incidental use occurred in late August and September, when the mature cones remained on the trees. Since most grizzlies do not climb, the only cones available to the bears during this time were those on the ground as a result of squirrel (*Tamiasciurus hudsonicus*) cuts and windthrow. Exclusive use occurred in October and probably November after cone disintegration and/or abscission. At that time, nuts and cones were abundant on the ground and grizzlies were linked directly to them. A move to higher-elevation ridges where whitebark pine is abundant was a response to cone disintegration and abscission.

Grazing on grasses and sedges was concentrated in dense stands of succulent forage at least 8 cm tall. Grizzlies usually grazed with a sideways motion of the head, which placed the muzzle perpendicular to the vegetation. The food was grasped with the molars and plucked. Feeding activity was rapid and was sustained for prolonged, uninterrupted periods.

Lake Economy

The lake economy consisted of Yellowstone Lake tributaries that supported spawning cutthroat trout (*Salmo clarki*) used as food by grizzlies. The economy functioned in the south, southeast, and Flat Mountain arms of the lake.

The food items contributing to the diet in the lake economy were similar in 1973 and 1974 but differed in rank and importance value, probably because of sampling differences. During the 2-year period, grass and cutthroat trout were the most important foods.

The feeding cycle was directly related to spawning activities of cutthroat trout, which extended from late June to early August. Time of occurrence of spawning trout varied among individual tributaries (Knight 1975).

Feeding activity was observed along a tributary at the tip of Flat Mountain Arm during the last half of July 1974. Estimated flow in the steam was 0.13 m^3/second, and estimated peak fish density was 6 fish per linear meter within 0.8 km of the mouth. Cutthroat trout in this segment averaged 38 cm in length and 0.6 kg in weight. Eleven different grizzlies were sighted fishing in the vicinity between 16 July and 18 July 1974 (Knight 1975). Grass, horsetail (*Equisetum arvense*), and elk thistle were heavily grazed in the area. Grizzly

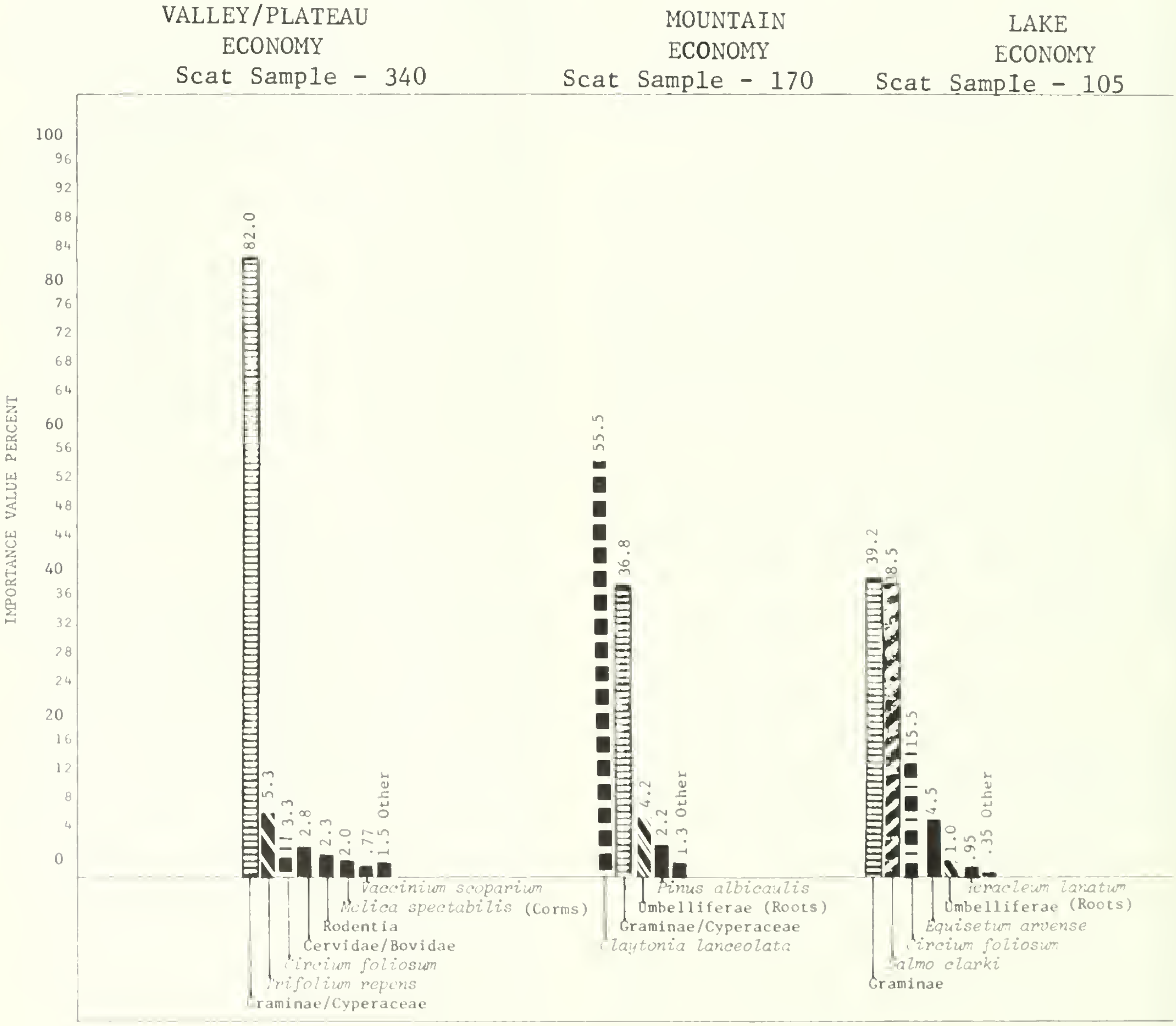

Fig. 2. Comparison of consumption of key food items by grizzly bears in different economics, Yellowstone National Park, 1973-74.

feeding activity was related to fish density in the tributary. On 2 August, peak fish density was estimated to be 0.5 fish per linear meter, and no fresh evidence of grizzly feeding was apparent.

Summaries

The 2-year summaries of food consumption for each of the economies show that grasses and sedges were the most important items in the valley/plateau economy, western springbeauty was the most important item in the mountain economy, and grass and cutthroat trout were the most important items in the lake economy (Fig. 2). The 3 economies were apparently oriented to: grasses and rodents (valley/plateau); springbeauty, grasses, and roots (mountain); and grasses and trout (lake).

Parkwide, the diet for each year was fairly constant. For the 2-year period, grasses and sedges were the top-ranked foods, with an importance value percentage of 78.5 (Table 1). Five of the 8 ranking food items were plants that represented 93.1 percent of total importance. The remaining 3 items, fish and mammals, represented 4.3 percent of the total importance value. Western springbeauty appeared to be the most highy selected of the major foods.

Food Quality and Apparent Digestibility

Five different samples of grass and grasses/sedges

Table 1. Summary of grizzly bear food consumption parkwide, Yellowstone National Park, 1973-74.

Food item	Use	Elevation (m)	Frequency occurrence percent	Percent composition per item	Percent of diet volume	Importance value	Importance value percent
Gramineae/Cyperaceae	Gramineae 95% stems leaves *Carex* sp. 5% heads	2,428	64.5	55.3	*35.70*	23.00000	*78.5000*
Claytonia lanceolata	Entire	2,821	15.1	79.9	*12.10*	1.80000	*6.1000*
Cirsium foliosum	Stems/heads	2,388	16.3	49.4	*8.00*	1.30000	*4.4000*
Trifolium repens	Stems/leaves/heads	2,369	11.0	57.0	*6.30*	0.69000	*2.4000*
Salmo clarki	Entire	2,376	9.3	57.8	*5.40*	0.50000	*1.7000*
Umbelliferae	*Perideridia gairdneri* 54% — roots *Lomatium cous* 46% — roots	2,525	10.9	41.6	*4.50*	0.49000	*1.7000*
Rodentia	*Thomomys talpoides* 63% *Microtus* spp. 35% *Marmota flaviventris* 2%	2,354	9.8	38.7	*3.80*	0.37000	*1.3000*
Cervidae/Bovidae	*Cervus canadensis* 90% *Odocoileus hemionus* 6% *Bison bison* 4%	2,318	8.1	56.5	*4.60*	0.37000	*1.3000*
Melica spectabilis	Corms	2,341	6.0	59.6	*3.60*	0.22000	*0.7500*
Equisetum arvense	Stems	2,409	5.5	49.3	*2.70*	0.15000	*0.5100*
Pinus albicaulis	Nuts	2,568	5.0	55.2	*2.80*	0.14000	*0.4800*
Vaccinium scoparium	Berries/leaves	2,408	4.2	63.4	*2.70*	0.11000	*0.3700*
Formicidae	Mature/larvae	2,504	8.8	9.6	*0.84*	0.07000	*0.2400*
Heracleum lanatum	Stems/leaves	2,463	3.1	47.1	*1.50*	0.04000	*0.1400*
Polygonum bistortoides	Entire	2,380	3.3	19.5	*0.63*	0.02000	*0.0700*
Russula sp.	Caps/stems	2,430	2.3	25.7	*0.59*	0.01000	*0.0300*
Fragaria virginiana	Fruits	2,447	1.6	18.4	*0.30*	0.00500	*0.0200*
Garbage		2,373	0.81	70.0	*0.57*	0.00500	*0.0200*
Taraxacum sp.	Stems/leaves/heads	2,426	0.81	54.0	*0.44*	0.00400	*0.0100*
Smilacina sp.	Rhizomes	4,447	0.65	71.3	*0.47*	0.00300	*0.0100*
Agoseris sp.	Stems/leaves/heads	2,223	0.49	76.6	*0.37*	0.00200	*0.0070*
Vespidae	Mature/larvae	2,347	0.65	24.1	*0.16*	0.00100	*0.0030*
Ribes setosum	Berries	2,621	0.33	100.0	*0.33*	0.00100	*0.0030*
Chlorophyceae	Entire	2,256	0.33	75.0	*0.24*	0.00080	*0.0030*
Forb — unidentified	Stems/leaves	2,149	0.33	75.0	*0.24*	0.00080	*0.0030*
Ranunculus sp.	Stems/leaves/flowers	2,405	0.49	30.0	*0.15*	0.00070	*0.0020*
Mertensia ciliata	Stems/leaves	2,842	0.33	50.0	*0.16*	0.00050	*0.0020*
Angelica sp.	Stems/leaves	2,408	0.33	27.5	*0.09*	0.00030	*0.0010*
Aster integrifolius	Stems/leaves	2,377	0.16	95.0	*0.15*	0.00020	*0.0007*
Pastinaca sativa	Stems/leaves	2,713	0.16	50.0	*0.08*	0.00010	*0.0003*
Ruppia pectinata	Stems/leaves	2,347	0.33	12.5	*0.04*	0.00010	*0.0003*
Anacharis sp.	Entire	2,377	0.16	20.0	*0.03*	0.00005	*0.0002*
					99.58	29.30455	*100.0755*

were analyzed along with corresponding scat material (Table 2). Protein was the primary nutrient utilized and the greatest source of energy. Protein digestibility of these samples compared favorably with the 54±12 percent reported for ruminants on roughage feeds including various grasses, legumes, and native western hay (Crampton and Harris 1969).

All 5 grasses and grasses/sedges were succulent when collected. The first 2 were collected before flowering, the last 3 after flowering. Protein content of preflowering material was higher than that of postflowering material; the opposite was true of nitrogen-free extract. Energy per gram generally remained constant. The data suggest a direct relationship between protein content and apparent protein digestibility. Highest protein digestibility was recorded for the higher protein content of preflowering samples; lowest protein digestibility was recorded for the lower protein content of postflowering samples. This result was to be expected because protein levels are highest in the aerial parts of plants during early growth stages, and plant cell contents at that time are most available for digestion before cell walls lignify (Klein 1965, Crampton and Harris 1969).

If values for nitrogen-free extract are accepted, a direct relationship between extract content and digestibility is also suggested. Apparent digestibility per gram of gross energy was fairly constant in spite of the differences in the relative amounts of protein and nitrogen-free extract and in their respective digestibilities. This finding suggests a digestive flexibility in grizzlies that may have provided a relatively constant energy intake regardless of changes in diet levels of protein and nitrogen-free extract.

Food quality of western springbeauty averaged 29.9 percent protein, 3.9 percent ether extract, and 45.7 percent nitrogen-free extract, which averaged 3.8 percent starch and 41.9 percent nonstarch. Calculated energy averaged 4.0 kcal/g. Digestibility of individual items averaged 61.8 percent for protein, 93.0 percent for starch, unknown for nonstarch nitrogen-free extract (7.5 percent if the values are accepted), and 30.5 percent per gram of gross energy (35.0 percent if nonstarch nitrogen-free extract values are accepted). Protein was the greatest energy source.

Averaged values for protein and ether extract content and digestibility for cutthroat trout were substantially higher than those recorded for succulent herbs. Ether extract of fish consisted primarily of triacylglycerols, which are the major components of storage fats in plant and animal cells; ether extract of the aerial portions of succulent herbs was probably made up primarily of phospholipids from cell membranes serving as structural elements (Lehninger 1973). Storage fats were more digestible than the waxy structural elements.

Averaged values for food quality and digestibility of Umbelliferae roots, melica and western springbeauty corms indicated that starch was a highly digestible energy-rich nutrient.

A summary of quality and digestibility of the most important grizzly foods indicates that animal material had the highest digestibility and the highest calculated energy content, and plant material had the lowest (Table 3). A direct relationship between food energy and digestibility is apparent; the higher the energy of the food, the greater its digestibility. Differential digestibility of plant and animal foods is apparent.

Nutritive Values

Five principal nutrient materials contributed to total energy intake of grizzlies. Protein from succulent herbs was estimated to be 42.8 percent digestible, protein and fat from animal material 78.1 percent digestible, fat and protein from whitebark pine nuts 73.6 percent digestible, and starch from herbs 78.8 percent digestible. The digestibility of sugar from berries and fruits of shrubs and herbs was undetermined but assumed to be high.

Seasonal grizzly nutritive values for 1974 were compared among the 3 economies. Each economy had a unique nutritional plane. The valley/plateau economy was nutritionally distinguished by the relatively high nutritive value of protein from succulent herbs. The mountain economy was distinguished by the relatively high nutritive value of starch, and the lake economy by the relatively high nutritive value of protein and fat from fish. Protein from succulent herbs appeared to be the primary and sustaining nutrient in all 3 economies.

For the 2-year period in the Park, protein from succulent herbs, with a nutritive value of 77.3 percent, was the grizzlies' most important source of energy (Fig. 3). Protein and fat from animal material ranked second, starch ranked third, and fat and protein from whitebark pine nuts ranked fouth. Energy contribution of sugar from fruits and berries is unknown, but its nutritive value percentage probably did not exceed 0.50.

DISCUSSION

In Yellowstone Park, grizzlies occupied fertile, primarily open grasslands, herblands, and parklands with adequate cover where protein, taken in large quantities primarily from succulent herbs and secon-

Table 2. Quality and digestibility of grizzly bear foods as indicated by chemical analysis.

Item: Gramineae/Cyperaceae
Consumption rank: 1
Importance value percent: 78.5

	Whole food material		Corresponding scat material		
	Proximate content	Calculated gross kcals	Apparent digested kcals	Concentration factor	Apparent digestibility percent
Item: *Agropyron* sp. — 50%, *Poa* sp. — 20%, *Bromus* sp. — 10%, *Phleum alpinum* — 10%, *Carex* sp. — 10%					
Economy: Mountain					
Condition: Preflowering, succulent					
Protein	22.9	128.2	63.8	0	49.8
Ether extract	3.7	34.4	Unknown	1.2	Unknown
Nitrogen-free extract	39.4	169.4	Unknown	Unknown(1.01)[a]	Unknown
Total		332.0	63.8		
Per gram		3.3	0.64		19.4
Item: *Poa* sp. — 50%, *Agropyron* sp. — 30%, *Phleum alpinum* — 10%, *Carex* sp. — 10%					
Economy: Mountain					
Condition: Preflowering, succulent					
Protein	25.6	143.4	68.9	0	48.0
Ether extract	3.6	33.5	Unknown	1.3	Unknown
Nitrogen-free extract	35.9	154.4	Unknown	Unknown (1.1)	Unknown
Total		331.3	68.9		
Per gram		3.3	0.69		20.9
Item: *Deschampsia caespitosa* — 80%, *Carex* sp. — 20%					
Economy: Mountain					
Condition: Postflowering, succulent					
Protein	14.0	78.4	31.9	0	40.7
Ether extract	2.7	25.1	Unknown	1.1	Unknown
Nitrogen-free extract	46.8	201.2	Unknown (24.5)	0	Unknown (12.2)
Total		304.7	31.9 (56.4)		
Per gram		3.0	0.32 (0.56)		10.7 (18.8)
Item: *Poa* sp. — 100%					
Economy: Valley/plateau					
Condition: Postflowering, succulent					
Protein	17.4	97.4	35.8	0	36.7
Ether extract	1.5	13.9	Unknown	1.9	Unknown
Nitrogen-free extract	62.2	267.5	Unknown (73.9)	0	Unknown (27.6)
Total		378.8	35.8 (109.7)		
Per gram		3.7	0.36 (1.1)		9.5 (28.9)
Item: *Calamagrostis canadensis* — 100%					
Economy: Valley/plateau					
Condition: Postflowering, succulent					
Protein	17.6	98.6	34.2	0	34.7
Ether extract	5.0	46.5	27.0	0	58.0
Nitrogen-free extract	41.9	180.2	Unknown (3.9)	0	Unknown (2.2)
Total		325.3	61.2 (65.1)		
Per gram		3.3	0.61 (0.65)		18.5 (19.7)

Averaged values					
Protein	19.5	109.2	46.9	0	42.0
Ether extract	3.3	30.7	5.4	1.1	11.6
Nitrogen-free extract	45.2	194.5	Unknown (20.5)	0	Unknown (8.4)
Total		334.4	52.3 (72.8)		
Per gram		3.3	0.52 (0.73)		15.8 (21.5)

[a] Nitrogen-free extract values are determined by difference and are subject to possible error. Results in this category are recorded as Unknown. Numerical values are given in this category and elsewhere in parentheses to show the result if the values are accepted.

Table 3. Summary of the quality and digestibility of grizzly bear food items.

Food item	Apparent digested kcals/g	Apparent digestibility percent	Calculated kcals/g whole food	Consumptive use rank
Cervidae/Bovidae	4.6	81.3	5.6	8
Salmo clarki	4.1 (4.2) [a]	73.2 (73.7)	5.7	5
Pinus albicaulis (nuts)	1.9 (2.1)	48.7 (52.5)	3.9	11
Claytonia lanceolata	1.2 (1.4)	30.5 (35.0)	4.0	2
Umbelliferae (roots) plus corms of *Melica spectabilis* and *Claytonia lanceolata*	1.0 (1.5)	25.7 (36.8)	3.9	6
Russula sp.	0.98 (1.3)	25.0 (33.0)	3.9	16
Gramineae/Cyperaceae	0.52 (0.73)	15.8 (21.5)	3.3	1
Trifolium repens	0.50 (0.79)	13.9 (21.9)	3.6	4
Equisetum arvense	0.37	12.8	2.9	10

[a] Results in parentheses include nitrogen-free extract values.

darily from artiodactyls, satisfied most of their energy needs. These needs were met because protein is convertible to fat and ketone bodies via the intermediary metabolism; such conversion occurs particularly when protein is taken in excess (Lehninger 1973). Because of their nutritional dependence on protein, Yellowstone grizzlies in 1973-74 occupied primarily a protein food niche.

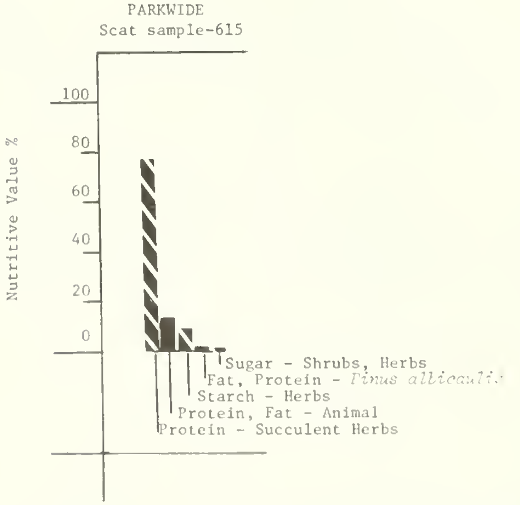

Fig. 3. Parkwide summary of the nutritive values of grizzly bear foods, Yellowstone National Park, 1973-74.

In this study, park grizzlies grazed for long periods on grasslands. Protein digestibility of grassland herbs was 42.8 percent, considerably lower than the indicated digestibilities of the other principal nutrient materials. Park grizzlies compensated for this relatively low nutrient digestibility by a high intake of succulent herbs that insured a high level of ingested protein and a consequent energy source and fat store. Geist (1974:207) noted a similar process in the perissodactyl, which can "compensate for poor forage of low digestibility by eating more and passing out the undigested portions relatively quickly. It can thus maintain a steady stream of energy and nutrients across the gutwall, but does so by digesting the forage less efficiently than do ruminants and by consuming more forage."

Davis (1964) discussed gut length and dentition of the Ursidae, and Hoffman and Pattie (1968) and Greer and Craig (1971) described both the teeth and feet of grizzly bears. Colbert (1969) discussed the adaptive significance of ursid dentition. Carnassial shearing teeth are absent in grizzlies (and all other bears) and have been replaced by crushing bunodont molars, an apparent adaptation to an herbivorous or omnivorous diet. The front claws of grizzlies are longer than 55 mm, allowing these bears to be effective diggers, possibly an additional adaptation to herbivory. The food niche (primarily plant protein) occupied by Yellowstone grizzlies is attributable in part to their relatively long gut length, bunodont molars, and long claws. These physical characteristics allowed utilization of plant materials without preventing a high digestibility of animal material. As a result, grizzlies were digestively flexible and were able to make maximum use of both plant and animal protein. This digestive flexibility accounted in part for the successful exploitation of the park's 3 different food economies.

Yellowstone grizzlies appeared to be adapted primarily to the most constant and abundant protein sources in their environment. Fertile grasslands and herblands provided a constant supply of protein because a relatively large portion of fixed light energy was available as food energy directly in succulent herbs and indirectly in herbivores. Conferous forests did not provide such rich souces of energy. In 1974, seasonal foods such as pine nuts and berries were relatively abundant and contributed importantly to the grizzly diet. In 1973, pine nuts and berries were not abundant and were relatively scarce in the diet. A periodic low annual production of nuts and berries, such as occurred in 1973, probably has no major impact on park grizzlies because nutritionally they are anchored to the more stable energy supply available from grasslands, herblands, and associated forested edges.

Relative scarcity of animal foods during the pregreen-up period probably sets absolute limits on the protein available to grizzlies at this time. This limited protein availability could in turn limit grizzly numbers when their demand for animal protein exceeds the supply. At such times, competition among grizzlies for animal food (Cole 1972) may result in population losses. Dispersal and direct mortality may cause losses among subordinate bears (Stokes 1970, Martinka 1976). The pregrowing season is the only time in the park when bears' supply of protein could be strictly limited. This period is likely to be the primary one in which natural regulation of grizzly populations occurs.

The grizzly population in the park has been estimated to be 178-270; the highest density, excluding the Yellowstone Lake area, has been estimated to be 1 bear per 5.7 km^2 in Hayden and Pelican valleys (Knight 1974). These estimates indicate a lower population level and a lower density than might otherwise be expected of an animal population at the primary consumer level in pristine grassland habitat (Odum 1971). Two explanations at least partially account for the grizzly population level and densities in the park:

1. Grizzlies are secondary consumers during pregreen-up periods, when they are probably subject to population-limiting pressures related to the amounts of available animal protein.
2. Grizzlies are relatively inefficient grazers because of their dentition and digestive structure. Hence, the available supply of areas providing the tall, dense stands of succulent protein-rich herbs that grizzlies require probably has a limiting effect on grizzly numbers.

Grizzly digestive capability with respect to succulent herbs was limited primarily to the extraction of protein. By comparison, artiodactyls digest protein, ether extract, fiber, and nitrogen-free extract from herbs in nearly any condition (Crampton and Harris 1969) and consequently obtain more energy per gram of vegetation than do grizzlies. To maximize energy intake and compensate for low energy per gram of forage, grizzlies sought out and ingested large quantities of succulent herbs growing in tall, dense stands. Such high-quality stands were extensive in the park but not unlimited.

Nutritionally, free-ranging Yellowstone grizzlies using natural foods were primarily herbivores and secondarily carnivores in 1973-74, obtaining protein from succulent herbs and artiodactyls. Digestive flexibility permitted maximum protein use of both plant and animal foods. The principal environmental requirement necessary for continued support of grizzlies in their multi- and mixed-level trophic niche appeared to be the availability of grasslands and herblands capable of maintaining elk and bison in sufficient numbers to provide adequate food for pregreen-up secondary consumption, of providing rodents for growing-season mixed consumption, and plentiful, succulent and nutritious herbs for growing- and postgrowing-season primary and mixed consumption.

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BROWN BEAR MOVEMENTS AND HABITAT USE AT KARLUK LAKE, KODIAK ISLAND

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Abstract: Since 1967, brown bears (*Ursus arctos middendorffi*) have been radiotracked in studies devoted to movements and use of habitat. A total of 487 contacts were made with 29 animals. The bears tended to move to Karluk Lake streams in July to feed on salmon. In August, they spent more time in the midlands to feed on berries. Midlands appeared to be preferred for hiding and resting. Uplands were primarily used for cross-country travel and for denning in winter. Denning usually occurred in alder patches on northeast-facing slopes at elevations of 483 m to 670 m. Home ranges of 7 males averaged 24.4 km^2 as compared with 14.3 km^2 for single females during the summer and 10.6 km^2 for females with young during the fall. More data are needed on the period from den emergence to summer before all the habitat requirements at Karluk Lake can actually be identified.

The U.S. Fish and Wildlife Service has conducted population studies of brown bears at Karluk Lake on Kodiak National Wildlife Refuge since 1958. One objective of these long-term studies was to determine home range and movement patterns. The conventional method of recapturing tagged animals was supplemented by a radiotracking program in 1967. The purpose of this paper is to augment the preliminary findings reported by Berns and Hensel (1972).

We wish to express our appreciation to our former co-worker, R. Hensel, who initiated the radiotracking program and also reviewed the manuscript. We also thank T. Grubb, J. Gilbert, and the late R. Blott for assistance in capturing and in monitoring the movements of radio-instrumented bears.

STUDY AREA

Kodiak is a mountainous island with rugged peaks rising to 1,362 m. The coastline is long and intricate with prominent headlands, cliffs, and deep, narrow bays. Other features include 11 watersheds and 15 large lakes with numerous tributaries. Temperatures usually range between −18 C and 24 C, with an annual mean of about 5 C. The average annual precipitation is 152 cm, and lowlands are often without snow cover because of mild winter temperatures and frequent rainstorms.

Our investigations were conducted on the southern part of the island in the Karluk Lake drainage (Fig. 1). Karluk Lake is at an elevation of 111 m, is 19 km long and 0.8 km wide, and is fed by 9 lateral and 2 large terminal streams. During the summer and fall, red salmon (*Oncorhynchus nerka*) spawn in the feeder streams and along the lake shores. The dominant vegetation is alder (*Alnus* sp.), willow (*Salix* spp.), and grasses (Gramineae), with cottonwood (*Populus trichocarpa*) along valley bottoms.

METHODS

The radiocollars consisted of a transmitter unit and battery pack as described by Tester et al. (1964). Movements of radio-equipped bears were monitored from a Piper Supercub aircraft and, to a lesser extent, from the ground. A detailed description of equipment and monitoring techniques were given by Berns (1968). Berns and Hensel (1972) described a modification of the Boundary Exclusive Method (Stickel 1954) used to determine size of activity areas. The *activity area* is intensively used for the purpose of food gathering or winter denning. *Home range* is an area in which all living requirements are fulfilled or in which an animal normally spends all of its time.

Most of our data were collected during the falls of 1972-75. Some additional observations were made during the summers.

RESULTS AND DISCUSSION

Habitat Use

Of 487 radio contacts with instrumented bears during summer and fall (Table 1), males were located in lowlands 69 percent, in midlands 12 percent, and in uplands 19 percent of the time. Corresponding figures for females (with or without offspring) were 60 percent, 27 percent, and 13 percent.

It was apparent that bears made extensive use of lowlands because they were attracted by the large numbers of migrating salmon using the spawning streams. By mid-August, bears were found less frequently along salmon streams and were more often found hunting for berries in the midlands. From late September through October, bears returned to the lowlands to feed on salmon along lake shores and outlets of tributary streams. Immature bears, less proficient in

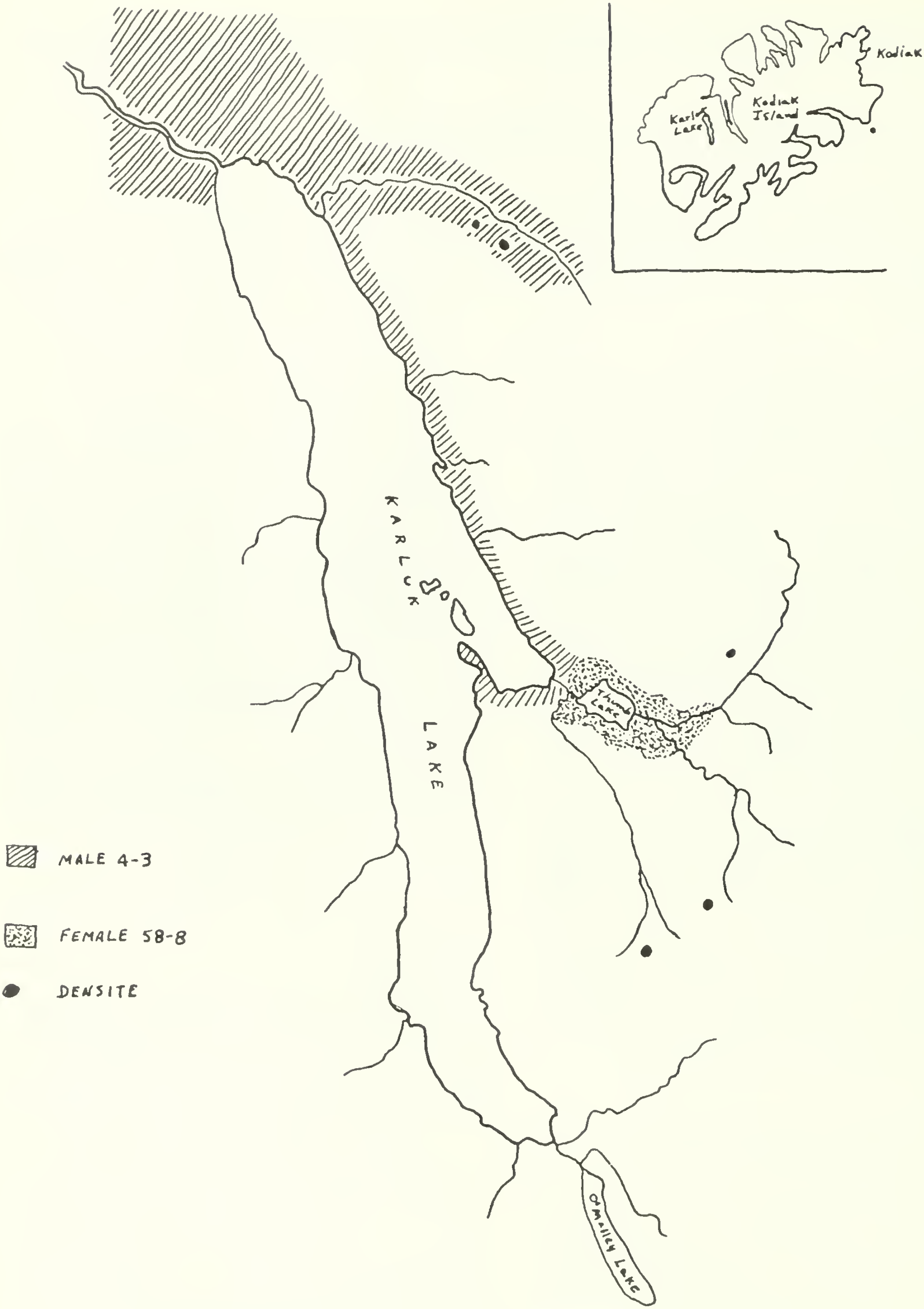

Fig. 1. Locations of 5 den sites and the ranges of 2 bears in the Karluk Lake drainage study area.

Table 1. Frequency of brown bears observed in different habitats, Karluk Lake, 1967-76.

	Total fixes	Lowland		Midland		Upland	
		Fixes	Percent	Fixes	Percent	Fixes	Percent
Females							
Summer	211	108	51	76	36	27	13
Fall	153	109	71	24	16	20	13
Total	364	217	60	100	27	47	13
Males							
Summer	45	35	77	6	13	4	10
Fall	78	50	64	9	11	19	24
Total	123	85	69	15	12	23	19

catching fish than mature animals, necessarily spent more time along the salmon streams than adult bears. This difference in skill may explain why midlands were used more frequently by adults, especially females with cubs, during the summer, when bear activity was greatest along the salmon streams. Alder patches at higher elevations were continually used by all bears as hiding and rest areas. Otherwise, the uplands received little use except for winter denning and, to a minor extent, cross-country travel. For example, of 36 contacts made with 4 bears in upland habitat during 1972-73, only 1 was of a bear moving toward another drainage. All other upland observations were of bears near denning sites.

Denning Activities

Some grizzlies have been known to travel 16-24 km during a 12-hour period and to range from 4 to more than 48 km from fall or summer foraging areas to den sites (Craighead and Craighead 1972). During our 1972-73 studies, in fall, a female brown bear traveled 7.2 km in a 24-hour period, but this movement was solely a feeding expedition. The longest single movement to a den site was made by a female with 1 yearling. After being instrumented, she stayed mostly in the upper midlands until 5 November 1972, when she moved 4 km to a denning site. On 10 November, after a light snow, the two bears were sighted digging a den in an alder patch at an elevation of 488 m.

In November 1972, a female, No. 13-72, with 1 cub moved 6.4 km from Karluk Lake in 5 days, where she eventually denned at an elevation of 580 m. On 19 November 1974, the female, alone at the time, was shot by a hunter while digging a den approximately 1.2 km east of her 1972 den site.

A subadult male, No. 1-3, was instrumented near the north end of Karluk Lake on 7 October 1973. He moved from the Karluk Lake area approximately 3.2 km to the Moraine Creek drainage on 20 October and denned in an alder patch at 580 m on 4 November.

Another subadult male, No. 4-3, was instrumented on 9 October 1973 near Camp Island. This bear moved to the Moraine Creek valley and visited the den of No. 1-3 on 12 November. The next day, he was sighted about 0.4 km away at an elevation of 518 m, preparing a den. He was seen on 16 November lying 14 m from his den, and he emerged from the den between 30 April and 6 May 1974.

The foregoing observations suggest that distances from major feeding areas to denning sites were not great. Grizzlies observed by Craighead and Craighead (1972) dug dens as early as 3 and 8 September but did not actually den until November. Brown bears apparently differ from grizzlies by remaining near or inside their dens for the duration of the winter. Den construction usually began late in October, often within alder patches on slopes of 487-670 m in elevation. Five of 6 dens of instrumented bears were on slopes facing northeast and 1 was on an east-facing slope (Fig. 1.).

Site selection and den construction by brown bears have been described by Lentfer et al. (1972). Couturier (1954) reported that the European brown bear often used natural shelters. Jonkel and Cowan (1971) stated that the bases of hollow trees were often used by black bears (*Ursus americanus*) for dens in the spruce-fir forest of Montana. There have been some reports of denning in natural rock caves, but none were found in the Karluk Lake area. All observed dens on the Alaska Peninsula and on Kodiak Island were excavated by bears.

Movements

Single bears of either sex moved greater distances than females with young, despite an abundant food supply in summer and fall. Home ranges of 7 males averaged 24.4 km^2, those of 6 single females averaged 14.3 km^2, and those of 17 maternal females averaged 10.6 km^2 (Table 2).

Table 2. Home range size for male, single female, and maternal female brown bears at Karluk Lake as determined from radiotracking 30 individuals, 1967-76.

Class of bears	Sample size	Home range size (km^2)	
		Average	Range
Males	7	24.4	2.6-49.2
Single females	6	14.3	9.0-19.9
Maternal females	17	10.6	0.5-36.2
Total	30	14.6	0.5-49.2

Areas used only 3 or 4 days were not considered a bear's activity area. Such casual movement could be described as wandering. Two examples of wandering included a single female, No. 58-8, who traveled 14.5 km into the adjacent Uyak drainage, and a male, No. 4-3, who moved 19 km from the north end to the south end of Karluk Lake. Both animals returned to their original areas within a few days.

Bears in the Karluk studies seldom traveled over 16 km, but a yearling male tagged in 1960 at Karluk Lake was killed in May 1967, 40 km from the tagging site. A trapper also found the collar of an adult male bear 45 km from his capture site. The yearling may have dispersed after family breakup and the adult male, tagged in the spring, may have traveled 45 km during the breeding season in search of females.

Established brown and black bears often return to their familiar home ranges if moved. Mundy and Flook (1973) reported that 2 transplanted bears returned 72 km in 7 days by the most probable direct route. Bader (1974) reported that an adult female black bear moved at least 160 km and crossed several major bodies of water to return to her capture site in less than a month. An adult male brown bear transplanted to Montague Island from Cordova returned 76 km in 28 days (Reynolds 1973). The bear had to swim a minimum of 11 km through strong tidal current to return to the capture site. A grizzly sow transported 113 km from her home site returned in 3 days (Pearson 1972).

Berns and Hensel (1972) observed that some brown bears used two activity areas and others used only one. For example, female No. 58-8 was instrumented 4 times in 5 years and was monitored 27 times by radio and sighted 13 times for a total of 40 contacts. All except 1 contact were in the Thumb-Karluk drainage. As a subadult, she once wandered a distance of 14.5 km but there after confined her movements to a home range of 10.6 km^2.

A subadult male, No. 4-3, emerged from his den between 30 April and 6 May 1974. Although his radio transmitter no longer functioned, the color-coded collar was retained until 25 August. Between 22 June and 16 July, the bear made 25 visits for salmon to the weir at Karluk Lake outlet. He was sighted on 25 July at Canyon Creek, 19 km away, near the south end of Karluk Lake. On 25 August, he was again observed at the outlet, where weir attendants saw him fighting with another bear. Later the same day, they saw him without his collar, catching fish near the weir. During the year, 62 contacts were made with this bear near Karluk Lake. Except for one 4-km movement to a winter den, his range was calculated to be 40.6 km^2 in a rather narrow band along the lake. No. 4-3 was killed by a hunter on 27 October 1974, within 1.6 km of the Karluk Lake outlet.

Although movements of bears Nos. 58-8 and 4-3 might be misleading because they continually frequented the Karluk drainage, both apparently spent a large part of their lives within a relatively small area. The use of relatively restricted areas by Kodiak brown bears may be attributed to an abundance of salmon and berries and nearby denning sites all in close proximity. The annual requirements of brown bears can perhaps be met within a comparatively small range at Karluk Lake. However, additional data are needed, particularly on the period after den emergence, to effect a better understanding of the ecological factors that support this unique assemblage of brown bears.

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BROWN BEAR SUMMER USE OF ALPINE HABITAT ON THE KODIAK NATIONAL WILDLIFE REFUGE

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Abstract: Brown bear (*Ursus arctos middendorffi*) alpine summer habitat use patterns were studied at the Kodiak National Wildlife Refuge in 1973, 1974, and 1975. Seven plant communities were described and mapped within the alpine and subalpine zones of the 56.5-km^2 study area. Single bears and family groups showed an almost exclusive preference for *Carex macrochaeta* as the primary food. Alpine activity areas, determined for 29 individually identified bears, were small; those of lone adults were twice the size of those females with young, 1.70 and 0.85 km^2, respectively. The average density was 0.85 bear/km^2 but rose to 2.60 bears/km^2 in an area where animals concentrated to feed. Bears spent 5-6 weeks in the high mountains, abruptly departing when young *Carex macrochaeta* plants were no longer being produced.

In Alaska, little effort has been directed towards studying brown bear use of alpine habitat. Alpine investigations have been confined to denning studies on the Alaska Peninsula and Kodiak Island (Lentfer et al. 1972). Annual alpine composition counts on the Kodiak National Wildlife Refuge have revealed many bears (*U. a. middendorffi*) in summer months. A study was conducted during 1973, 1974, and 1975 to determine the reasons for their presence.

Brown bears (*U. a. arctos*) in Europe, and Russia (*U. a. beringianus*) also commonly use high mountains in summer. Curry-Lindahl (1972), referring to European bears, states that these animals visit alpine areas in late summer to feed on berries. He comments on Scandinavian populations by adding (p. 78) that some "subalpine birch forests . . . are characterized by a luxurious vegetation, which offers the bear optimal habitats." Novikov (1956) reported that brown bears in interior Russia make regular seasonal vertical migrations into the mountains, frequenting the alpine zone to an altitude of 2,800 m or higher. In eastern Siberia, where the habitat resembled that of southwestern Alaska, Kistchinski (1972:70) says that brown bears "often" move up to the alpine zone at 1,500-1,800 m by July. Brown bears in the Austrian Alps (Krott 1962) and in Italy's Abruzzo National Park (Zunino and Herrero 1972) move into the alpine zone in late spring to graze on the freshly sprouted greenery of the high mountain meadows.

Grizzly bears (*U. a. horribilis*) also utilize alpine vegetation. In Canada, Mundy and Flook (1973) report that grizzlies move from avalanche slopes and lower forests in the spring and early summer to alpine meadows in midsummer and back to lower elevations in autumn. These authors further state that the movements seem related to the availability of natural foods and that the greater density of these bears in Glacier National Park can be attributed to the highly productive alpine and subalpine vegetation.

Brown bear habitat in Alaska is under disruptive pressures from several sources. The Alaska Native Claims Settlement Act is causing millions of hectares of wildlands to be transferred from public to private ownership, with potential exploitation of natural resources likely in many areas. On the Kodiak National Wildlife Refuge, 140,000-224,000 ha of bear habitat will be patented to Native villages. The search for oil on the Alaska Peninsula and in the Gulf of Alaska, with attendant construction of onshore staging facilities, and increased timber harvests in coastal southcentral and southeastern Alaska, all pose threats to bear habitat. As man continues to infringe on these wildlands, effective management schemes will have to be based on a sound knowledge of the bears' habitat use patterns if more than remnant populations are to be perpetuated.

The study objectives were (1) to define the major plant communities in the study area, (2) to measure bear use of each community and determine the most important plant species sought, and (3) to determine summer alpine activity areas (a unit of alpine habitat used to fulfill normal living demands) used by family groups and single bears.

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STUDY AREA

The Kodiak Island group (Fig. 1) is positioned in the Gulf of Alaska southeast of the Alaska Peninsula. Kodiak, the largest of the 3 main islands, is approximately 96 km by 160 km. It is typified by fjord-like bays penetrating as far inland as 50 km. These bays and associated cirques and U-shaped intermountain valleys were created by the scouring action of Pleistocene glaciers. The result is a succession of mountain spurs flanked by fjords and valley extensions (Karlstrom and Ball 1969). Rugged mountains rising to a maximum of 1,360 m dominate the island's interior. Sharp crested alpine peaks protrude from the main northeast-trending axis of the range, and broad ridges extend to the northwest.

The island's climate is influenced by the Japanese Current; therefore, temperatures are mild, with extremes at sea level seldom fluctuating below -18C or above 27 C. Frost occurs every month of the year at altitudes higher than 700 m. Annual precipitation is 157 cm, with drizzle and fog common. Cyclonic lows move in from the Aleutian Islands and cause frequent precipitation and windstorms throughout the year.

The most characteristic vegetation of Kodiak Island, from sea level to the brush line at about 580 m, is an alder (*Alnus* sp.) - willow (*Salix* spp.) complex that is interspersed with lush grass-forb meadows. Cottonwood (*Populus trichocarpa*) grows along river valleys and stunted birch (*Betula papyrifera* var. *kenaica*) occurs on gentle slopes below 250 m. The 1 conifer present, Sitka spruce (*Picea sitchensis*), is confined to the northeast section of the island.

About 80 percent (7,200 km^2) of Kodiak Island's southwest portion constitutes the Kodiak National Wildlife Refuge. On one of the remote mountain spurs within the refuge, a 56-5 km^2 alpine study area was selected because of heavy summer use by bears (Fig. 1). The study area, which dips into the subalpine zone, is about 9.7 by 5.8 km, and is comprised of mountainous terrain ranging in elevation from 305 to 1,316 m. It is located on the west side of Kodiak Island between Uganik Lake and the head of the South Arm of Uganik Bay, 64 km west-southwest of municipal Kodiak.

METHODS

The study area was monitored each year with a fixed-wing aircraft, commencing in late April, to determine when bears first moved to the high country. Flights were conducted at approximately 10-day intervals until the field crew was on site. Personnel stayed in the mountain study area as long as bears remained. To minimize disturbance, party size was limited to 2. Plant identifications were based on Hultén's (1968) *Flora of Alaska and Neighboring Territories* and were corroborated by D. Murray, curator of the University of Alaska herbarium. Plant communities were identified by using Hjeljord's (1971) Kodiak alpine vegetation analysis as a reference and were then mapped for the entire study area at a scale of 1:15,840. In determining the communities, Hanson and Churchill's (1961:66) generalized definition was followed, i.e., "a group of stands that are similar in species composition and structure and occupy similar habitats." The term *alpine* as used in this paper refers to the entire study area, and unless stated otherwise, includes the subalpine zone comprised of the Willow Field - Subalpine Meadow and protruding tongues of the Alder Community's upper limits.

Bear observations were made daily, using variable-power (20-45X, 15-60X) spotting scopes at distances of 50 m to 2 km. With little vegetation to hide them, bears were easily observed in the high mountains. The entire study area was searched once a week, but locations where these animals concentrated, as determined from aerial and ground surveys, were monitored every 1 or 2 days. Thus, the same bears were usually seen several times a week and frequently for several consecutive days during each week. Bears were observed continuously for as long as conditions allowed. Their activities were noted and coded in sequence so that an observation usually consisted of a series of activities.

Repeated observations of the same bears in open country allowed the field team to identify many animals individually. Size, conformation, deformities, pelage shedding patterns, pelage color, and scars were distinguishing characteristics. Sex, age, family groupings, and behavior traits were also distinguishing factors, leading to high confidence in the identification of individuals. Other investigators have used similar physical and behavioral peculiarities to identify individual animals (Burkholder 1959, Meehan 1961, Woodgerd 1964, Craighead et al. 1974, Martinka 1974).

Boundaries of activity areas were established by connecting the outermost position locations, as determined from ground observations, with straight lines.

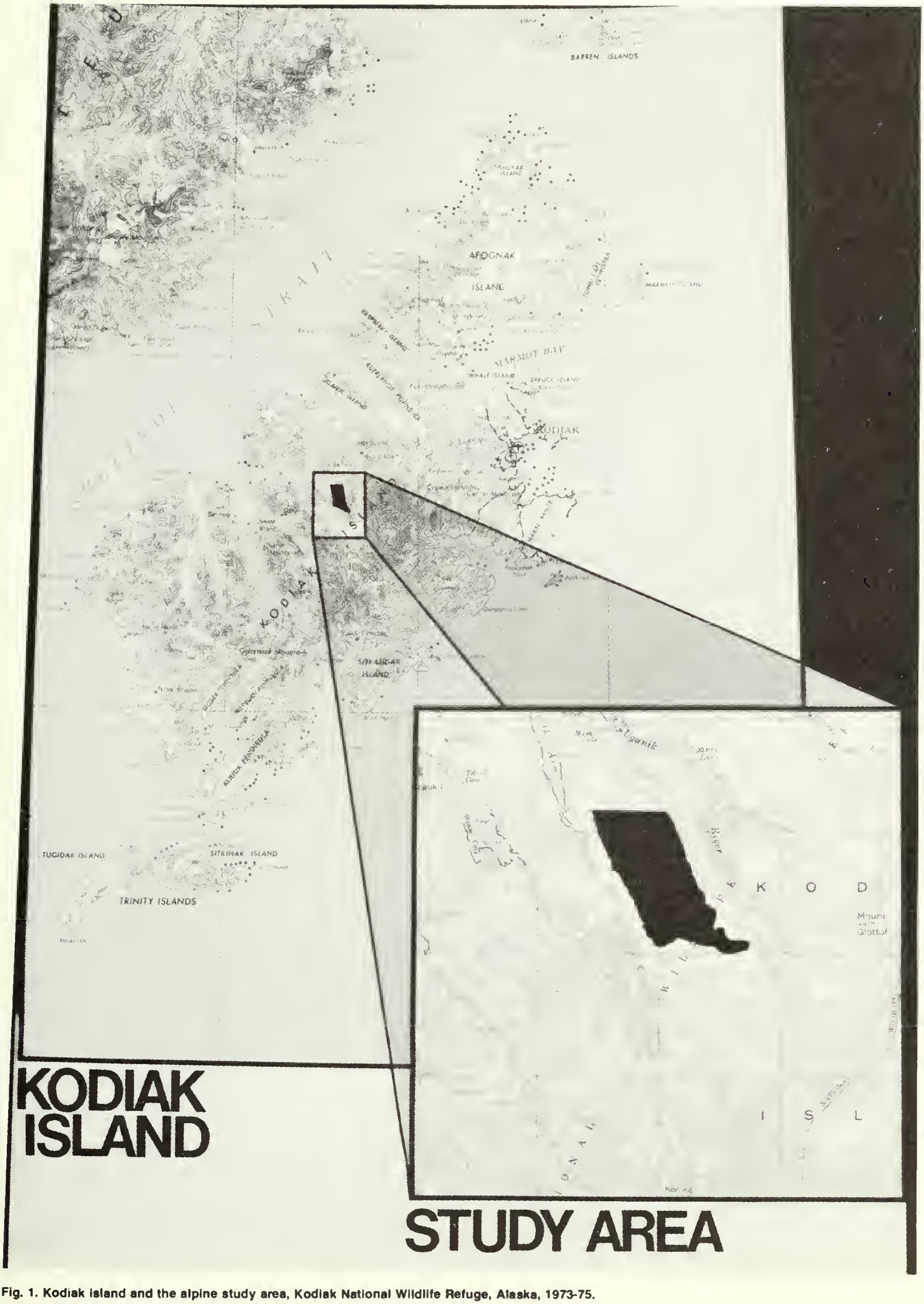

Fig. 1. Kodiak island and the alpine study area, Kodiak National Wildlife Refuge, Alaska, 1973-75.

The alpine zone was never completely without snow, the amount varying at any given time from year to year. In both 1973 and 1975, the study area remained completely snow-covered through the first 3 weeks of May. New growths of grasses, sedges, and forbs did not appear on snow-free areas until the first week of July. Snow in gullies, hollows, and chutes receded gradually through mid-August, continuously releasing shoots of fresh vegetation.

By contrast, the spring of 1974 was unusually warm and sunny; a few ridges and knolls were exposed the first week of May. By the second week of June, snowslides had cleared some south- and southwest-facing slopes and plant growth occurred. Snowmelt, and consequent plant development, were 2 weeks earlier in 1974 than in 1973 and 1975.

RESULTS

Plant Communities

The identity of 99 different plant species was established and 7 communities were recognized (Table 1).

Table 1. Plant community criteria for the alpine and subalpine zones of the study area, Kodiak National Wildlife Refuge, Alaska, 1973-75.

Plant community	Characteristics	Most common species	Altitude range	Aspect	Slope
Carex-Forb Meadow	A thick, nearly continuous growth of *Carex macrochaeta* mixed with numerous broad-leaved species. Ericaceous plants are absent. Soil fertility is high and the sites, frequently located below snowbanks and rocky outcroppings, are well supplied with moisture.	*Carex macrochaeta, Calamagrostis canadensis, Anemone narcissiflora, Lupinus nootkatensis, Geranium erianthum, Veratrum eschscholtzii, Angelica lucida, Arnica latifolia.*	670-945 m	South and southwest	30-50°
Ericaceous Knolls and Hummocks	Differs from Carex-Forb Meadows in having overall gentler topography, lower average fertility, and the presence of interrupted mats of Ericaceae species. Both xeric and mesic conditions exist and, together with a wide variety of soils and microenvironments, contribute to species diversity.	Rocky, exposed knolls are dominated mainly by *Empetrum nigrum, Cassiope stelleriana, Oxytropis nigrescens, Sedum rosea, Loiseleuria procumbens, Salix arctica,* and *Arnica lessingii.* Rolling hummocks and mixed meadow slopes between the rocky knolls are densely vegetated with *Carex macrochaeta, Festuca altaica* tussocks, *Poa arctica, Calamagrostis canadensis, Empetrum nigrum, Anemone narcissiflora, Lupinus nootkatensis, Salix reticulata,* and *Salix barclayi.*	670-790 m	No specific aspects.	0-40°
Rocky Carex-Forb Meadow	Moderately vegetated, very precipitous, and interrupted by extensive rocky outcroppings. Ordinarily situated immediatcly above Carex-Forb Meadows.	Most of the same species found in Carex-Forb Meadow, but also some hardier plants found on higher-stress sites such as Ericaceous knolls; these include *Cassiope stelleriana, Empetrum nigrum, Rhododendron camtschaticum,* and *Geum rossii.*	790-1,130 m	South and southwest	50-80°

Table 1, Continued

Plant community	Characteristics	Most common species	Altitude range	Aspect	Slope
Talus Slope and Bare Rock	This community is characterized by rocks, volcanic ash, and little vegetation. It is a xeric community, even though it becomes snowfree late in the year.	Scattered clumps of *Luzula wahlenbergii.*	Usually above 915 m but occasionally as low as 760 m in areas covered by snowbanks most of the summer.	Most frequently on steep north-facing slopes but may be found on almost any aspect.	Mainly 40-90° but sometimes 30-40°
Luzula-Congeliturbation Slope	These slopes are sparsely vegetated, xeric, and of low fertility. They are located where environmental conditions are severe. Loose volcanic ash is interspersed with rock slides and barren late snow-free areas. Frost action is manifest in soil lobes with obvious downslope creep; frost scars and miniature stone rings may be present.	*Luzula wahlenbergii, Sedum rosea,* prostrate *Salix* sp., *Saxifraga bronchialis, Papaver alaskanum, Potentilla villosa, Oxytropis nigrescens, Carex* sp., *Geum rossii, Silene acaulis, Minuartia* sp., and *Luetkea pectinata.*	760-1,220 m	North	15-50°
Willow Field-Subalpine Meadow	This type encompasses the transition zone between the true alpine and lower Alder Community. Fertile soil and an abundant moisture supply make it high in plant productivity.	*Carex macrochaeta, Calamagrostis canadensis, Salix barclayi, Salix glauca, Salix* sp., *Geranium erianthum, Arnica latifolia, Heracleum lanatum, Rubus spectabilis,* and *Alnus crispa.*	490-730 m	Any aspect	0-35°
Alder	This community is characterized by a discontinuous belt of *Alnus crispa* interspersed with dense meadows of grasses, sedges, ferns, and forbs, the result of deep, fertile soil and a good moisture supply.	*Calamagrostis canadensis, Carex macrochaeta, Athyrium filix-femina, Rubus spectabilis, Sambucus racemosa, Salix* spp., *Heracleum lanatum, Geranium erianthum,* and *Alnus crispa.*	580 m and below	Any aspect	0-65°

There was considerable variation in community size (Table 2). As the largest, Ericaceous Knolls and Hummocks covered 40 percent of the study area. The Alder and Willow Field-Subalpine Meadow communities were second at 19 percent each, with the remaining 4 plant aggregations accounting for a total of 22 percent of the land area.

Bear Use of Alpine Habitat

Bear tracks first appeared on the study area in early May each year but were not common until late May. Bear occurrence was not continuous until the last week of June or the first week of July when new vegetation was available in quantity on the snow-free south- and southwest-facing slopes. Ground team observations began after continuous occupation by bears. Bear numbers generally increased through the second and third weeks of July, then slowly declined. In the first half of August, the animals abruptly left the study area.

A total of 804 hours were spent, during the 3 years, observing 305 individual bears and family groups (Table 3). Activity sequences for this period numbered 2,077. An average of 29 different bears was individually identified yearly. An average of another 42 was seen too infrequently to establish sufficient criteria for field recognition. These latter individuals were mainly transient animals, but undoubtedly some bears with established identities were occasionally included in this category when seen for only brief periods.

Fifty percent of the time that bears were under observation, they were feeding; plants consumed were identified in about half the instances. These plants in-

Table 2. Comparison of plant community sizes within the study area, Kodiak National Wildlife Refuge, Alaska, 1973-75. Water surface areas are excluded.

Plant community	Area (ha)	Percent of study area
Ericaceous Knolls and Hummocks	2,247	40
Alder	1,071	19
Willow Field-Subalpine Meadow	1,072	19
Carex-Forb Meadow	492	9
Talus Slope and Bare Rock	339	6
Luzula-Congeliturbation Slope	287	5
Rocky Carex-Forb Meadow	100	2
Total	5,608	100

Table 3. Total brown bear observations by year on the study area, Kodiak National Wildlife Refuge, Alaska, 1973-75.

	1973	1974	1975	Total
Number of observations (may include more than one observation of same animal)	84	120	101	305
Number of activity sequences (a series of all activities documented while an animal was under observation)	448	884	745	2,077
Number of different individually identified bears (does not include young in company of an adult)	15	44	29	86[a]
Total observations of individually identified bears	46	47	86	179
Bears not individually identified	38	73	15	126
Time bears were observed (hours)	164	366	274	804

[a] Only 1 animal with known identity was observed each of the 3 years.

cluded *Angelica lucida, Carex macrochaeta, Carex* sp., *Equisetum arvense, Heracleum lanatum, Lupinus nootkatensis,* and *Salix* sp. When bears fed on known plant species, they were almost exclusive in their choices and concentrated on *Carex macrochaeta* 97 percent of the time. Bears frequented the steep Carex-Forb Meadow Community on south- and southwest-facing slopes in the 670- to 945-m altitude range where *Carex macrochaeta* grew in lush and almost pure stands (Table 1). The Carex-Forb Meadow prevailed in areas having a good moisture supply. In these locations, bears fed along the hillsides in a manner similar to that of grazing ruminants, and, as has been noted for other grazers, they probably select the highest-quality forage available (Klein 1970). *Carex macrochaeta* was pulled, rather than bitten off, and separated from the roots to expose whitish basal stems. Several mouthfuls were taken before the material was chewed and swallowed.

As snow receded in depressions, new growths of *Carex macrochaeta* were continuously released through July. By the second or third week of August (first week in 1974), the perimeters of the snowbanks had melted, exposing ash and scree. These areas ordinarily are snow-covered for so much of the year that they are devoid of vegetation.

The early development, extreme abundance, apparent palatability, and high utilization of *Carex macrochaeta* made it the most important component in the bears' alpine diet. Second to sedges, bears preferred feeding on flowers of *Angelica lucida, Heracleum lanatum,* and *Lupinus nootkatensis.*

Eighty-two percent of the bears' time was spent in 2 plant communities in which 88 percent of their feeding occurred (Table 4). By far the most important community was the Carex-Forb Meadow, where the bears spent 65 percent of their time and which accounted for 73 percent of their feeding. Apparently, bears concentrate in these areas because of the key alpine food *Carex macrochaeta*. Although this sedge is available in several communities, it is only abundant in Carex-Forb Meadow and Willow Field-Subalpine Meadow complexes (Table 5). Because of steeper slopes, which trigger snowslides earlier in the higher Carex-Forb Meadows, spring shoots emerge about 2 weeks earlier there than in the Willow Field-Subalpine Meadows. In addition, *Carex macrochaeta* concentrations in the former community are more nearly pure.

Table 4. Percentage of time brown bears were observed in each of 7 plant communities within the study area, Kodiak National Wildlife Refuge, Alaska, 1973-75.

Plant community	All activities combined (percent)	Feeding only (percent)
Carex-Forb Meadow	65	73
Willow Field-Subalpine Meadow	17	15
Ericaceous Knolls and Hummocks	8	8
Rocky Carex-Forb Meadow	6	2
Luzula-Congeliturbation Slope	2	1
Alder	1	1
Talus Slope and Bare Rock	1	0
	Observations total 801 hours	Observations total 393 hours

Activity Areas

In a sample of 17 individually identified family

Table 5. *Carex macrochaeta* **occurrence by plant community within the study area, Kodiak National Wildlife Refuge, Alaska, 1973-75.**

Community	*Carex macrochaeta*
Carex-Forb Meadow	Abundant in nearly pure stands
Willow Field-Subalpine Meadow	Extensive and predominant, but in mixed stands
Alder	Moderate, but mainly in mixed stands
Ericaceous Knolls and Hummocks	Light, with occasional almost pure pockets
Rocky Carex-Forb Meadow	Light and scattered
Luzula-Congeliturbation Slope	None
Talus Slope and Bare Rock	None

groups composed of females with cubs or yearlings, the average activity area was 85 ha (Table 6). When 1 aberrantly large activity area of 834 ha is included, the average becomes 127 ha. For 12 solitary adults assumed to be mostly males, the average activity area was 170 ha, twice the average for females with young. In a paired *t*-test this difference was significant ($P < 0.025$). Apparently, the dense stands of *Carex macrochaeta* made it unnecessary for bears to move long distances for food, as demonstrated by the size of alpine activity areas.

Table 6. Sizes of activity areas of single adult brown bears and family groups within the study area, Kodiak National Wildlife Refuge, Alaska, 1973-75.

	Sample size	Number of position locations	Activity area average size (ha)
Females with cubs-of-the-year	10	135	94
Females with yearlings	7	57	72
Females with young (above 2 categories combined)	17	192	85
Single adults	12	195	170
	29	387	120

Activity areas for succeeding years were determined for only 1 animal — No. 06-73 (Fig. 2). One hundred and seven position locations for this bear were recorded during the 3 years. Locations were concentrated in the Carex-Forb Meadow Community adjacent to 2 cirque lakes. No. 06-73 returned to the same alpine area each year but made occasional feeding forays, of less than 3 days each, up to 1.6 km east over a low pass. The straight-line distance of these trips increased in 1974 and 1975. As a result, the activity areas became larger: 1973 — 166 ha, 1974 — 209 ha, and 1975 — 472 ha.

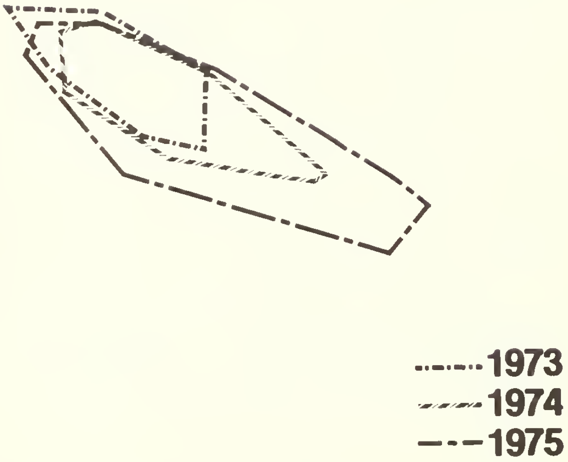

Fig. 2. Alpine activity areas of brown bear No. 06-73 for 3 consecutive years (1973-75), Kodiak National Wildlife Refuge, Alaska.

Bears tended to congregate, as reflected in the overlapping activity areas shown in Fig. 3. On 2 August 1975, 32 bears were under observation simultaneously in an area roughly 2.5 by 5.0 km, for a density of 2.6 bears/km^2. Even with these high concentrations, intraspecific strife was not common. Occasionally a female with cubs chased a solitary adult that wandered too close, or 1 lone adult ran at another, but no encounters that we witnessed ever ended in physical contact.

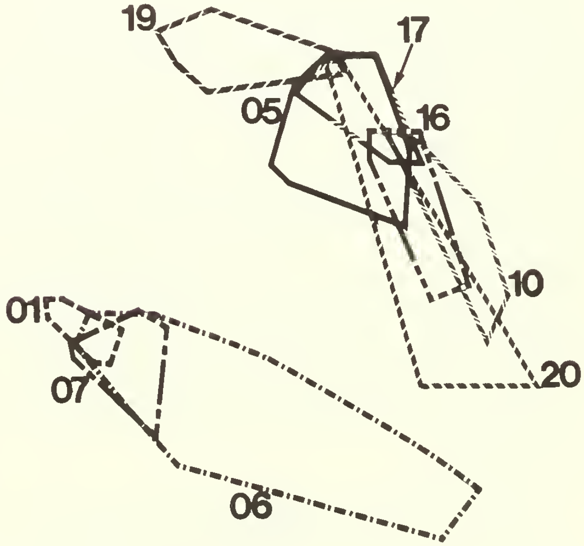

Fig. 3. Alpine activity areas of individually identified brown bears on the study area, Kodiak National Wildlife Refuge, Alaska, 1973-75.

Age Composition of Bears

Age composition for the 581 bears seen during the study is compared with aerial count data in Table 7. The most obvious differences occur in the cub and subadult categories. Particularly lush growths of the preferred *Carex macrochaeta* may attract and concentrate family groups, which would account for the higher percentage of cubs. Females with cubs, while on the study area, were apparently able to obtain their food in relatively small units of alpine habitat.

Table 7. Composition of brown bear age classifications as determined by aerial and ground counts, Kodiak National Wildlife Refuge, Alaska, 1973-75. Aerial counts were conducted annually on predesignated alpine units of which the study area represents 17 percent.

Age classification	Aerial counts		Study area ground counts	
	Number	Percent	Number	Percent
Adults	196	48	261	45
Subadults (2.5-3.5 years old)	55	13	32	5
Yearlings	68	17	90	15
Cubs	89	22	198	35
Total	408		581	

Migration From Study Area

Bears typically left the study area rather abruptly each year. This migration coincided with a marked decrease in availability of sedge shoots. In 1973, bear observations were numerous through 17 August but only 2 sightings were recorded afterwards. The bears departed earlier in 1974 than in either of the other 2 years but not as abruptly. During the 1975 field season, bears were consistently located in moderate numbers through 10 August; only 1 animal was found after that date.

Salmon (*Oncorhynchus* spp.) began arriving in Kodiak Island's spawning systems adjacent to the study area in early June but were most numerous during the second half of August. In the nearest stream, the Uganik River, peak counts during the study by biologists of the Alaska Department of Fish and Game averaged 77,000 salmon per year. These fish became available and were heavily utilized by bears when new sedge shoots were no longer being produced in the alpine zone.

DISCUSSION

Bears appeared to have been attracted to the study area each summer primarily by *Carex macrochaeta* — a localized but abundant, fast-growing, and probably highly nutritious food (Mealey 1975). This sedge is one of the earliest plants to emerge after snowmelt. Initial growth is rapid because of the large amounts of carbohydrates stored in the roots and rhizomes (Johnson and Tieszen 1973). Klein (1970) has stated that the highest nutritive quality of most forage plants coincides with the early stages of growth, which is probably true of *Carex macrochaeta*.

Cubs only 6-7 weeks out of the den have rapid growth rates, placing heavy dietary requirements on their lactating dams, who in turn must not only feed their young but must also recover from the vicissitudes of denning. The lush stands of *Carex macrochaeta* may satisfy these needs.

The bear density was high on the study area, 0.85 bear/km^2, determined from individually identified animals seen on 2 or more occasions. This density approximates the 0.65 bear/km^2 found by Troyer and Hensel (1964) in a 249 km^2 study area at Karluk Lake on Kodiak Island, where brown bears had concentrated to feed on salmon, another easily available and probably nutritious food (Mealey 1975). Kistchinski (1972:69), citing Lavov et al. (1963), quoted figures of 1.2-2.0 bears/km^2 for parts of Paramushir Island (Kurile Islands, USSR) rich in fish, but did not include the size of the land mass involved.

Activity areas were small and frequently overlapped. Troyer and Hensel (1964) found brown bear movements to be similarly limited in the vicinity of dense spawning areas. Most animals remained there for several weeks within 1.6 km of their food supply.

Brown/grizzly bears are known to congregate seasonally at sources of preferred foods and in this study the Carex-Forb Meadow Community was especially important. There, and to a lesser degree in the Willow Field-Subalpine Meadow, activity areas frequently overlapped. Animals so localized would be those whose home ranges encompassed the feeding area, as reported for black bears (*Ursus americanus*) by Jonkel and Cowan (1971). One individually identified bear returned each year to the same part of the study area, which indicates that others may have done the same.

After 5-6 weeks of grazing in the high mountains, the bears abruptly left. Their departure coincided with the return of spawning salmon, similar to what Kistchinski (1972) reported for eastern Siberia. Whether the presence of salmon at Kodiak Island attracts the bears from the alpine areas is not known; however, the bears' departure occurs at the time salmon become readily available. Most likely, as alpine plants become less palatable with age, the bears merely leave to seek substitute foods and the salmon fulfill this need.

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SEASONAL MOVEMENTS OF AN ALASKA PENINSULA BROWN BEAR POPULATION

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Abstract: On the central Alaska Peninsula, 344 different coastal brown bears (*Ursus arctos* L.) were immobilized and marked during 5 spring seasons. Between 1970 and 1976, the observed locations of 123 marked bears were determined 354 times, and the locations of 139 marked bears killed by hunters during spring and fall hunting seasons were recorded. Bears moved greater distances per unit of time during spring than during other seasons of the year. Summer movements were restricted as bears concentrated along streams to feed on salmon. Dispersal away from streams began in late summer. Denning usually began by mid-November, but some bears remained out of hibernation through mid-December. The seasonal ranges of 30 adult females averaged 293 km^2 and those of 4 adult males averaged 262 km^2. Limited movement data for adult males suggested that males spent more time than females in or near escape cover. The mobility and spring distribution of adult females were related to changes in their reproductive status. Single adult females moved further than females accompanied by young. Females with 1- to 3-year-old young utilized open lowland areas during the spring and tended to be in mountainous terrain when breeding and when accompanied by young through age 6 months. Subadult males were more transient than females, tending to move out of their maternal seasonal range after family separation; subadult females tended to remain. The seasonal range of 5 subadult males and of 6 subadult females averaged 740 km^2 and 224 km^2, respectively.

This paper describes seasonal distribution and movements of brown bears on a 8,547 km^2 study area located on the central Alaska Peninsula. The Alaska Peninsula extends 680 km southwest from mainland Alaska into the Pacific Ocean. It contains probably the largest remaining parcel of prime brown bear habitat yet unaltered by man. The region supports a large population of bears and annually contributes about 25 percent of the total statewide harvest (average, 200 of 800). About 50 of the 200 bears are taken on the study area. Increased hunting pressure has required increasingly restrictive and complex hunting regulations to stabilize bear population levels. In recent years, there has been a marked increase in mineral exploration and other related industrial activities, all of which may ultimately prove detrimental to this bear population. Also, land ownership patterns are changing as provisions of the Alaska Native Claims Settlement Act of 1971 are implemented. Administering bear management programs on federal, state, Alaska Native, and private lands will be difficult.

Information on movements of coastal brown bear populations is limited, especially for populations that receive heavy hunting pressure and for bears that depend on salmon (*Oncorhynchus* spp.) for food. Craighead (1976) reported the strong influence of earth-filled garbage dumps on grizzly bear density and movements within and beyond Yellowstone National Park. Berns and Hensel (1972) described summer and fall activities of 14 brown bears on Kodiak National Wildlife Refuge and discussed the size of activity areas in connection with food-gathering and denning. Glenn et al. (1976) noted that bears were strongly attracted to salmon in Alaska's McNeil River State Game Sanctuary during July and August. The purpose of this study is to provide resource managers with information on the general pattern of movements of a coastal brown bear population.

This study was conducted by the Alaska Department of Fish and Game and was funded by Alaska Federal Aid in Wildlife Restoration Project W-17-2 through 8. A. Egbert, J. Faro, A. Franzmann, C. Irvine, E. Klinkhart, C. McIlroy, K. Pitcher, B. Rausch, and K. Schneider, Alaska Department of Fish and Game, assisted in the field and laboratory. Credit for piloting skills and field assistance is given to J. Farwell, A. Gretchen, G. Jarvella, G. Kitchen, B. Lyons (deceased), C. Martin, B. Morgan (deceased), J. Osgood, R. Shower, and J. Swiss.

STUDY AREA

The study area (Fig. 1) is approximately 110 km long and 65 km wide and lies between two semi-active volcanoes: Mount Aniakchak (1,021 m) on the northeast and Mount Veniaminof (2,226 m) on the southwest. These mountains are dominant features of the portion of the Aleutian Range that extends through the study area. A broad, flat coastal plain with many small lakes and meandering streams lies between the mountains and the coast of Bristol Bay. Lowlands of the coastal plain are poorly drained and remain flooded until streams subside, usually in the third week of June. Mountains of the Aleutian Range gradually ascend from the coastal plain, with peaks averaging 850-975 m above sea level. On the Pacific side of the mountains, habitat is characterized by steep slopes with alder (*Alnus* sp.) covered foothills. The broad valley of the Meshik River and Black and Chignik lakes bisect the Alaska Peninsula. Dominant vegetation is sedge (*Carex* spp.) and willow (*Salix* spp.) in tundra areas and dense alders, willows, crowberry

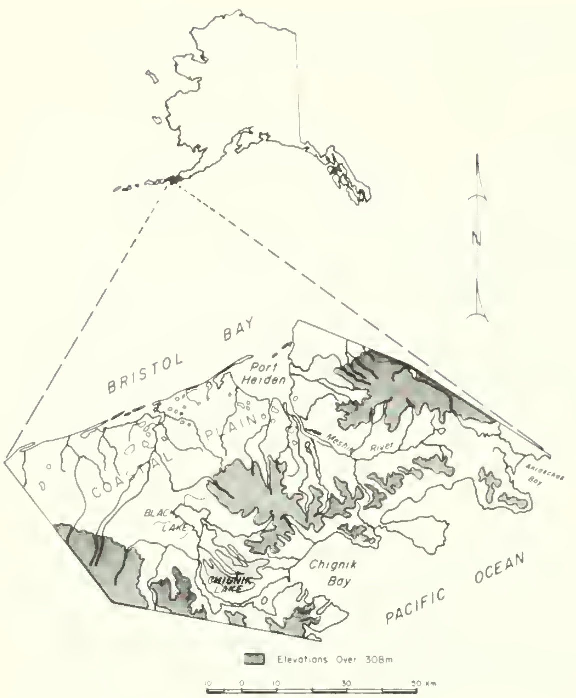

Fig. 1. Map of study area and Alaska location map.

(*Empetrum nigrum*), blueberry (*Vaccinium* spp.), lowbush cranberry (*V. vitis-idaea*), and grasses in mountainous areas. Weather is characterized by high winds, overcast skies, fog, and rain showers in the summer, and by snow showers and cloud cover in the winter. The resident human population is sparse. Access to the area is by aircraft or boat.

METHODS

Bears were captured and marked in spring only, beginning in 1970 and continuing through 1975, excluding 1973. Three hundred forty-four different bears were marked; about 46 percent of these bears were recaptured 1 or more times. Sixty-two marked adults were relocated by individually identifiable markings 188 times, and 61 subadults were relocated 123 times. The locations of 139 marked bears that were killed during spring and fall hunting seasons were recorded.

Bears were located and captured with the aid of a Bell 206A Turbo helicopter and a fixed-wing Piper PA-18 aircraft. The fixed-wing aircraft was used as a spotter plane. Radio communication between the two aircraft directed the helicopter pilot to the located bear. Bears were located by random excursions over the study area.

Bears were immobilized from the helicopter by injecting Etorphine (M-99) or phencyclidine hydrochloride (Sernylan) into the rump muscles with Palmer Cap-Chur darts. When a female with young was located, the adult always received the first drug injection. The pilot then moved the helicopter a short distance away and herded the family group to keep them together and away from thick escape cover and wet areas where they might drown. After the female was immobilized, the same procedure was used to capture the young (except cubs-of-the-year). Cubs-of-the-year were captured by hand.

Most bears (451 of 502) were captured in valleys and foothills below the alder zone or on the coastal plain, where the helicopter could be safely maneuvered; the other bears were captured in the mountains. One upper first premolar tooth and one lower first premolar tooth were removed from each captured bear older than cubs-of-the-year. The teeth were sectioned to determine age from cemental layers (Mundy and Fuller 1964, Craighead et al. 1970, Willey 1974). All captured bears were marked with ear tags and were tattooed on the groin and on the inside of the upper lip. A numbered nylon-and-fiberglass identification collar designed to permit visual identification by observers in fixed-wing aircraft was developed, tested and used to mark 38 adult bears. Fifteen adult bears were collared with radio transmitters manufactured by AVM Instrument Company, Champaign, Illinois.

The movements of collared bears were monitored by periodic aerial surveys. Each survey aircraft was equipped with a portable receiver and a 3-element yagi antenna attached to the wing strut. The position and direction of movement of marked bears were plotted on 1:250,000 U.S. Geological Survey topographic maps.

A state regulation requires that successful bear hunters present their bear skulls and hides to Department of Fish and Game personnel for recording of kill data. This regulation allows department personnel to interview successful bear hunters or their guides in order to establish precise locations of bear kills. This system was used to determine kill locations of tagged bears. Marked bears were detected in the harvest by the presence of fiberglass collars or radiocollars, ear tags or holes in the ears, lip and groin tattooes, and missing upper and lower first premolars.

Because this investigation was concerned with bear movements that may bias population censusing, emphasis was placed on spring distribution. Mean airline distances traveled by bears away from their original spring capture sites were determined in order to show the extent of movement. The term *subadult* refers to a single bear 2-4 years of age. A *seasonal range* is an area used during spring, summer, or fall but excludes the denning area (Craighead 1976), and is determined by marking the location sightings on a map and connecting the peripheral points.

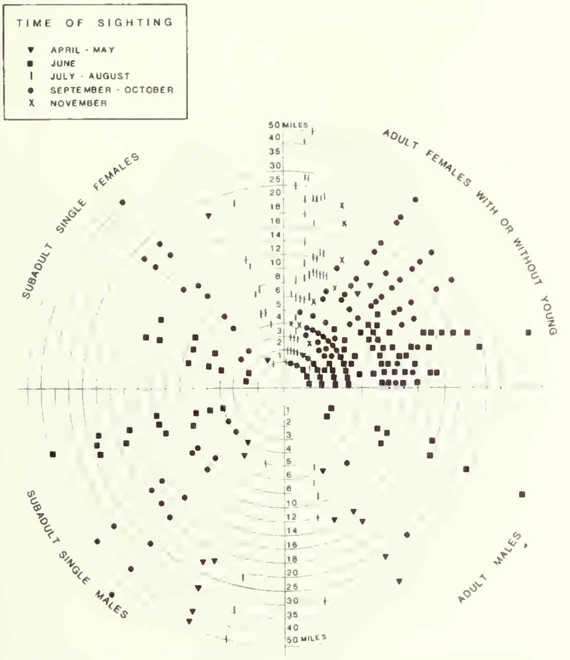

Fig. 2. Dispersal in miles (1.61 km), by season, from spring capture sites for adult male and female brown bears and young (both sexes) captured as subadults and relocated in subsequent years at any age.

RESULTS AND DISCUSSION

Fig. 2 summarizes the seasonal dispersal of marked bears away from original spring capture sites. The 1:1 ratio of marked to unmarked bears captured during June 1975 and the locations of marked bears killed by hunters support the conclusion that tagged bears were distributed throughout the population.

Spring Movements

Lentfer et al. (1972) reported that the greatest proportion of Alaska Peninsula brown bear dens was located in the Aleutian Range at an elevation of about 396 m. In our study, most brown bears had moved away from den sites to lower elevations by 25 May. Emergence from dens usually began in early April and continued to the end of May. The high proportion of adult males killed during the early part of spring bear hunting seasons (average, 89 percent before 20 April and 72 percent after 10 May) indicates that males emerged from dens earlier than females. Females with cubs-of-the-year were observed near den sites as late as 6 June; females with older young were not observed near den sites after 25 May. Craighead and Craighead (1972) reported that some females with cubs-of-the-year remained in the vicinity of their dens until the snow had disappeared.

Bear movements during June were complex. Except for females with cubs-of-the-year, bears moved greater distances per unit of time than during other periods of the year. Bears descended from mountainous subalpine areas onto the coastal plain. Time spent on the plain varied with the individual; most bears were observed only once, but some remained longer than 16 days. The rates of capture success in lowland areas provided indices of changes in bear density. Between 28 May and 10 June, an average of 0.6 bear was captured per hour of aerial search; between 15 and 30 June, the capture rate increased to 1.3 bears per hour. Bears were attracted to Bristol Bay to feed on dead gray whales (*Eschrichtius robustus*), walruses (*Odobenus rosmarus*), harbor seals (*Phoca vitulina*), and other marine mammals that washed ashore. Although caribou (*Rangifer tarandus*) calving areas did not appear to attract bears, they were observed preying on caribou calves. Bears were observed catching moose (*Alces alces*) calves and feeding on adult caribou and moose. The coastal plain provided a source of protein food that was especially attractive to females with young older than cubs-of-the-year. The observed density of bears on the plain reached a peak in mid-June, remained high until about 30 June, and then declined rapidly as bears moved to salmon spawning streams, located primarily in the foothills of the Aleutian Range.

Summer Movements

The arrival of salmon in streams was responsible for the most dramatic seasonal shift in bear distribution and density. By 15 July, the previously dispersed bear population had concentrated near salmon spawning streams, remaining there during the peak of spawning in August. Brown bears began feeding on salmon in early July and some bears were observed eating salmon in late November.

There are approximately 75 streams within the study area that provide habitat for spawning salmon. Because bears are strongly attracted to the salmon food source, the chronology of salmon migration into 2 major freshwater spawning systems is briefly described here. The Black Lake-Chignik River watershed supported the largest salmon-rearing area on the lower Alaska Peninsula and attracted the largest summer bear population. For example, on salmon spawning tributaries near Black lake in early August, it was common to count more than 100 different bears during a 3-hour aerial bear survey. Bears began feeding on red salmon (*Oncorhynchus* *nerka*) about 7 July as the fish began moving into 11 salmon spawning tributaries that comprise the Black Lake-Chignik River system. Red salmon spawning terminated in 10 of these tributaries about 1 September. Silver salmon (*O. kisutch*) spawned in the remaining streams into October. The Port Heiden Bay-Meshik River watershed supported the second largest salmon-rearing area in the study area. Red, chum (*O. keta*), and king (*O. tschawytscha*) salmon entered Port Heiden Bay and Meshik River tributaries on 1 July. The peak of spawning occurred here between 1 and 15 August when it was common to count more than 35 different bears during bear surveys flown along these tributaries. Silver salmon arrived in late August and spawned in some of these streams into December. (Salmon chronology is provided by A. Shaul, Area Fisheries Biologist, Alaska Department of Fish and Game, personal communication.)

Fall Movements

At the end of August, bears began moving away from streams and supplemented their fish diet by feeding on berries. Although berries were available near spawning streams, some bears traveled to higher elevations to feed. The bear population continued their dispersal through September. During October, the numbers of bears using the coastal plain increased noticeably, although numbers recorded in spring were much greater. By mid-November, some bears presumably had denned, since fewer were observed during aerial reconnaissance. Some bears remained out of hibernation through mid-December. Further study is required to determine conditions that influence predenning movements and time of denning. Most bears observed during fall were in the subalpine alder zone and alpine areas.

Movements of Adults

The seasonal ranges of 30 adult females average 293 km^2 (range, 26-1,098 km^2), and those of 4 adult males averaged 262 km^2 (range, 62-749 km^2). The small size of the male sample restricted comparison of adult male and female ranges. Radiocollars attached to adult males provided little movement information because they were easily shed; the average neck diameter for 9 males (30 cm) was similar to their average zygomatic width (27 cm). Limited straight-line distance data for 2 adult males suggest that range size is larger than that previously reported: The first male was captured 28 June 1970 near the beach on the south side of Port Heiden Bay and was recaptured 28 June 1972 on the Aniakchak River, 8 km from the Pacific Ocean. Between age 6.5 and 8.5 years, this male traveled the entire width of the Alaska Peninsula (82.0 km). The second male, 8.5 years old, was captured 7 July 1972 near the beach on the Pacific Ocean side of the Aleutian Range and was killed by a hunter near Chignik Lake on 14 May 1976, having traveled 98.0 km within the Aleutian mountains. The capture locations of 7 males 8-14 years old indicated that these males remained in the mountains until late June and then moved to streams to feed on salmon.

There was considerable variation in the seasonal ranges of female bears. Craighead (1976) stated that home range size was influenced by availability and distribution of food, proximity of mates, den site requirements, habitat preference, foraging habits, age, sex, condition of the animal, and other factors. Results of this study support conclusions by Craighead (1976) and demonstrate the complexities involved in providing a detailed description of population movements. Three examples illustrate variations in movements of adult females: (1) Female No. 19 (seasonal range, 26 km^2) was never observed on the coastal plain. She apparently used the mountains and lowland areas adjacent to the mouth of West Fork River. (2) Females No. 728 and 731 (combined seasonal ranges, 345 km^2) usually traveled half the width of the Alaska Peninsula as they moved from mountains located near the center of the peninsula to salmon spawning tributaries east of Black Lake. These females were never observed far out on the coastal plain but were observed within 10 km of the foothills during spring and fall. Females No. 747 and 773 (combined seasonal ranges, 614 km^2) usually traveled three-quarters of the width of the peninsula as they moved from the mountains east of Black Lake to the beach on the coastal plain and back. They were never observed on the coastal plain in fall.

Females with 1- to 3-year-old young tended to be recaptured each spring in open lowland area; females with cubs-of-the-year were seldom captured because they were generally observed in mountainous terrain. Only 1 of 12 females with 6-month-old cubs was captured before 19 June, and most (9) were captured after 24 June. Three of 12 females with cubs-of-the-year were captured on the coastal plain, and 9 were captured in valleys and foothills of the Aleutian Range. Observations before 15 June indicated the locations of 14 females with cubs-of-the-year. Ten of these family groups were located in rugged alpine areas and 4 were located in dense alder thickets in the foothills. Aerial surveys conducted during August, when bears were easily observed along salmon spawning streams, showed that about 50 percent of the young in family groups were cubs-of-the-year. Eighty-three percent of the captured young ($N = 153$) in family groups were older than cubs-of-the-year. These data reflect the reluctance of females with 6-month-old cubs to move away from protective cover before 20 June.

The observed distribution of apparently estrous females supports capture findings that most breeding females remained in or near the mountains. Thirty estrous females over 5 years of age were captured in open lowland areas during June. Of these females, 8 were in the company of young males (5-7 years old); 12 were single and may have already bred, and 10 were single and lactating, indicating that family separation had recently occurred. During the same month, we captured and frequently observed mated bears in mountainous terrain. The higher density of males over 7 years of age in the mountains as opposed to the coastal plain appeared to influence the spring distribution of estrous females. Whether the distribution of adult males is natural or is influenced by bear hunting is unknown. Hunting is focused on single bears because females with young are protected. Since young usually remain with adult females for 2.5-3.5 years, greater hunting pressure is exerted on adult males. Adult males whose seasonal ranges include exposed lowland areas run a greater risk of being shot. This hunting pressure may explain why few males over the age of 6 years were captured on the coastal plain and why most breeding females were observed or captured in the mountains.

The mean seasonal distances traveled by adult male and female bears away from their original spring capture sites are shown in Table 1. The cumulative 6-year movements of 13 adult males were greater than those of 49 adult females. During a single annual cycle, females with cubs 6-11 months old traveled a mean distance of 13.5 km; females with older young traveled a mean distance of 17.5 km. Single adult females traveled farther than all other females, 20.8 km. These movements support the conclusion that annual mobility of adult females is associated with changes in their reproductive status.

Table 1. Distance (km) moved from original capture sites by adult female brown bears with different-aged young during a single annual cycle and by adult and subadult male and female bears on the central Alaska Peninsula, 1970-76.

Sex and age	Number of bears	Number of observations	Distance (km) Mean	Distance (km) Range
Female				
Subadult single[a]	26	88	21.8	2-82
Adult single	10	20	20.8	2-45
Adult with cubs	7	14	13.5	2-34
Adult with yearlings	18	37	17.5	2-81
Adult with young aged 2+ years	14	27	17.4	3-66
All adult females	49	165	16.6	2-81
Male				
Subadult single[a]	35	79	48.5	6-134
Adult	13	23	31.5	5-98

[a] Captured as subadults and relocated in subsequent years at any age.

Females normally separate from their young within their home ranges. One female (No. 433) 19 years old, however, traveled 64 km southwest of the center of her home range before separating from her 2 young, aged 3.5 years (Nos. 434 and 435). When captured with her young on 15 June 1974, the adult female's vulva was swollen, indicating her estrus cycle had begun. Fifteen days later, she returned alone (56 km to the northeast) and was captured while breeding with a male 5.5 years old. Female offspring No. 434 was killed 29 km southwest of her 15 June capture site during the October bear hunting season. Female No. 433 was located alone on 24 October 1974 and 7 October 1975 within 6.4 km of her original capture site.

The speed of travel of male No. 714, aged 6.5 years, provides evidence of the potential rate of mobility. While on the coastal plain, this male moved 25.8 km between 19 and 22 June and 72.5 km between 22 and 26 June.

Homing movements were also recorded and provide information on the speed of movement through mountainous terrain. Female No. 89, 3.5 years old, was captured on 24 June in the village of Chignik Lagoon, located on the Pacific side of the Aleutian Range. This bear was transported by helicopter to the northwest side of Black Lake and released. After recovering from the effects of the immobilizing drug, she returned to the village of Chignik Lagoon, an airline distance of 40.2 km, within 24 hours. Excluding travel in deep snow during periods of warm weather, there appeared to be few geographical barriers that restrict bear movements.

Movements of Subadults

The seasonal ranges of 5 males bears between mean ages of 3.3 and 5.5 years averaged 749 km^2 (range, 111-2,109 km^2). The ranges of 6 females between mean ages of 3.3 and 5.9 years averaged 244 km^2 (104-420 km^2). Males tended to move out of their maternal seasonal range; females tended to remain. This characteristic was emphasized by computing the mean distance traveled by male and female bears captured as single subadults and observed at any age thereafter (Table 1). The mean age of 35 subadult males at first capture was

3.3 years and of 26 subadult females was 3.5 years. In subsequent years, these bears were relocated 167 times. The mean airline distance traveled by males was 48.5 km, or about twice that of females, 21.8 km. When these bears were last observed, the mean age of males was 5.2 years (range, 2.5-9.5); that of females was 5.3 years (range, 2.5-10.5). The distance moved by young females was similar to that of single adult females, 20.8 km. Since distances moved between time of family separation and first capture were unknown, these averages were considered minimum.

We also computed the difference in distance traveled by 14 subadult males and 9 subadult females before and after family separation. Movements by these bears provided further evidence that males were more transient than females. The average age of males when first captured with their mothers was 2.2 years; the average age for females was 1.8 years. When last sighted, these 23 bears were alone; the average age of males was 5.3 years, that of females 5.9 years. After family separation, males were relocated a mean distance of 83 km and females a mean distance of 27 km from their original capture sites. When these young were with their mothers, the family groups moved a mean distance of 16.4 km from their capture sites. When the movements of these males captured with their mothers were compared with those of males captured as single subadults and relocated at any age thereafter, the data indicated that males travel long distances during the first few months after family separation.

The longest recorded distances were made by 5 young males (mean distance, 126 km) that were killed outside the study area: (1) Yearling male No. 80 was captured with his mother near the beach on the south side of Port Heiden Bay. When he was 4.8 years old, he was killed by a hunter, 166 km southwest of his original capture site. (2) Male No. 799 was 2.5 years old when captured alone near Black Lake. He was reported killed at age 6.8 years, 134 km to the northeast. (3) Male No. 865 and sibling male No. 866 were captured with their mother near the Meshik River when 2.5 years of age. Male No. 865 was killed at age 4.8 years, 107 km to the southwest. (4) Male No. 866 was killed when he was 6.8 years old, 95 km to the southwest of his original capture site. (5) Male No. 142 was captured alone near the mouth of Ocean Creek when he was 3.5 years old. The next spring he was killed 129 km to the southwest. About 50 percent ($N = 66$) of young males captured in family groups when 1.5-3.5 years of age have not been relocated. On the basis of kill locations of marked males, it appears that many of these bears have moved outside the study area.

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MORPHOMETRIC CHARACTERISTICS OF BROWN BEARS ON THE CENTRAL ALASKA PENINSULA

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Abstract: On the central Alaska Peninsula 344 different brown bears (*Ursus arctos* L.) were measured during 502 captures in 5 spring seasons, 1970-75. Height at shoulder, chest girth, total body length, body length, neck circumference, hind-foot length, zygomatic width, skull length, total skull size, and body weight were measured and classified by sex and cementum age. Growth rates were plotted. No morphometric differences were detected between sexes at 6 months of age, but sexual dimorphism was evident by 1.5 years of age and persisted through life. Except for zygomatic width, female bears attained at least 95 percent of ultimate body dimensions between ages 4 and 6 years and males between ages 6 and 8 years. Zygomatic width was the last dimension to attain ultimate size. Extensive size overlap was demonstrated among bears 1.5 years and older of the same sex. Superior size-weight correlations were derived from zygomatic width. It was demonstrated that the sex of bears over 9 years of age could be determined on the basis of total skull size. Serial measurements of adult bears were tested for accuracy of repetitive measurements. Skull dimensions were the least affected by inaccuracies in measuring technique. Correlations (r^2) for models tested revealed that skull dimensions were the best indicators of growth rate. Of the 10 dimensions studied, none provided a reliable age substitute for counting cemental annuli.

Rausch (1962) and Pearson (1975) mentioned the small size of brown bears inhabiting interior regions of Alaska and Canada. There are few published data, however, that described size of brown bears inhabiting coastal regions of southern Alaska. The Alaska Peninsula and Kodiak Island group may contain the largest living brown bears. Erickson (1965) reported that exceptional specimens from these areas may attain weights of 590 kg. Coastal bears are usually larger than interior forms; differences in size are probably genetically determined and influenced by climatic and nutritional conditions. The objective of this investigation was to describe morphometric characteristics, using sex and age correlates, of a brown bear population in a coastal environment of southwestern Alaska. I also evaluated the utility of body dimensions as indicators of age, sex, and weight.

This study was conducted by the Alaska Department of Fish and Game and funded in part by Alaska Federal Aid in Wildlife Restoration Project W-17-R. Persons assisting in the field were J. Faro, A. Franzmann, C. Irvine, E. Klinkhart, C. McIlroy, L. Miller, K. Pitcher, R. Rausch, and K. Schneider, all of the Alaska Department of Fish and Game.

STUDY AREA

The study area (approximately 8,547 km²), located on the central Alaska Peninsula, is bounded on the southeast by the Pacific Ocean, on the northwest by Bristol Bay, on the northeast by Mount Aniakchak (1,021 m), and on the southwest by Mount Veniaminof (2,226 m). A detailed physiographic description of the region was presented by Glenn and Miller (1980).

METHODS

Bears were immobilized and marked using techniques described by Glenn and Miller (1979). Approximately 100 bears were captured each June from 1970 through 1972, and in June 1974 and 1975. Because all measurement data were collected in spring, size difference associated with seasonal variation was small.

A steel tape graduated in millimeters was used to record 6 different body and 2 different skull measurements from 344 immobilized brown bears; 502 sets of measurements were taken. Most of these bears were also weighed.

Body dimensions were as follows: height at shoulder — distance from superior angle of the scapula to the tip of the longest claw; body length — excluding tail, the distance along the lateral side of the body between the tuber scapulae and the base of the tail; total length — distance between the tip of the nose and tip of the tailbone, with the measuring tape following the contour of the head and spine; hind-foot length — distance from the heel to the tip of the longest claw; chest girth — circumference of chest just posterior to the posterior edge of the scapulae; neck circumference — distance between the occiput and the base of the neck. Circumferential measurements were made with the steel tape held snugly.

Cranial measurements were taken by positioning the points of calipers and pressing them firmly against the skin and underlying bone. Skull length was determined by measuring the distance between the most anterior surface of a first upper incisor and the posterior protuberance of the parietal crest. This measurement was taken after the bear's head had been tilted toward its chest, thereby providing better exposure of the posterior reference point. Zygomatic width was measured at the widest point of the zygomatic arches. For purposes of this paper, total skull size was considered to be the sum of zygomatic width and skull length, and total body size the sum of the 8 variables.

Bears weighing less than 90 kg were weighed with a hand-held 90.7-kg capacity spring scale. Heavier bears were suspended beneath a helicopter in a cargo net, and weights were recorded by the pilot from a digital readout electronic weighing system (Chadwick Inc., Beaverton, Oregon) accurate to ±2.3 kg.

One upper first premolar and one lower first premolar were taken from each bear older than cubs-of-the-year. Age of these animals was determined by sectioning these teeth and counting cemental layers (Mundy and Fuller 1964, Craighead et al. 1970, Willey 1974).

Because few adult males were captured, fleshed skulls of Alaska Peninsula bears over 9 years of age, obtained from hunters, were used to compare cranial differences between sexes. To allow conversion of fleshed skull measurements to the live head size, a conversion factor was developed for a subsample ($N=4$) of skulls from male bears by comparing the difference in size before and after skulls were fleshed. The conversion factor for skulls from females was based on the difference between the mean skull size of the fleshed sample ($N=22$) and the mean skull size of the live sample ($N=54$). The zygomatic width of fleshed skulls averaged 93 percent of the live head width for males and 97 percent for females; skull length of fleshed skulls averaged 97 percent of live head length for both sexes, and total skull size of fleshed skulls averaged 96 percent of live head size for males and 97 percent for females.

For purposes of comparison, skull dimensions were considered ultimate by 15 years of age and body measurements were considered ultimate by 10 years of age. The value for percentage of each ultimate body dimension was determined by dividing the mean size of each age-class by the mean value of the ultimate body size. For example, mean body length of 6-month-old females, 46.9 cm, divided by 123.4 cm, the mean size of the 10+−year-old (ultimate size) females, is 38 percent.

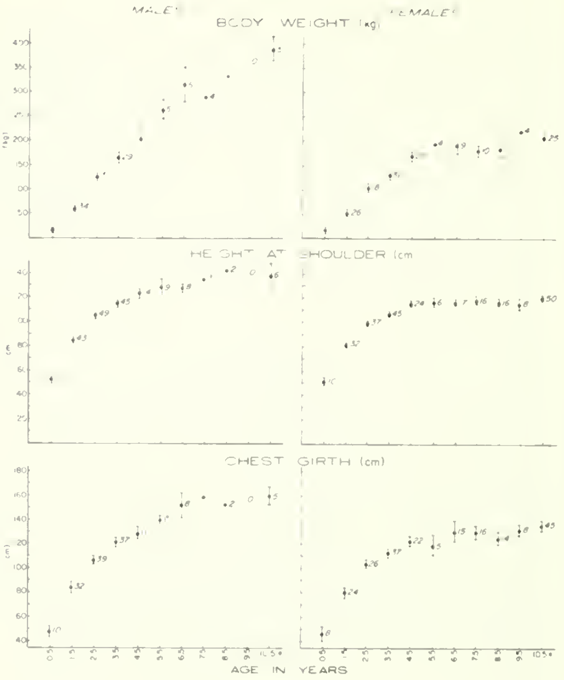
RESULTS

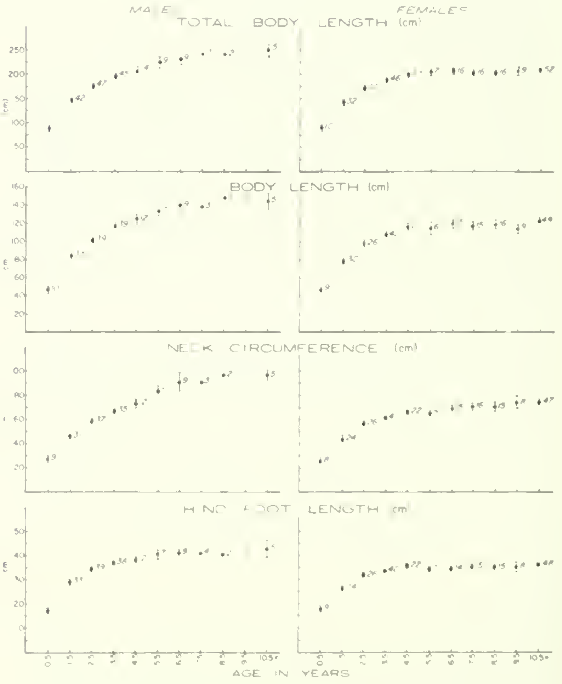
Characteristics of Growth

Fig. 1 provides a graphical presentation of body measurements made on Alaska Peninsula brown bears, reflecting the rate and duration of growth by sex and age. Sample size varied with each dimension but usually included more than 225 females and more than 150 males.

No sex-related differences in body size were apparent at age 6 months, but yearling males were significantly larger ($P<0.001$-0.05) than yearling females in zygomatic width, total skull size, height at shoulder, and hindfoot length. Males at age 2 years were significantly

Fig. 1. Change in body size by age-class of brown bears captured on the Alaska Peninsula during June 1970-72 and 1974-75. Vertical lines extending through the means represent 95 percent confidence limits on means. Numbers represent sample sizes.





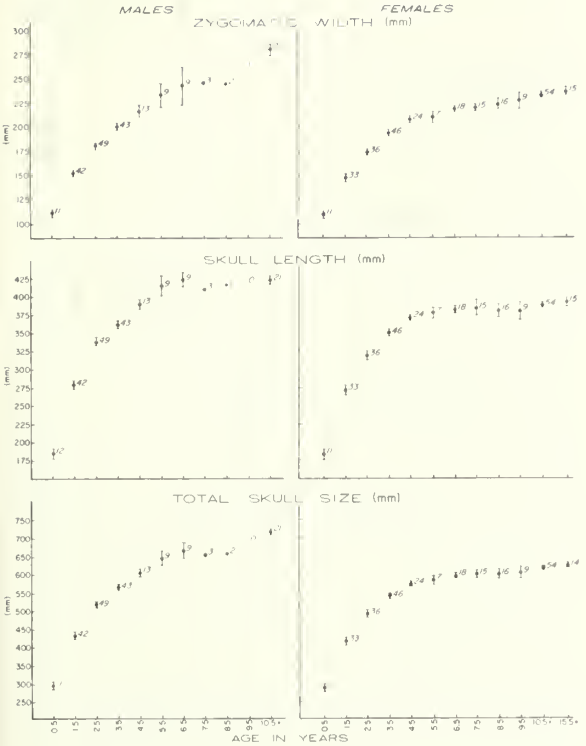


Table 1. Percent of ultimate size completed by Alaska Peninsula male and female brown bears at specific ages.

Age in years	Mean total body size completed	
	Female percent	Male percent
0.5	42	36
0.5-2.5	37	35
2.5-5.5	13	19
5.5-10.5+	8	10

Age in years	Mean cranial size completed			
	Zygomatic width		Total length	
	Female percent	Male percent[a]	Female percent	Male percent[a]
0.5	46	40	47	42
0.5-3.5	36	31	43	41
3.5-6.5	10	15	7	12
6.5-15.5+	8	14	3	5

[a] Ultimate size of males was determined from a sample of fleshed skulls adjusted to the live head size.

larger ($P < 0.01\text{-}0.02$) in skull length and body weight, and at age 3 years and older, all dimensions of males were significantly larger ($P < 0.0005\text{-}0.02$) than those of females.

By the age of 6 months, females had completed a greater percentage of their ultimate size than males (Table 1). As reflected in total body size, both sexes experienced a period of rapid, continuous growth between the ages of 6 months and 2.5 years. Between the ages of 6 months and 3.5 years, cranial dimensions showed a similar trend. A period of moderate growth then occurred, but size of males increased at a faster rate. A slow period of final growth followed. Of the variables considered, sexual differences in growth were most pronounced for cranial dimensions between the ages of 6.5 and 15.5+ years. During this time, the rate of males' growth was approximately twice that of females.

At least 95 percent of ultimate female dimensions of height at shoulder, total body length, body length, hind-foot length, and skull length were completed by age 4 years; weight, chest girth, neck circumference, and total skull size by age 6 years; and zygomatic width by age 8 years. The same percentage of ultimate male dimensions of height at shoulder, total body length, body length, hind-foot length, skull length, chest girth, and neck circumference were completed by age 6 years; weight and total skull size by age 8 years; and zygomatic width by age 10 years. The adult male sample was small within older age-classes (age 7 years and older, $N = 10$) and did not provide a clear indication of the duration of growth. Serial data within adult age-classes indicated, however, that growth in males was 95 percent complete by the aforementioned ages.

The largest captured male (784) was 13 years and the largest captured female (825) was 15 years old. Differences in their respective sizes were as follows: weight, 390-275 kg; height at shoulder, 152-130 cm; total length, 264-228 cm; hind-foot length, 44-38 cm; neck circumference, 90-80 cm; chest girth, 159-157 cm; body length, 140-127 cm; skull length, 473-403 mm; and zygomatic width, 311-251 mm. When all measurements were combined, mean total body size of 5 males over 9 years of age was 19 percent larger and their mean body weight was 88 percent heavier than the sizes and weights of 25 females of comparable age.

Figs. 2 and 3 present the predicted spring weights of male and female bears. Both the power curve fit for girth (males, $r=0.99$; females, $r=0.98$) and linear regression for zygomatic width (males, $r=0.99$; females, $r=0.99$) demonstrate a strong relationship and appear to provide a suitable method to estimate body weight. Correlations (r) were lower for other dimensions.

The summer weight gain of 1 yearling male (704) was

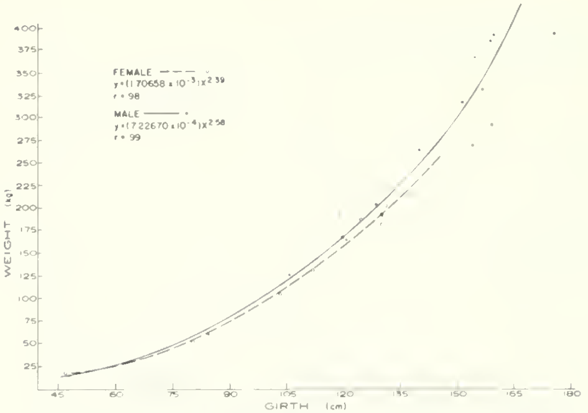


Fig. 2. Curvilinear relationship of chest girth to spring weight of live-captured brown bears, Alaska Peninsula, 1970-72 and 1974-75.

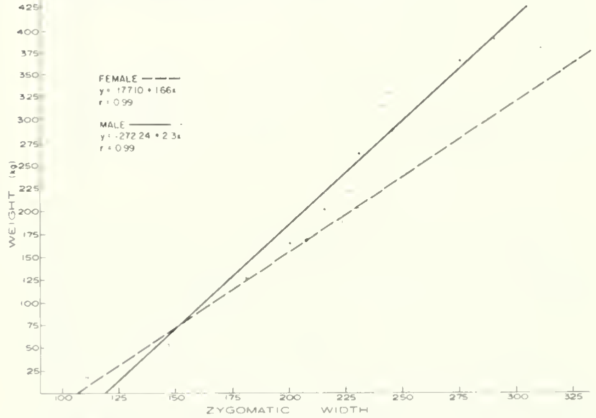


Fig. 3. Linear relationship of zygomatic width to spring weights of live-captured brown bears, Alaska Peninsula, 1970-72 and 1974-75.

recorded. Between 23 June and 15 August, this male increased in weight from 97.8 kg to 125.0 kg, a net increases of 27.3 kg (22 percent) in 53 days.

Size overlaps among age-classes characterized the Alaska Peninsula bear population. Statistical comparison (0.05 level of significance) by sex between age-classes for the expected range in body dimensions resulted in the following conclusions: (1) no dimension overlap occurred between bears aged 6 months and 1.5 years; (2) except for cranial dimensions and weight of males, yearling bears, were separated in size from bears 4 years old and older but not from bears 2 and 3 years old; and (3) except for weight and skull dimensions, sizes of 2-year-old males overlapped the sizes of other males in most age-classes between ages 1.5 and 6.5 years, and 2-year-old females overlapped in size between 1.5 years and older. When cranial dimensions and weights of males were considered, size separation for each sex was evident in bears between ages 1 and 3 years. Beyond ages 3.5 years in females and 4.5 years in males, these dimensions overlapped. When the actual range in each body dimension was compared with the expected range, data support conclusions at the 0.05 level of significance.

Measurement Reliability

Computing the coefficient of determination (r^2) for the linear fit of weight data and the logarithmic fit of body size data (ages 6 months through ages 10 years and older) provided an indication of dimension value. For these models, correlations were highest for the 3 skull dimensions (males, r^2=0.92-0.94; females, r^2=0.85-0.91) and lowest for the 6 body size dimensions (males, r^2=0.84-0.88; females, r^2=0.76-0.79). Correlations for weight were similar to correlations for body size (males, r^2=0.82;females, r^2=0.84).

Serial measurements on 13 females 10+ years old captured 28 times provided data with which to calculate the degree of reliability of measurements. The difference between maximum and minimum size for each dimension for each year was determined and expressed as a percentage of the maximum measurement. The mean percentage value was then determined for the sample. Each dimension with its corresponding percentage values follows in order of decreasing reliability: skull length, 0.9 percent; total skull size, 1.3 percent, zygomatic width, 2.1 percent; total body length, 5.2 percent; hind-foot length, 5.3 percent; height at shoulder, 5.4 percent; body weight, 6.3 percent; body length, 6.8 percent; chest girth, 10.1 percent; and neck circumference, 10.5 percent.

Characteristics of Skull Growth

Annual increments in zygomatic width and skull length were analyzed to determine their applicability for predicting mean age of male and female bears. The power curve and formulae used to show this relationship are presented in Fig. 4. Zygomatic widths show a higher relationship (males, r=0.98; females, r=0.97) than skull lengths (males, r=0.95; females, r=0.92). These data made it possible to accurately predict mean age of young bears. Corresponding ages for mean zygomatic width were discrete through age 3 years for females and through age 4 years for males. Age predictions within older age-classes were not precise but closely approximated true mean age.

Zygomatic width was at least 98 percent complete in 12 of 14 recaptured females by age 10 years. Five females had attained this maximum growth dimension by age 8 years. One female (19) was captured at ages 5, 6, 8, and 10 years; her respective zygomatic widths at these ages were 210 mm, 213 mm, 216mm, and 216 mm. Another female, captured at ages 8 and 11 years

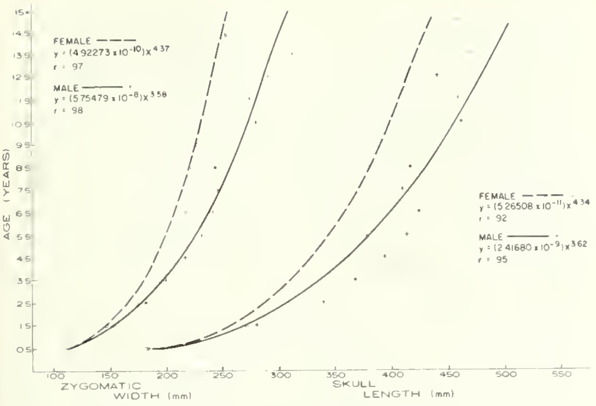


Fig. 4. Curvilinear relationship of zygomatic width and skull length to age of brown bears captured on the Alaska Peninsula during June 1970-72 and 1974-75.

(864), maintained a width of 219 mm. After females had attained the age of 8 years, annual increments in serial skull widths were difficult to detect. Skull length was at least 98 percent complete in most recaptured females by age 6 years. Two females attained this dimension by age 5 years. One female (747), captured at ages 5, 6, 7, 9, and 10 years, had respective skull lengths of 384 mm, 391 mm, 395 mm, 396 mm, and 394 mm. After females had attained the age of 6 years, annual increments in serial skull lengths were difficult to detect, as indicated in the preceding example. Sample size was too small to determine the mean ages at which males complete 98 percent of ultimate skull width and length. Serial measurements of 2 adult males, however, suggested that zygomatic width is 98 percent complete by age 12 years and skull length by age 8 years.

There was no overlap in total skull size of male and female bears older than 9 years. The minimum size of fleshed male skulls was greater than 644 mm and maximum skull size of females was smaller. Similarly, there were no overlaps between the expected ranges in fleshed total skull sizes of males (range, 651-727) and females (range, 577-636). Within the sample of live males, those older than 9 years had significantly larger ($P<0.001$) skulls than female bears of the same age. Findings were also similar when comparisons were made between the sample of fleshed male skulls and the sample of live female skulls adjusted to fleshed skull size. The total skull size of the smallest capture male (423, age 11 years) was 681 mm (654 mm converted to fleshed size); the skull of the largest female (825, age 15 years) measured 654 mm (634 mm fleshed). Bear harvest records ($N=535$) show that the largest adult female skull (certificate no. 4230) originating from the Alaska Peninsula measured 638 mm fleshed.

DISCUSSION

Although between-year comparisons of body dimensions of males aged 6 years and older and of females aged 10 years and older were based on small samples, serial measurements of adult bears and measurements derived from all family members of family units both supported definition of size characteristics.

Because there were no statistical differences in size between 6-month-old male and female bears, morphometric data for both sexes can be combined. Beyond age 6 months, *t*-tests and range values for the expected dimensions of body size justify separation of male and female morphometric data. As age increased, there was an increasingly apparent difference in body dimensions between sexes (Fig. 1). Maximum female growth was attained approximately 2 years before that of males.

Except for zygomatic width, weight, and the weight-related dimensions of neck and chest girth, females reached 95 percent of ultimate size by age 4.5 years and males by age 6.5 years. The female age of physical maturity corresponds to the age of sexual maturity reported by Glenn et al. (1976) for brown bears at McNeil River, Alaska. Pearson (1975) reported that observed known-age female brown bears of the Yukon Territory, Canada, were not sexually mature under age 6.5 years.

Spring weights of female bears increased rapidly through age 5 years. Subsequent weight gain appear to depend mostly on a bear's individual size and seasonal physical condition. Serial between-year weights of ultimate-size bears indicated less than 10 percent variation. The heaviest male (18) weighed 442 kg and was 10 years old. The heaviest female (825) weighed 277 kg and was 15 years old. Mean weights of 5 males and 25 females over 9 years of age were 389 kg and 207 kg, respectively. The weights of these adults were considerably heavier than mean weights given by Pearson (1975) for adult (minimum age and dates of weighing not given) brown bears in interior Canada. Data comparisons indicate that Alaska Peninsula males were 2.8 times heavier and females 2.2 times heavier than interior Canada males (139 kg, $N=40$) and females (95 kg, $N=21$) respectively. The degree of size difference attributable to environmental or to genetic factors has yet to be determined. Growth rates of brown bears raised in captivity suggested that adult size is generally fixed. Growth response under captive conditions, however, may not reflect comparable size response in free-roaming bears that are subjected to extreme changes in climatic, dietary, and other environmental conditions.

Chest girth and zygomatic width showed a close correlation to weights. Subjective examination of the power curve for chest girth (Fig. 2) indicates that male and female weight data can be pooled as 1 model that would serve to estimate weight. Although either measurement can be used to estimate spring weight, in certain instances 1 measurement may prove more applicable than the other when models are determined at other seasons of the year.

Only within broad limits does body size relate to age. Beginning at age 1.5 years, bears of the same sex and age exhibited a wide range in body size within and between litters. Differences in size are probably influenced by genetics, time of birth, nutrition, parental care, sibling competition, and many other factors. Two examples serve to illustrate these differences. The weights of 3 sibling males (80, 82, 83) ages 1.5 years were 27.3 kg, 31.8 kg, and 48.2 kg, respectively. Their respective total lengths were 116 cm, 123 cm, and 145 cm, and heights at shoulder were 69 cm, 74 cm, and 78 cm. The stage of eruption of the permanent canine teeth also varied greatly among these yearling males. The lengths of their left upper canine, as measured above the gum line, were 8 mm, 0 mm, and 11 mm, respectively. In the other example, the average weight of 2 sibling females (24, 25) ages 1.5 years, 30.7 kg, was considerably less than that of 3 sibling females (840, 841, 842) of the same age in a different litter, 53.6 kg. Adult skull sizes varied greatly. For example, the total skull size of male 423 at 16 years was 681 mm, which is considerably smaller than the 720-mm total skull size of male 112 at age 6 years. All body dimensions exhibited a high degree of variation beyond that attributable to age.

Variation in size of young was so great that visual age determination is essentially impractical. Trained observers on the ground could distinguish cubs up to age 8 months from older animals with little difficulty, but by late October aerial observers flying in fixed-wing aircraft or helicopters had difficulty distinguishing large, well-furred cubs 10 months old from small young older than 1.7 years. Except for cubs-of-the-year, it is unlikely that experienced observers could accurately determine age of free-roaming young in family groups. Even after capture, errors occurred in estimating age of young within 15 of 62 family groups (24 percent error). Age estimates were further complicated by the fact that some adult females retained their young for 3.5 years. (It is normally considered that young are retained only until 2.5 years of age, Glenn et al. 1976.)

When sex and age are known, all body measurements have descriptive value; only a few, however, are of practical significance. Of the 9 dimensions considered, skull measurements were the best indicators of growth rate and measurement reliability. This conclusion is supported by serial data, tested for dimension variation, and by correlations (r^2) for dimension models. Such data demonstrated that skull measurements provided the most sensitive indicators of annual growth increments and were least affected by any or all of the following variables: position of the body when measured, tension on the measuring tape, use of indistinct reference points for measurements, annual differences in the bears' physical condition, and individual differences in technique of measurement. For these reasons, collection of skull measurements should receive priority.

On the Alaska Peninsula, the sex of bears over 9 years old can be determined on the basis of total skull size. This finding is especially useful when the sex of a fleshed skull of a mature bear is unknown. If age determined from tooth cemental layers is greater than 9 years, a fleshed skull can be considered that of a female if its size is less than 644 mm. Conversely, it can be considered the skull of a male if its size is greater than 644 mm at any age.

The potential for age prediction based on mean skull dimensions was tested by using models for zygomatic width and skull length (Fig. 4). Although correlations (r) between zygomatic width and age were high, I believe the method has almost no utility in predicting the age of individual bears because of the wide range in skull size among bears of the same sex and age. At this time it appears that counting of cemental layers is the only reliable method for determining the age of individual bears.

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THE ECOLOGY OF WINTER DEN SITES OF GRIZZLY BEARS IN BANFF NATIONAL PARK, ALBERTA

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Abstract: Forty-seven completed and partially dug grizzly bear (*Ursus arctos*) dens were examined in Banff National Park, Alberta, Canada, in 1975-76. The following environmental parameters were measured or estimated at most den sites: slope, aspect, altitude, soils, vegetation, snow accumulation, and age. Most environmental parameters studied had low variability. They appeared to be important in relation to dens that were physically stable for at least 1 winter, and where snow accumulation and perhaps thermal inversion contributed to energy conservation within the den. When environmental parameters associated with dens in Banff Park are compared with those found for grizzly/brown bear dens elsewhere, some parameters, such as slope angle and snow accumulation, are similar; others, such as elevation and aspect, are dissimilar. Despite the differences, which appear to be due to local biogeoclimatic factors, a comparison of data from various areas yields a consistent, general picture of the ecology of grizzly bear den sites.

Characteristics of grizzly bear winter dens were first described in the scientific literature by Murie (1944, 1961) and Clarke (1944). In Banff National Park, our study area, McCowan (1936) reported that grizzlies denned at high elelvations, but he gave no further details. Today a fairly extensive literature describes aspects of grizzly/brown bear winter den ecology in different biogeoclimatic zones (Ustinov 1960, Sokov 1969, Craighead and Craighead 1972, Lentfer et al. 1972, Zunino and Herrero 1972, Pearson 1975, Harding 1976).

In northern latitudes, winter dens are normally dug into the earth and certain environmental parameters related to the den sites appear to be reasonably consistent from area to area. Examples of these parameters are: slope angle where the den is dug, snow-holding ability of the site, and drainage of the soil. Exceptions are the 10 undug dens that were found in rock caves located on the north slope of the Brooks Range (Quimby 1974). Other environmental parameters associated with dug dens, such as compass orientation and altitude, vary from one area to another. In a broad perspective, grizzly/brown bears in northern latitudes appear to prefer dens that will remain physically stable for the duration of at least 1 winter and where snow and accumulation contributes to energy conservation by the bear during hibernation.

Because den site selection by grizzly bears depends partly on local conditions, certain environmental parameters of the den sites are different in each biogeoclimatic zone. For this reason, persons responsible for managing grizzly bears in a given biogeoclimatic zone require specific information on den site ecology. The present study, which was undertaken within the boundaries of Banff National Park, was intended to identify specific den locations and conditions and to describe environmental parameters that could be used to predict possible future denning areas. Winter den sites should have similar environmental parameters in other portions of the eastern slopes of the Rocky Mountains in Alberta. Exceptions might occur in far northern and southern portions of the range or in areas where prevailing wind direction is different during winter months.

The study was assisted by many people. D. Hamer, D. Holroyd, and P. Perren each contributed very substantially. F. Jaggi helped us find 1 major denning area. Several other members of the Banff Park Warden Service assisted in locating dens. The project would not have been possible without the services of J. Davies of Bow Helicopters, who not only flew for us but also found dens in his spare time. The study was financially supported by Parks Canada and the National Research Council of Canada.

STUDY AREA

The physiography of Banff National Park is one of extreme relief. The lowest valley bottoms lie at 1,300 m above sea level, and the higher summits extend up to 3,000-3,500 m. The mountain system consists of a complex series of parallel-aligned ranges: the eastern mountains comprising the Front Ranges are separated by a major thrust fault from the mountains of the western Main Ranges. Important climatic and vegetative differences are associated with these different mountain ranges.

The climate is continental, and over much of the park the air masses are dry, humidity is low, and precipitation and snowfall are low, especially toward the Front Ranges. Annual and winter temperatures are low, and there is a wide range in daily maximum and minimum temperatures and in seasonal temperatures. The continentality of the climate decreases westward into the Main Ranges and with increasing elevation. Here there is greater total precipitation and deeper snowfall. The maximum precipitation occurs in winter.

Several biogeoclimatic zones occur in Banff National Park (Ogilvie 1976): the Douglas-Fir Forest Zone (1,200-1,500 m) on the warm, dry, southerly-facing slopes; the Subalpine Forest Zone (1,300-2,300 m) which forms an extensive forest band from valley bottom to timberline; and the Alpine Zone (2,200-3,000 m) above timberline.

Banff National Park covers 6,564 km^2; approximately a third of this area (2,188 km^2) was surveyed from a helicopter in our search for dens. Intensive exploration for dens took place both from helicopter and on foot throughout a 128 km^2 portion of the study area. Winter den sites of grizzly bears were found within the Upper Subzone of the Subalpine Biogeoclimatic Zone at 2,000-2,300 m. Here, the total precipitation and snowfall are high, and the growing season is brief. The continuous forest becomes diffused with glade openings and is fragmented into islands at higher elevations. Ultimately it becomes small scattered colonies of dwarf krummholz. The tree species forming the forest are subalpine fir (*Abies lasiocarpa*), subalpine larch (*Larix lyallii*), Engelmann spruce (*Picea engelmannii*), and whitebark pine (*Pinus albicaulis*). The most widespread plant associations of this subzone are the grouseberry (*Vaccinium scoparium*)-heather (*Phyllodoce* spp.-*Cassiope tetragona*) association and the false azalea (*Menziesia ferruginea*)-rhododendron (*Rhododendron albiflorum*) association. Avalanche tracks cutting into this forest are dominated by the tall herb-grass meadow (*Elymus* spp.-*Bromus* spp.) association on southwesterly slopes and the willow (*Salix* spp.) association on northeasterly slopes.

METHODS

In April 1975, we began helicopter flights to acquire information on winter den sites and early spring movements of grizzly bears. We found the first den on 9 May 1975. Discovery of this den gave us a preliminary idea of the environmental parameters related to choice of den sites. From then on, we employed a combination of aerial searches supplemented by ground searches to discover dens.

Dens were visible from the helicopter when snow was on the ground in spring (3 dens) and also during nonsnow seasons (8 dens). A pile of tailings material accumulated during den excavation extended 3-7 m below what we assumed were completed dens. Whenever the vegetation was sufficiently open and there was no snow on the ground, these tailings piles were easily seen from a helicopter.

Once a den site was discovered by aerial search, it and the surrounding area were thoroughly explored on foot. Normally, a helicopter was used for morning placement of personnel near a suspected den sit.

One group of dens was found in response to observations made by a Banff townsite resident. Another den was found during a study of grizzly bear food habits and habitat preferences.

Our methods for discovering dens were subject to certain biases. Although we were unlikely to find dens that were well hidden in trees, many dens were discovered in forested areas. These discoveries, however, usually occurred after a den was located in a nearby open or semi-open area. We also searched forested areas that we thought had appropriate environmental conditions for dens but where no dens had been seen from the air. The biases could be checked through the use of biotelemetry, but at the time of the study the park had a policy of not employing this technique.

Another bias of the study was the different intensity of search effort accorded to various areas of the park. Some portions, especially the Cascade Valley, were searched intensively, other areas less intensively, and some possible denning habitat has not yet been searched.

Each den site was eventually examined on the ground. While there, we numbered and photographed the den site and recorded environmental parameters. A clinometer was used to record slope angle and a steel tape was used to take standardized measurements of the den. Altitude was estimated with a pocket altimeter that had been set that morning in Banff. Exposure was recorded by taking a compass bearing. Estimates were made of the relative abundance of different species within tree, shrub, herbaceous, and ground layers near the den. In one instance, measured plot analysis was carried out.

The soil profile was examined from a newly exposed section at the den opening for horizon, depth, color, texture, structure, and consistency. The soil morphology and classification were based on criteria of the Canadian Soils Classification System (Canada Department of Agriculture 1974).

RESULTS

Results reported in this paper are for the period 20 April 1975-20 November 1976. During this time we recorded data for 47 den sites. Twenty-nine of these were judged to be completed dens, previously used by grizzly bears during winter. The remainder were partially dug dens, most likely made by grizzly bears but probably not used during winter. These partially dug dens averaged 1.1 m in overall length. They usually did not have a chamber.

We assumed that a den had been used during a winter if it appeared similar in size to the dens where we actually saw grizzly bears inside (1 den) or saw fresh tracks just outside the den (2 dens). We consider it unlikely that the excavations that we assumed were made by grizzly bears where in fact made by black bears (*Ursus americanus*) or other animals. A few black bear dens have been found in Banff National Park (Herrero 1970, wardens' wildlife observation cards), but all were at lower elevations. In addition, black bears are very rare or absent in the upper portions of the Cascade Valley, where 13 completed dens and 3 partially dug dens were found. The paucity of black bears in this region was confirmed during intensive field work during 1974-76. This work included the use of ungulate carcasses to attract bears. No black bears were observed to visit these carcasses.

We considered the possibility that the holes that we called winter dens might in fact be day beds for warm-season use. Despite possible confusion in this regard (Craighead 1972, Craighead and Craighead 1972), we consider a misjudgment unlikely. During the past 3 years of field work on grizzly bears in Banff Park, numerous day beds were found. These beds were always shallow excavations very unlike winter dens. Also, most sites where we found dens were not foraging areas, except perhaps casually near the den site.

Ages of Dens

The dens that we found were estimated to be of various ages (Table 1). The age of most of those dens where grizzly bear or fresh tracks were not seen was estimated by noting the vegetation regrowth on the tailings pile or den mouth (Fig. 1) and the extent of collapse of the den. According to estimates by our plant ecologist, after a maximum of 75-100 years, vegetative or geomorphological traces of collapsed grizzly bear dens are no longer readily discernible. Age estimates were not made for some dens.

Fig. 1. Grizzly bear den in avalanche meadow vegetation type, Banff National Park, spring 1976. Photo of same den, taken from a helicopter, is shown in Fig. 8.

Table 1. Estimated ages of grizzly bear dens, Banff National Park, 1975-76.

Estimated age (years)	1-2	3-4	6-9	10-15	15-20	20-25	>25
Number of dens	10	7	3	6	1	1	3

Spatial Distribution of Dens

Several dens were usually found near one another. These dens were separated by as little as 40 m or as much as several kilometers. Dens probably tended to be clustered because only a small portion of the total area of Banff Park seemed to provide suitable conditions for grizzly bear dens. Table 2 shows the number of completed and partially dug dens found in 11 topographically distinct areas.

Table 2. Number of completed and partially dug grizzly bear dens in each topographically distinct area, Banff National Park,1975-76.

Area	A	B	C	D	E	F	G	H	I	J	K
Number of dens	2	14	2	2	2	7	6	5	2	1	4

To avoid disturbing grizzly bears in denning areas, specific locations are not given; they are on file with the Banff Park Warden Service.

Time of Denning and Emergence

Warden wildlife observation cards and reports from other reliable observers suggest that in Banff National Park, most grizzlies normally den sometime during November and emerge about early April. Detailed field observations were carried out in the Cascade Valley from October 1975 through November 1976. During fall 1975, the last grizzly bear tracks, those of a female and 2 cubs-of-the-year, were seen on 13 November. The first grizzly bear tracks appeared on 20 March 1976. The last tracks in 1976 were made about 15 November. In Jasper National Park, which is in a similar biogeoclimatic zone, the use of radiotelemetry revealed the latest denning date to be 16 December (Russell, personal communication). We assume that, on the average, grizzly bears in Banff National Park spend 4.5 months in or near their den sites. Variations in this time span have been reported elsewhere and are related to age- and sex-classes of grizzly bears (Craighead and Craighead 1972, Lentfer et al. 1972, Pearson 1975) as well as to climate.

Physical Configuration of Dens

Dens were dug approximately horizontally into slopes. They appeared to contain (or have contained) a tunnel and a chamber, the chamber being larger in height and width than the tunnel. The average dimensions for the 29 dens that we judged to have been used were: width of entrance, 0.72 m; height of entrance, 0.68 m; total length from entrance to back of den, 2.20 m; maximum width of chamber, 1.22 m; maximum height of chamber, 0.84 m.

Partially Excavated Dens

The partially dug dens that we found were all located near completed dens. They appeared to be excavations that grizzlies had begun but had abandoned when unsuitable microenvironmental conditions were encountered. Often a large rock blocked further excavation. In altitude, aspect, and slope angle, partially dug dens did not appear to differ from completed ones. Because of the environmental similarity between partially dug and completed dens, data on both are presented together.

ENVIRONMENTAL PARAMETERS OF DEN SITES

Altitude, Aspect, and Thermal Inversion

Both types of dens were found within a rather narrow altitudinal band (Fig. 2). The distribution approximated a statistically normal one, except for skewing on the low elevation end. The sharper cut-off at higher elevations was probably due to such environmental factors as increased stoniness of ground, shallow soils, and exposure to wind near ridgetops. Both types of dens were usually located quite high up in the valley sides but were beneath the ridge crests (Fig. 3).

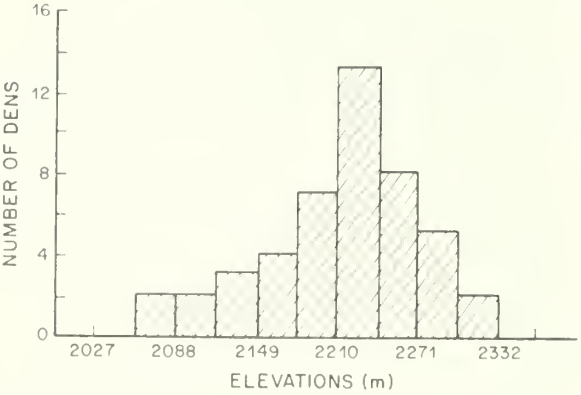

Fig. 2. Altitudes of grizzly bear dens, excluding 1 located at 1,729 m. Banff National Park, 1975-76.

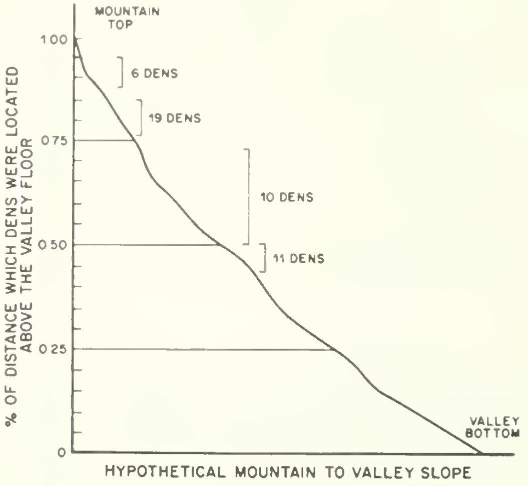

Fig. 3. Histogram and drawing depicting locations of grizzly bear dens expressed as a percentage of the elevation from valley floor to mountain top, Banff National Park, 1975-76.

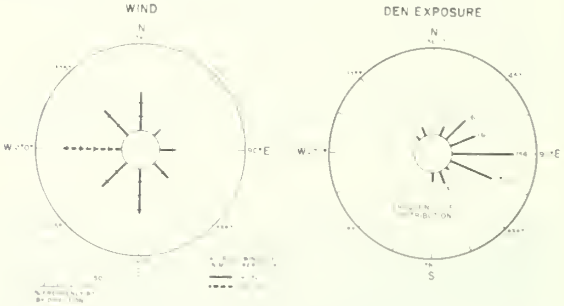

Fig. 4. Aspect of grizzly bear dens (Banff National Park, 1976) and wind force vectors (Calgary. Alberta, January 1961).

The aspects of 36 of 47 den sites were between 45° (NE) and 112.5° (ESE) (Fig. 4). The wind force vectors for Calgary, the nearest area for which such data are synthesized, are also shown in Fig. 4. The strongest wind force vector comes from the west and the most frequent den site aspect was eastward, exactly to leeward of the west wind. Den sites were located on leeward slopes, within zones of inferred snow deposition.

Thermal inversion is another environmental variable that may be related to the altitude of den locations. In the Rocky Mountains, inversions are prevalent east of the western Main Ranges and occur in most valley systems within the study area. When thermal inversions occur, a layer of warm air functionally traps a lower layer of cold air beneath it, resulting in cooler temperatures at lower elevations. Grizzly bears dens were located at alititudes where preliminary data suggests that thermal inversion is a prevalent phenomenon.

Slope Angle

Fig. 5 shows that grizzly bear dens were quite specific with regard to slope angle of the den locations. The mean slope angle for completed and partially dug dens considered together was 33°. All dens were on slopes greater than 22°, with 36 of 46 dens between 30° and 38°; none were on slopes over 40°.

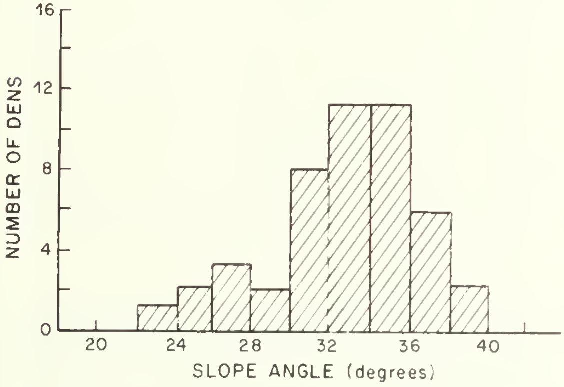

Fig. 5. Angle of slope where grizzly bear dens were located, Banff National Park, 1975-76.

Soils and Vegetation

The soil profiles of the dens consist of Podzolic, Brunisolic, Chernozemic, and Regosolic soils. The soil parent materials include tills, colluvium, and fragmented or weathered bedrock. The rock types include limestones, shales, sandstones, conglomerates, and quartzites. The vegetation in which the dens are located consists of mature forest, krummholz, meadow, and shrub communities.

The soil and vegetation data are summarized for 38 dens under the following 6 vegetation types (Ogilvie 1966). Soils and vegetation data were not collected for the remaining 9 dens. The major plant species are listed, by strata, in order of dominance.

1. Grouseberry-Heather Vegetation Type. *Picea-Abies-Larix/Vaccinium scoparium* Association (Figs. 6, 7).

Seventeen completed and partially dug dens.

Shallow Podzolic Soils (LFH, Ae, Bf, C); parent material: scattered to very abundant colluvial fragments of shale, sandstone, or limestone. The vegetation is characteristic of the upper subalpine and timberline area, consisting of mature closed stands, stands with openings, and low krummholz colonies. The tree composition is spruce, subalpine fir, and sometimes subalpine larch. The stand structure varies from small openings under the tree canopy to large glades. There is very deep snow accumulation that increases with increasing size of the glade.

Fig. 6. Aerial photograph of grizzly bear den in grouseberry-heather vegetation type, Banff National Park, spring 1976.

Fig. 7. Close-up photograph of den shown in Fig. 6. Note supporting tree root.

Trees: *Picea engelmannii, Abies lasiocarpa, Larix lyallii.*

Shrubs: *Vaccinium scoparium, Phyllodoce glanduliflora, P. empetriformis, Cassiope tetragona, Vaccinium myrtillus.*

Herbs: *Arnica latifolia, A. cordifolia, Pedicularis bracteosa, Erigeron peregrinus* var. *callianthemus, Valeriana sitchensis, Potentilla diversifolia, Hieracium gracile, Silene lyallii, Castilleja rhexifolia, Antennaria racemosa, A. lanta, A. alpina.*

Mosses and lichens: *Dicranum scoparium, D. fuscescens, Timmia austriaca, Peltigera aphthosa, Cladonia* spp.

There are 4 important variants of this habitat type:

a. Shallow bedrock variant: the bedrock occurs close to the surface and the shallow soil mantle consists of coarse quartzite rock fragments; the soil profile is Regosolic (LFH, (B), C).

b. Moist seepage variant: the soil profile is a Seepage Regosol (LFH, B, C); the parent material is compact clay loam with coarse shale fragments. The seepage indicator species are: *Salix vestita, Parnassia fimbriata, Equisetum scirpoides, Anemone parviflora, Senecio lugens*.

c. Dense krummholz variant: the vegetation consists of a dense colony of *Abies*, with very sparse occurrence of other species: *Arnica cordifolia, Valeriana sitchensis*. The soil profile is a leached Brunisol (LFH, Bf, C); the parent material is abundant, hard shale fragments.

d. Large glade with deep snow accumulation: the deep snow indicator species are: *Salix arctica, Myosotis alpestris, Stellaria monantha*. The soil profile is Shallow Chernozemic Black (LFH, Ah, B, C); the parent material is sandy loam with scattered stones.

2. False Azalea-Rhododendron Vegetation Type. *Picea-Abies-Larix/Menziesia-Rhododendron* Association.

Five completed dens.

Deep Podzolic Soils (LFH, Ae, Bf, C); the soil parent material is variable: tills of stones and loam, weathered shales of very fine particles or with stone fragments. This vegetation type occurs at slightly lower elevations than the previous one; it consists of old, mature, closed stands of spruce, fir, and occasionally larch.

Trees: *Picea engelmannii, Abies lasiocarpa, Larix lyallii*.

Shrubs: *Menziesia ferruginea, Rhododendron albiflorum, Vaccinium membranaceum, V. myrtillus, V. scoparium*.

Herbs: *Arnica cordifolia, A. latifolia, Viola orbiculata, Cornus canadensis, Lycopodium annotinum, Pedicularis bracteosa*.

Mosses and lichens: *Hylocomium splendens, Peltigera aphthosa, Dicranum fuscescens*.

3. Fir Krummholz-Rock Willow-Herb Vegetation Type. Krummholz *Abies/Salix vestita-Thalictrum* Association.

Five completed dens.

Deep Podzolic Soils (LFH, Ae, Bf, C); the parent material is coarse colluvial limestone rubble.

There is deep snow, with surface avalanching down to the top of the krummholz vegetation. This vegetation type occurs at timberline and consists of dense fir krummholz.

Trees: *Abies lasiocarpa* (krummholz form).

Shrubs: *Salix vestita*.

Herbs: *Thalictrum occidentale, Senecio lugens, Valeriana sitchensis, Arnica cordifolia, Epilobium angustifolium, Fragaria virginiana* var. *glauca*.

Mosses and lichens: *Brachythecium* sp., *Peltigera aphthosa*.

4. Subalpine Herb-Meadow Vegetation Type.

Two completed/dens.

Shallow Podzolic Soil (LFH, Ae, B, C); parent material: loam with scattered stones.

The structure of the vegetation is an herb-meadow glade-opening in the upper subalpine forest.

Trees: *Abies lasiocarpa, Picea engelmannii, Larix lyallii*.

Herbs: *Hedysarum sulphurescens, Epilobium angustifolium, Heracleum lanatum, Fragaria virginiana* var. *glauca, Achillea millefolium, Valeriana sitchensis, Thalictrum occidentale, Erythronium grandiflorum*.

5. Avalanche Meadow Vegetation Type. *Elymus innovatus-Bromus pumpellianus-Hedysarum sulphurescens* Association (Figs. 1, 8).

Seven completed dens.

Fig. 8. Aerial photograph of grizzly bear den in avalanche meadow vegetation type, Banff National Park, spring 1976. A female and 3 cubs-of-the-year were inside.

Shallow Chernozemic Black Soil (Ah, B, C) and Shallow Brunisolic Soil (LFH, (Ah), Bf, C); parent material: loam and shale fragments. This vegetation consists of rich meadows of mixed grasses and forbs occupying avalanche tracks cut into the upper subalpine closed forest.

Shrubs (infrequent): *Juniperus communis*.

Herbs: *Elymus innovatus, Bromus pumpellianus, Hedysarum sulphurescens, Aster foliaceus, Fragaria virginiana* var. *glauca, Danthonia spicata, Epilobium angustifolium, Poa* spp., *Festuca scabrella*.

Mosses and lichens (infrequent): *Tortula ruralis, Bryum* sp., *Brachythecium* sp., *Peltigera canina.*

There are 2 variants of this vegetation type:

a. With additional grass species: *Agropyron trachycaulum, Trisetum spicatum, Phleum alpinum, Danthonia spicata, Aster foliaceus.*

b. With heavier shrub cover: *Juniperus communis, Arnica cordifolia, Elymus innovatus.*

6. Subalpine Shrub-Herb Meadow Vegetation Type Two dens.

Shallow Chernozemic-Regosolic Soils (LFH, (Ah), B, C); parent material: colluvial limestone fragments.

The vegetation occurs in the upper subalpine krummholz and consists of mixed shrubs and meadow herbs.

Trees (krummholz form): *Abies lasiocarpa, Picea engelmannii.*

Shrubs: *Juniperus communis, Potentilla fruticosa, Salix glauca.*

Herbs: *Aster* spp., *Solidago multiradiata, Epilobium angustifolium, Fragaria virginiana* var. *glauca, Achillea millefolium, Agropyron latiglume, Bromus pumpellianus.*

Summary of Typical Den Site Conditions

A "typical" den was located in the upper subalpine-timberline area at a mean elevation of 2,280 m. The mean slope angle was 33°, and the orientation was between 22.5° (NNE) and 112.5° (ESE). Slopes of typical dens are leeward of prevailing winds and partly because of their lee position have stable, deep snow cover. Surface avalanching may occur but does not normally extend to the ground surface.

Soils are well-drained; wet-seepage soils are avoided. The typical den may be located in diverse geological bedrocks and parent materials. Shallow bedrock soils are avoided. The soils have a wide range of stoniness and amounts of sand, silt, and clay. Extremes of soil textures are avoided, e.g., massive rock blocks or very fine clays. The structural coherence of the soil mass is variable, ranging from weak to strong. Weakly coherent soils may be structurally reinforced by a network of roots of trees, shrubs, and herbs and by being frozen during winter usage of the den.

Aberrant Dens

Some dens varied so much from the norm that special mention is required.

One den was much lower in elevation (1,769 m) than the others. The roof of this den was formed by a substantial root of a spruce tree. Then den was large enough to have been used and could have been either a black bear or grizzly bear den.

Five dens were oriented either southerly or northwesterly, possibly exposing them to strong wind or winter sun. We have an impression that local microclimatic factors (such as nearby ridges) lessened the potential adverse effects of wind. However, some of these dens did not seem to be as climatically buffered as were most dens.

Two dens located about 40 m apart appeared to have collapsed during their first winter. When we found them they appeared to be less than a year old. One was probably unused and the other used for a month or two before it collapsed. Near these sites, 38 trees had broken limbs or boles. Limbs were removed to a height of 4.6 m, apparently indicating that the bear had climbed the trees since maximum snow depths would not have exceeded 2 m. A substantial ground bed, at least 30 cm thick when we examined it during late summer, was located in front of 1 den. We surmised that the bear had spent the remainder of the winter or spring on this bed.

Observations of Grizzly Bears at a Den Site

On a helicopter search flight on 12 April 1976, we saw a female grizzly and 1 cub-of-the-year at an open den entrance. At this time there were no tracks in the snow outside of the den. On 17 April, the den was checked again and there were still no tracks. On 21 April, a single track appeared outside the den. From 23 April to 25 April, one of us used the helicopter to set up a bivouac camp about a kilometer from the den. The bears and the den site were observed from this camp with the aid of a spotting scope (20X, 20-45X). The den occupants were a female grizzly bear with 3 cubs-of-the-year. During the time the den site was observed, the bears were outside for 2-4 hours per day, spending each night (23 and 24 April) inside the den. While the female was outside, her behavior and that of the cubs differed markedly. The cubs either played or nursed, or occasionally rested, when outside. Their play was vigorous and prolonged but never took them farther than 20 m from the female. One of their play activities was to climb up a snow slope and then launch themselves down it. They sometimes started their slide from about 4 m above the den mouth. At these times their slide normally stopped when they landed on the head of the female who sat in the den entrance. Her movements in general, even on those occasions, were lethargic. She allowed the cubs to fall off or climb down her back without taking action herself. When walking she would sometimes take slow, exaggerated steps, somewhat slothlike but faster. She occasionally ate snow, and subsequent examination of the site suggested that she dug some *Hedysarum sul-*

phurescens roots. She appeared still to be in her winter lethargy, conserving energy. The cubs were actively exploring their local environment.

The female built 2 day beds in patches of trees, 12 m and 15 m away from the den entrance. Trails worn in the snow connected these sites with the den. Other worn trails led to another patch of trees and to nearby assumed feeding areas where the snow had sloughed. The entire zone of activity was no greater than 50 m in diameter.

On 30 April, the den was checked again and the bears were gone. Snow coverage of tracks suggested that the bears may have left 2 or 3 days earlier. Therefore the family appeared to have spent about a week sleeping at night in the den and sometimes going outside during the day. Lentfer et al. (1972) found evidence that 3 family groups of grizzly bears in coastal Alaska had beds outside their dens. Their data indirectly suggest similar usage to that described here. Craighead and Craighead (1972) reported another similar observation for a female and 2 yearlings that remained near a den site for about 3 weeks after emerging.

DISCUSSION

This project was designed to conform to a Banff National Park policy directive that requested all possible information on winter den sites of grizzly bears but did not allow direct disturbance of the bears in any way. Because biotelemetry was not used, most of our work was necessarily inferential. We may have oversampled dens which were visible from the helicopter, and undersampled dens obscured by trees or thick shrubbery. We focused on the study of environmental parameters associated with den sites.

As was found in coastal Alaska (Lentfer et al. 1972), in the interior Yukon (Pearson 1975), and on the Arctic coast (Harding 1976), helicopter or fixed-wing aircraft is an efficient tool to help locate dens. In Banff National Park, it was profitably combined with searches on foot.

Most of the den sites that we investigated were older than a year. We found that most dens begin to disintegrate after the first winter and that after 75-100 years they are difficult to detect, even with experience. Reuse of dens in our area is unlikely because of collapse.

Environmental parameters associated with den sites were quite consistent in our study area. Dens of grizzly bears in Banff National Park appeared to be situated in areas when a deep insulating layer of snow would accumulate at the den entrance and above, and where the soils were cohesive enough during the first winter to maintain the physical stability of the den. The stored heat of the earth and the metabolic heat of the bear appear to have been conserved within the den.

The vegetative type widely used for winter dens is the grouseberry-heather association. Deep snow accumulates between widely spaced trees or in the glade openings in the stand. Another vegetative type frequently used for denning is the grass and forb meadows on avalanche tracks cut into the closed subalpine forest stands. Fewer dens were found in the krummholz shrub meadows and in the herb meadow glade openings. Some dens were found at lower elevations in the closed mature forest of the false azalea-rhododendron tall shrub vegetation type.

A common feature of all these vegetative types is the deep and long-lasting snow accumulation that we infer was associated with them. The specific action of avalanching in some of these communities is of importance here. The elevation of many dens and their locations on the leeward side of mountains often put them near the trigger zones of winter avalanches. Although the avalanche near the release point may pass directly over a den, it is unlikely that winter avalanches would often remove the snow cover to a depth that would seriously affect the insulation of the den. Winter avalanches of major size in the study area are normally released by a soft slab breaking in the trigger zone. This soft slab is usually only the upper layer of the snowpack. At these elevations, also, not many days would elapse after a surface avalanche released until a new layer of snow would be deposited, either by snowfall, wind action, or both, and any loss of insulation would be restored. After the avalanche has gained enough momentum going down the mountain, it will move the entire snowpack, but this would happen only at elevations lower than where grizzly dens are normally located.

The type of avalanche that does take the snow to the ground at elevations where dens are located is the wet spring avalanche. This type, however, is not likely to be a problem to the bears since it occurs in late spring, after the bears have left the dens.

Of the considerable diversity of soils and parent materials at the den sites, some common features should be mentioned. The soil profile types — Podzolic, Brunisolic, Chernozemic, and Regosolic — are all well drained; there are no Organic, Gleysolic, or Alluvial profiles. Soil texture, structure, stoniness, and consistency are highly variable, ranging from fine loams to coarse rock fragments and from loose coherence to very firm consistency. There are numerous combinations of these soil physical factors that can provide the requisite stability for dens during a single winter occupancy: a minimum amount of structural coherence of the rock fragments and fine soil particles, combined with the binding effect of a dense network of roots of trees, shrubs, and sod-grasses, along with the solidifying effect of the frozen soil mass.

There is no relationship between the dens and the bedrock geology. A wide range of rock types occur: limestones, shales, sandstones, conglomerates, and quartzites.

When the environmental parameters associated with den sites in Banff National Park are compared with those found elsewhere, a fairly consistent picture of denning ecology emerges. Environmental parameters are either consistent from area to area or much of the variability can be explained by considering local biogeographic conditions, the experience of a given bear, and perhaps human influence both today and over many generations.

Rock cave dens as found by Quimby (1974) are excluded from the following discussion.

The mean slope angle of den sites in Banff National Park was 33°, which compares closely with the findings of Lentfer et al. (1972) (9 dens, 0°-30°; 14 dens, 30°-45°; 5 dens, 45°-60°), Pearson (1974) (mean slope angle, 35°), and Harding (1976) (most dens, 30°-60°), Pearson (1974) (mean slope angle, 35°), and Harding (1976) (most dens, 30°-50°). We agree with Harding (1976) that slope angle seems to be important for trapping snow at the den entrance but not in the chamber and for easy removal of material dug during construction. A more important reason for choosing slopes of a certain angle may be related to the stability and thermal properties of the den. Grizzly bears normally dig straight into a slope. If they dug downward, the den would be a less efficient heat trap. If they dug straight into slopes of less than 25°, there would be a thinner covering of soil over the den and the chances of collapse would probably increase. Shallow, unstable soils, and the lesser ability of steeper slopes to hold snow are probably the factors that prevent grizzly bears from using very steep slopes.

Although the soils associated with Banff National Park dens were found under 6 different plant associations, all soil types were normally well drained and stable at least during the first winter. Amongst the exceptions were 2 dens that appeared to have collapsed during the first winter (see Aberrant Dens, RESULTS section). Perhaps these dens were made by inexperienced grizzly bears. Craighead and Craighead (1972) hypothesize that experience in den construction serves to improve what is for the most part genetically programmed behavior. Learning, both from the mother grizzly bear and from individual experience, would also be important within each biogeographic zone. Because specific environmental parameters vary from area to area, learning is a necessary adjustment.

Most authors have reported that willow and alder (*Alnus* spp.) shrubs are present at den sites (Lentfer et al. 1972, Pearson 1975, Harding 1976) or that dens are buttressed by tree roots (Craighead and Craighead 1972). Although some of our dens had buttressing tree or shrub roots (Fig. 7), most were in small glade openings in subalpine forest, in subalpine herb meadows, or in avalanche meadows. Buttressing tree or shrub roots were absent at many of these sites although typically there was adequate soil development and root penetration by herbs. Synthesizing from all reported studies, it appears that roots help bind the soil at dens, but in some areas like ours, trees or shrubs are not essential to support the dens, to hide them, or to catch snow.

The vegetation at den sites indicates that dens in Banff National Park are located in areas that accumulate snow. The aspect (predominantly NNE to ESE) of dens, form of vegetation, average mean altitude (2,280 m), and direction of prevailing winds (prediminantly W) are all favorable to early and prolonged snow accumulation at den sites. If the bears denned at lower elevations they would receive significantly less insulation from snow. Lower down, the snow comes later, is generally more dense, and is not as deep. In late fall, after heavy frosts, grizzlies appear to have difficulty finding adequate food. They move toward higher denning areas when ordinarily there is little snow in valley bottoms. Perhaps they go to the highest elevation where they still find good soil, aspect, and slope. It would seldom be long before snow would cover and thus insulate the den. The average altitude of den sites in Banff National Park also suggests the possibility that colder temperature normally associated with higher altitude may be ameliorated by thermal inversion effects.

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TIME-LAPSE CAMERAS AS AN AID IN STUDYING GRIZZLY BEARS IN NORTHWEST WYOMING

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Abstract: Time-lapse cameras were effective for gathering limited distribution and population data on grizzly bears (*Ursus arctos*) and black bears (*Ursus americanus*) in northwest Wyoming. Thirty-six stations, each consisting of a camera and a lure, were monitored for 551 camera-days; 83 rolls of film were exposed. Five different lures were tested. Thirty-one bears (5 grizzly, 25 black, 1 unknown bear) were identified at 15 stations. Young:adult and young:female ratios observed (0.4 and 1.5 for black bears and 0.7 and 2.0 for grizzlies) corresponded well with those of other researchers in the region. One sighting recorded on film extended the known range of the grizzly bear in the Shoshone National Forest.

Effective management of wildlife populations requires knowledge of distribution, abundance, and composition. Numerous methods have been used to collect these data, but none has proven completely satisfactory when applied to black bear and grizzly bear populations. Harvest information does not always give a true representation of a population's age structure or sex ratio. In Michigan, Erickson et al. (1964:84-87) found that hunters reported a larger segment of the bear population to be males than was verified by the study personnel. Sex ratios of captured bears have varied from the expected 1:1 and these variations have been attributed to the method of capture. Poelker and Hartwell (1973:124) found that trapping gave the highest proportion of males, dog hunting was selective for females, and still hunting showed no selectivity.

The use of tracks in estimating bear populations (Spencer 1955, Edwards and Green 1959, Klein 1959) was affected by many variables such as berry production and abundance of salmon and other preferred foods. Aerial censuses were affected by time of day, wind velocity, and abundance of vegetation, but were considered valid when used in conjunction with hunter-caused mortality, and direct and sign observations (Erickson and Siniff 1963; Knight et al. 1975:11-13, 1976:7-9). Direct observations at dumps, roadsides, bait stations, and streamsides have been used to gather information on population dynamics (Hornocker 1962, Troyer and Hensel 1964, Barnes and Bray 1967, Jonkel 1967, Craighead et al. 1974). Researchers used marked individual bears and computed total numbers by using the Peterson Index and the Schnabel method (Schnabel 1938).

This paper described and evaluates the adaptation of a time-lapse camera system (Diem et al. 1973) for monitoring grizzly and black bear populations in northwest Wyoming. Impetus for the study was the need for base-line data from Wyoming for the Interagency Grizzly Bear Study being conducted in Yellowstone National Park and the surrounding areas in Wyoming, Montana, and Idaho. The objective of the study reported in this paper was to provide data on distribution, abundance, and age-classes of grizzly and black bears as a means of evaluating the potential usefulness of the camera system in bear population studies.

I wish to thank the personnel of the Wyoming Game and Fish Department for supplying cameras and equipment and for their valued assistance throughout the study. I also appreciate the assistance obtained through the Department of Zoology and Physiology, University of Wyoming, Laramie. R. Hede provided valuable field assistance during the 1976 field season, and the U.S. Fish and Wildlife Service, Wildlife Research Center, Denver, Colorado, supplied several of the lures used during the study.

STUDY AREA

The study area included approximately 2,800 km^2 in northwestern Wyoming (Fig. 1). The area is rugged and mountainous, with large ranges of exposed basaltic rock interspersed with meadows and dense coniferous forests. Elevations range from 1,400 m near Cody, Wyoming, to 3,680 m at the summit of Fortress Mountain. Seventy percent of the area is roadless wilderness and travel was by horseback or foot.

METHODS

Fourteen automatic super-8 time-lapse cameras, as described by Diem et al. (1973), were used to monitor 36 stations at various elevations and in various habitat types from 3 July to 21 October 1975 and from 3 June to 14 September 1976 (Fig. 1). The system incorporated an intervalometer circuit that functioned as a light

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[1] This study was completed while the author was a temporary employee of the Wyoming Game and Fish Department and a graduate student in the Department of Zoology and Physiology, University of Wyoming, Laramie 82071.

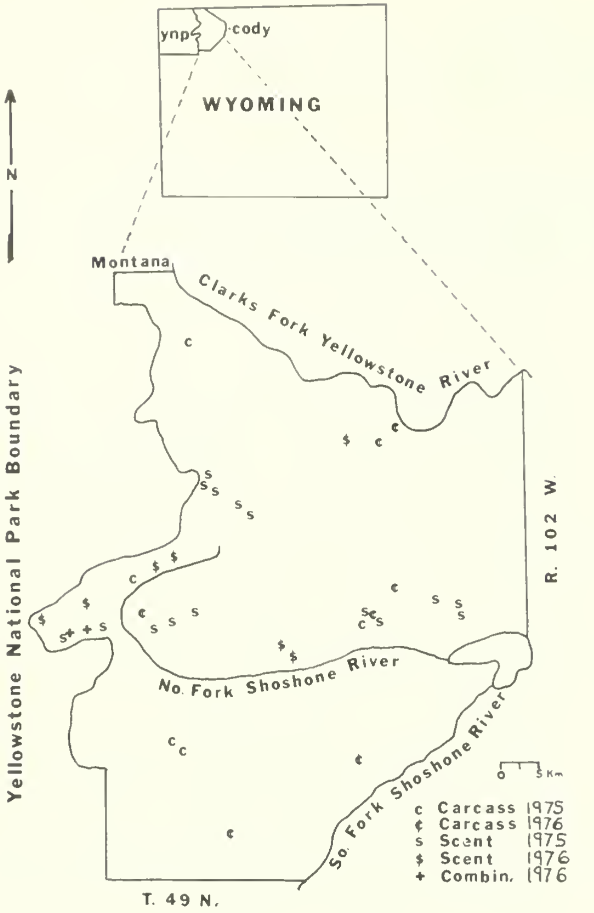


Fig. 1. Map of study area, Wyoming location map, and locations of camera/bait stations for bears.

activation-timer, pulse generator, and electric switch. A photosensor activated the camera at dawn and turned it off at night.

The cameras were equipped with zoom lenses, allowing the horizontal field of view to be varied with the type of lure monitored. Fields of view ranged from 8 m for scent and combination stations to 15 m for carcass stations. Cameras were positioned facing north or south to reduce glare, and most were fitted with a sunshade over the front of the camera box. The stations, each consisting of 1 camera and a lure, were located in areas of known or suspected grizzly bear range. The lures were placed a minimum of 150 m from major trails to reduce human disturbance, with the camera box mounted to a nearby tree with large eyebolts, nylon webbing, and a chain for security.

Preliminary investigations showed Kodak Ektachrome film (ASA 160) produced the best picture quality and resolution. Film was advanced at 1 frame/2 minutes at all stations in 1975, but to compensate for the reduced time that the bears spent at nonconsumable baits, film speed was increased to 1 frame/1.5 minutes at all stations except carcass baits, which remained at 1 frame/2 minutes.

Three categories of lures were used: scents (nonconsumable), carcasses (consumable), and combination lures (scent and carcass). Except for 1 winter-killed elk (*Cervus canadensis*) used in spring 1976, the monitored carcasses were horse baits put out by big game outfitters or hunters to lure black bears. The scents that were used would lure bears into the area but would not provide a major source of food. Thus, bears would visit the area and then move on. The scents used were fish and chicken (FC), synthetic fermented egg (SFE), putrid fish (PF), pheromone, and estrous grizzly bear urine (EGBU). Two to 3 kg of FC were placed in a burlap sack and suspended between 2 trees at a height of 3 m. Cans of sardines were nailed to the trees or dry dog food was spread below the baits to help keep bears within the field of view long enough to be photographed.

In 1976, this technique was modified to use concentrated scents. Surplus metal 7.62-mm ammunition cans held and protected the lures. The cans were perforated on 4 sides with holes 7-10 mm in diameter spaced about 2 cm apart to allow the scent to escape. Liquid baits were poured over absorbent paper placed loosely in the cans, and solid lures were sprinkled into cans without paper. For each lure station, 250 ml of PF or EGBU, 15-20 of pheromone, or 12-15 g of SFE were used. Cans were tied to trees and their contents replenished every 14 days.

The formula used for the PF was modified from Taber and Cowan (1971). Water was added to the rotten fish to prolong its liquid state because volatility was lost as the mixture solidified from evaporation. The SFE and the formula for the pheromone lure were supplied by the U.S. Fish and Wildlife Service, Wildlife Research Center, Denver, Colorado. Estrous grizzly bear urine was obtained from 2 adult females in captivity at the Denver Zoo, Denver, Colorado.

Film exposed during the study was analyzed in 2 stages. Preliminary analysis was done with a manually operated film editor (Argus, Model 2804). A Bell and Howell multimotion projector (Model 1623Z) was used for final editing. Bears photographed were identified as to species, and distinguishing features (natural markings, size, family groups) that might enable individual recognition were noted. When a bear could not be recognized as a new individual, the visit was considered a return and the bear was not added to the total number identified.

RESULTS.

Stations were monitored for 551 camera-days (1 camera at a site for 1 daylight period), exposing 83 rolls of film. At carcass stations, the 1 frame/2 minutes interval supplied at sufficient number of photos to identify the bear. A standard 15-m roll of film lasted up to 7 camera-days, depending on day length. This same interval was inefficient at scent stations in 1975. It provided enough photographs for positive species identification of only 4 of 5 bears. When trying to determine distribution and population dynamics of a particular species of bear, this 20 percent rate of failure could greatly affect the results of the study. The more efficient 1 frame/1.5 minutes interval used at scent or combination stations in 1976 used a 15-m roll of film in about 5 camera-days.

Thirty-one potentially different bears (5 grizzly, 25 black, 1 unknown bear) were identified at 15 stations. None of the identified bears was recognized at more than 1 station; however, all were unmarked, and thus a bear could have visited more than 1 lure station without being recognized as the same individual. At several stations, the same bear was identified returning to the site.

Although the sample size was small, the young:adult and young:female ratios recorded on film (0.7 and 2.0 for grizzly and 0.4 and 1.5 for black bears) (Table 1) compared favorably with the results obtained by Roop (1976) from grizzly bear sightings and sign records in northwest Wyoming and by Barnes and Bray (1967:144) for black bears in Yellowstone National Park.

Table 1. Young:adult and young:female ratios of bears photographed in northwest Wyoming, 1975 and 1976.

Year	Species	Females with subadults	Females with cubs	Other adults	Young: adult	Young: female
1975	Black	-	-	5	0	0
1976	Black	-	4:6	11	0.40	1.5
1976	Grizzly	1:2	-	2	0.67	2.0
1975-76	Both	1:2	4:6	18	0.35	1.6

The small number of bears photographed in 1975 (4 black, 1 unknown) corresponds well with the reduced number of bears observed by Knight et al. (1976:15) and Roop (1976:4) using aerial censuses, backcountry observations, and time-lapse cameras. Knight et al. (1976:15) attributed the below-average number of observations, relative to the 2 preceding years, to lush vegetation and an abundance of natural foods, induced by a wet spring and early summer. Since bears concentrate in areas with succulent vegetation (Mealey 1975:119), the widespread availability of vegetation throughout the summer probably enabled bears to find abundant forage without resorting to carrion.

Carcass Stations

Baits were monitored for 157 camera-days exposing 20 rolls of film. Eight bears were identified, 1 grizzly and 7 blacks. No bears were photographed near the 5 carcasses monitored in 1975, although 3 were visited by bears. In 1976, bears were photographed at 4 of the 7 stations monitored.

No interspecific or intraspecific interactions were observed at any of the stations. This lack of direct competition for carcasses conflicts with the observations of Barnes and Bray (1967:83-89) and may relate to the abundance and availability of preferred vegetable foods (Tisch 1961, Mealey 1975). Knight et al. (1976) stated that observations from time-lapse cameras used by the Interagency Grizzly Bear Study Team indicated that some bears prefer succulent herbage to carrion. An investigation of black bear hunter success on my study area showed that many baits remained untouched by bears even in areas known to support high bear populations.

In 1976, a single grizzly was photographed feeding at station 22. This bear is believed to be 1 of a group of 3 bears, a female and 2 subadults, observed at the carcass by a hunter 3 days before the camera was installed, and represents an extension of the known range of the grizzly bear in northwest Wyoming.

Scent Stations

A total of 22 scent stations (Fig. 1) were monitored for 313 camera-days exposing 48 rolls of film. Fifteen bears (4 grizzly, 10 black, 1 unknown bear) were identified at 10 stations.

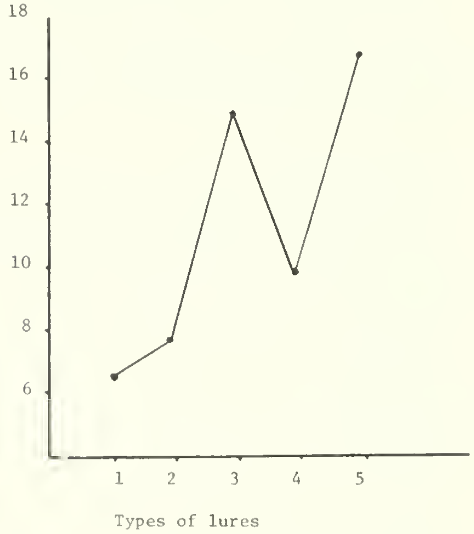
In 1975, 5 bears (4 black, 1 unknown bear) were photographed in 7 visits. Two of the cameras were disturbed by bears without the bears being photographed. Claw marks and hair confirmed that bears were responsible for the disturbances. Seven scent stations were monitored in 1976, with bear activity recorded at 5 locations. Ten bears (4 grizzly, 6 black) were identified from 19 rolls of exposed film.

The cool temperatures in 1975, especially at higher elevations, slowed, and sometimes prevented, putrefaction of the FC bait. Bears probably were not attracted to some stations because the lures were not odorous. Therefore, scents used during 1976 were odorous by design, eliminating the problem of delayed putrefaction. The use of concentrated lures also solved another problem. It was very difficult to prevent bears from tearing down the FC bait and eating it, thus making it unavailable to attract other bears. By changing to concentrated lures and placing them in sealed containers, this problem was eliminated.

Combination Stations

Two stations using a combination of a scent and a carcass as a lure were monitored for 82 camera-days in 1976, exposing 15 rolls of film. One objective of using a combination lure was to conduct a further test of the attracting power of the various concentrated scents by trying to enhance an already existing lure. The results were inconclusive, although 4 bears were observed at each station. At 1 stations, bears had almost totally consumed the carcass by the time the camera and lure were put into position. Bears continued to come to the station and investigate the lure even after the carcass was completely consumed. At the second station, bears had not used the carcass before installation of the lure and camera and did not begin coming to the station until the 32nd day of monitoring.

The mean number of days until a station was first visited by a bear was calculated for the various types of lures (Fig. 2) to determine which scent had the greatest attracting power and whether prebaiting could increase film economy. Because all carcass baits were in place for at least 1 week before monitoring began, and most had already been visited by bears, they were not included in the calculations. Data indicated that (1) scents most closely representing a natural food source (FC and PF) attracted bears most rapidly, and (2) film economy could be increased by prebaiting a station for 1 week (shortest $\overline{X}$ time, 6.5 days) before activating the camera. PF was the only nonconsumable lure at which grizzlies were photographed.



1 Fish and chicken (6.5)
2 Putrid fish (7.8)
3 Pheromone (15.5)
4 Pheromone and horse (9.9)
5 Synthetic fermented egg and horse (16.5)

Fig. 2. Mean number of days until the first visit by a bear for 5 different types of lure, northwest Wyoming, 1975 and 1976.

DISCUSSION AND RECOMMENDATIONS

The time-lapse camera system had several merits. It eliminated the need for numerous trained observers to monitor lure stations and allowed me, in effect, to be in several places at once by providing a permanent film record of concurrent bear activity at different stations. This permanent record is especially valuable at times when a particular sighting has special significance (i.e., a range extension), because it can be examined repeatedly for verification by other viewers.

Although limited in quantity, the system can supply data about population distribution and abundance that have value when used to augment more traditional methods of survey and inventory. It can probably be used most efficiently to monitor stations in habitat types such as dense timber or heavy brush, which restrict the use of other survey methods.

Lures

None of the lures was particularly successful in attracting bears, especially during midsummer to late summer, when amply vegetable foods were available. Since carrion and those lures that represented carrion were the most efficient, maximum advantage can be achieved by monitoring carcasses and bait stations in early spring, before large quantities of vegetation are available. The system can be used throughout the summer but decreased use of the stations can be expected. To maximize efficiency, stations should be prebaited for at least 1 week or until the site shows signs of being used. A bear will often return to a site where it has obtained food, at which time it can be recorded on film.

Some bear activity was missed because the cameras did not operate at night. The exact amount is undeterminable, but the loss appears to be minimal. Usually, close examination of the station and the surrounding area will reveal that a bear was at the site, and often the film will show that the bait has been disturbed and on what night the disturbance occurred. Bear activity was assumed whenever the position of a carcass bait was shifted more than slightly or large quantities were consumed in a short time.

Study Area

To prevent loss of data, the study area should be small enough to allow the film to be replaced as soon as exhausted.

Using the cameras in conjunction with a marked population sample would reduce the need to rely upon natural markings or characteristics to identify individual animals and would provide more information on population numbers, since a capture-recapture technique could be used for analysis.

Film Speed

The film advance speed used to monitor a station should be determined and tested prior to the initiation of the study to insure that a sufficient number of photographs will be obtained. For most studies, 1 frame/1.5 minutes may be a good starting speed because, although it is a fairly rapid cycle, it provides some film economy. Cartridge jamming can be reduced by advancing the film 25-30 frames manually when it is first placed in the camera.

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POSSIBLE IMPACTS OF HUNTING ON THE GRIZZLY/BROWN BEAR, A THREATENED SPECIES

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Abstract: Is hunting detrimental to bear populations? Or do harvests stimulate compensatory reproduction and decrease natural mortality among the survivors? When the literature was reviewed to evaluate support for the various sides of this controversy, data were found still inadequate for conclusions to be drawn. At best, available information can aid in distinguishing which additional data are most critical and which hypotheses are most likely to be heuristic. Among six *U. arctos* populations in North America, those with lowest proportions of adult males had highest reproductive potentials, and vice versa. Likewise, within Yellowstone National Park, there was a strong negative correlation between numbers of adult males during a given year vs. number of offspring. However, those populations with highest reproductive potentials were also in the best habitats. So whether the former relationships were due to (a) effects of adult males on conception and survivorship, or (b) a coincidental product of nutritional differences, must still be tested. For 2 black bear (*U. americanus*) populations in Idaho, 1 in good habitat which was hunted heavily and the other in poorer habitat that was hunted lightly, higher natality in the former was attributed not to hunting but to better nutrition. When trophy hunting was simulated on a formerly little-exploited population of black bears in Alberta, the natality rate was not obviously altered.

Dispersal of a once seasonally aggregated population of grizzly bears was apparently followed by marked increase in cub survival, perhaps because of lowered exposure of cubs to aggression by older bears. However, evidence does not confirm the idea that depletion of mature males substantially increases survivorship of cubs or otherwise offsets losses due to hunting. In fact, under some circumstances, trophy hunting may indirectly increase cub mortality. Aside from this aspect and the possible impacts of inverse culling on gene pools, trophy hunting may be less detrimental to bears than to certain ungulates, where fully-adult males regulate aggression by adolescent males and serve other important social roles.

Within the contiguous United States the grizzly is a "Threatened Species". One critical question for its management is whether we should allow any of the remaining populations to be hunted, and if so whether these should be trophy hunts concentrated on adult males or whether harvests should be unselective. Proponents of hunting partly justify their position by claims that aggression of adult males against other age-sex classes is detrimental to the populations. But this is just the opposite to what we find for at least some species of ungulates, where adult males play critical social functions; their depletion by trophy hunting can markedly lower viability of a population (Bubenik 1971; see also Stringham and Bubenik 1975). Would properly regulated hunting really enhance reproduction and survivorship in grizzly/brown bear populations? Or would it merely speed their extinction?

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Preliminary assessment of the stated problem was made by comparing 3 hunted populations with 3 protected populations. The former are on Kodiak Island (KI), Chignik-Black Lake (CBL), and the eastern Brooks Range (EBR) in Alaska. The protected populations are at McNeil River State Game Sanctuary (MRSGS) in Alaska, Kluane Game Sanctuary (KGS) in the Yukon, and Yellowstone National Park (YNP) in Wyoming. KI, CBL, and MRSGS are all mountainous coastal habitats; the latter 2 are on the Alaska Peninsula. The EBR encompasses part of the Brooks Range as well as tundra extending towards the Arctic Ocean. KGS and YNP are inland mountain habitats. Each summer for about 6 weeks, McNeil Falls within MRSGS hosts one of the largest aggregations of *U. arctos* in the world, as they fish for salmon. Comparable concentrations occurred at garbage dumps in YNP before they were closed (1968-70); hence, data before vs. after closure are treated separately where appropriate. In KI and CBL, bears were more dispersed along salmon streams; hunting pressure there is focused on trophy bears, especially adult males. In EBR, it is apparently less selective. Sanctuary bears (MRSGS, KGS, YNP) whose home ranges extend beyond sanctuary boundaries are also vulnerable to hunters; males tend to range more widely than females and are correspondingly more vulnerable. Among nuisance bears removed from YNP, there has been a small bias towards adult males. Troyer and Hensel (1964), Hensel et al. (1969), Craighead et al. (1969, 1974), Knight et al. (1975), Pearson (1975), Cole (1975, 1976), Egbert and Stokes (1976), Glenn et al. (1976), Glenn (1975), Reynolds (1976). Hence, relative proportions of adults, even adult males, are at best rough indicators of intensity of trophy hunting (Table 1).

The difference in mean proportions of adult males between KI and CBL (4.8 percent) vs. MRSGS, YNP, and KGS (24.3 percent) is highly significant ($P < 0.005$) by the chi-square test. By contrast, relative proportions of females and immatures do not differ significantly. At EBR males are plentiful; adults constitute about two-thirds of the known population, despite hunting.

QUALITY OF THE DATA AND ESTIMATES

Reproduction

Maturation rate. — Evaluation of sexual maturity is based on condition of the mammae and external genitalia, estrus behavior, and age when the first known litter is produced. The fact (Craighead et al. 1969; Glenn et al. 1976) that some females display signs of estrus and may even copulate as early as one year before their first confirmed conception, adds to the uncertainty of accessing maturity level. But we cannot yet estimate how much this may bias inter-population comparisons. For the purposes of this preliminary analysis, puberty was assumed to have occurred one year prior to production of the first confirmed litter, and vice versa in cases where the author did not provide a definite figure. The most extensive and reliable data on female maturation rates (Table 2) come from KI (Hensel et al. 1969), YNP (Craighead et al. 1969, 1974), and MRSGS (Glenn et al. 1976). Glenn (pers. comm.) is also preparing a detailed report for CBL; for now, all we have is an estimated mean. Figures from KGS (Pearson 1975) and EBR (Reynolds 1976) are questionable. Three KGS females had not conceived by age 6, nor is it known when they did. So minimum age at puberty for them was at least 7, giving a minimum mean for the entire female population ($n = 8$) of 6.85, and more likely older; a mean of 7 years was assumed for this analysis (Table 2). Data from EBR cover only two years, so in order to obtain a reasonable sample size, Reynolds estimated age at first litter for several females (aged by tooth annuli). While the estimates are reasonable, each could be off by a year.

Interval between litters. — The time interval between birth of 1 litter and birth of the next is a function

Table 1. Age-Sex Structure of Six North American *Ursus arctos* Populations.

	Number and percent ( ) of Population						Adult sex ratio M/100F
	Cubs	Yearlings	Other Immatures	Male Adults	Female Adults	TOTAL	
HUNTED							
Kodiak Island[a]	42 (25.8)	36 (22.1)	44 (27.0)	9 (5.5)	32 (19.6)	163 (100%)	28
Chignik-Black Lake[b]	140 (25.0)	84 (15.0)	169 (30.2)	23 (4.1)	143 (25.6)	559 (100%)	16
Eastern Brooks Range[c]	------------32------------ (32.3)			33 (33.3)	34 (34.3)	99 (100%)	97
PROTECTED							
McNeil River[d]	9.7 (15.0)	6.0 (19.3)	8.7 (13.5)	17.7 (27.4)	22.4 (34.7)	64.5+ (100%)	79
Yellowstone Natl. Park 1959-70[e]	31.4 (17.5)	22.6 (12.6)	43.8 (24.5)	37.7 (21.1)	43.8 (24.5)	179 (100%)	86
Kluane Game Sanctuary[f]	3 (7.3)	7 (17.1)	13 (31.7)	10# (24.4)	8# (19.5)	41 (100%)	131#

References:
[a] Troyer and Hensel (1964)
[b] Glenn (1975)
[c] Reynolds (1976)
[d] Glenn et al. (1976)
[e] Craighead et al. (1974)
[f] Pearson (1975)
* Figures calculated from data in source cited.
\+ Excluding 5 bears of unknown age.
\# Rough estimate for use in this preliminary analysis.

Table 2. Statistics for density, reproduction, and cub-vs.-yearling litter size differences.

	Mean value, standard deviation; and sample size ( )										
	$\frac{1}{\text{density}}$ (km²/bear)	Females: Age at puberty	Females: Age at first litter	Litter size Cubs	Litter size Yrlgs.	Litter size difference Cubs vs. Yrlgs. (percent)	Interval between litters (years)	Potential Natality Index t_{11} PNI	Potential Natality Index t_{11} lnPNI	Food supply	Dispersal
HUNTED											
Kodiak Island	1.6[a]	4[b]	5[b]	2.23[b] ±0.87 (98)	2.00[b] ±0.74 (103)	−10[b] (201)	3[b]	7.04	1.95	good	medium
Chignik-Black Lake[c,d]	15$^+$	4	5	2.20	2.02[o]	−9 (342)	3	6.92	1.93	good	medium
Eastern Brooks Range[e]	260	9$^+$ ±1.36 (20)	10	1.8 (13)	2.0 (7)	+10 (20)	4	2.53	0.93	poor	high
Lake Becharof[f]				2.0	2.0	0					
PROTECTED											
McNeil River[c]	--	5 ±1.07 (8)	6	2.1 (41)	1.8 (69)	−13 (110) −38 (13)#	3.58 ±1.24 (12)	5.12	1.63	good	low
Yellowstone Natl. Park 1959-70[g]	13.5	5.14 ±1.10 (14)	6	2.18 ±0.23 (173)	1.5$^+$	−31#	3.21 ±1.17 (68)	5.49	1.70		
1959-68[g]				2.23 ±0.20 (147)						good	low
1969-74[h,i]				1.87 ±0.12 (83)						fair?	medium?
Kluane Game Sanctuary[j]	27	7$^+$ (>6.89)*	8$^+$	1.7 (11)	1.5 (11)	−12	3$^+$ (3-5)	3.60	1.28	poor	high
Glacier Natl. Park, U.S.A.[k]				1.7 ±0.68 (35)	1.8 ±0.66 (30)	+6					
Mountain Parks,[l] Canada				2.0 ±0.70 (108)	1.93 ±0.72 (45)	−4					
Katmai Natl. Monument[f]				2.0	1.8	−10					

References:
[a] Troyer and Hensel (1964)
[b] Hensel et al. (1969)
[c] Glenn et al. (1976)
[d] L. Glenn (1975, personal communication)
[e] Reynolds (1976)
[f] Troyer (cited by Faro 1977)
[g] Craighead et al. (1969, 1974)
[h] Cole (1975, 1976)
[i] Knight et al. (1975)
[j] Pearson (1975)
[k] Martinka (1974)
[l] Mundy and Flook (1973)
*Figure calculated from data in source cited.
+ Rough estimate for used in this preliminary analysis
[o] Combined figure for yearlings and older young still accompanying an adult female
Only these data are from known litters compared at ages 0.5 vs. 1.5 years. Hence, the figure for sample size at McNeil of 13 is equivalent to 26 litters of unidentified cubs vs. yearlings.

of at least 2 variables: (1) age at which the cubs are weaned and dissociated from the mother, and (2) capability of the mother to conceive and gestate progeny. Only the YNP data (Craighead et al. 1969, 1974) (Table 2) are extensive enough to document successive litters for a substantial number (n=68) of females. There, most conceived a new litter the same year as they dissociated from the previous one — confirming the claim by Erickson and Nellor (1964) that a female does not come into heat again while she is lactating. Birth occurs the following winter. A female dissociating from cubs during their third spring of life (age 2.5 years) would thus have at least 3 years between birth of that and the next litter. So mean age at which cubs dissociate is sometimes used to estimate the *minimum* mean interval between litters, where specific data on inter-litter interval are lacking. However, the reliability of such estimates is questionable, since under certain circumstances black bear females may remain barren one or more additional years after dissociation (Rogers 1976). Figures for inter-litter interval from YNP, KGS (Pearson 1975), and MRSGS (Glenn et al. 1976) are derived from data; those from the other populations are primarily estimates based on age at which mothers dissociate from their cubs. Reynolds (1976) reported a range of 2.5 to 4.5 years for age of young at weaning in EBR, with emphasis on longer durations. So the mean minimum interval was roughly estimated as 4 years for this paper (Table 2). Pearson (1975) gave a range of 3-5 years for KGS, with only 1 female each at the 4 year and 5 year intervals; a rough mean of 3 years was estimated by me. Because of the uncertainties in determining inter-litter intervals and small sample sizes for some populations, there is no basis yet for concluding that the intervals vary significantly between the populations.

Litter size. — In the black bear populations where many females give birth in alternative years, there is roughly a biannual fluctuation in cub production (Free and McCaffrey 1972; Kemp 1976). In the year of most numerous litters, cubs tend to be most frequent but yearlings least so, and vice versa. Among grizzly/brown bear, where inter-litter interval averages at least three years, fluctuations in number of litters could be even more complex. Effects of that on natality could be compounded by variations from year to year in mean litter size, as documented at YNP (Craighead et al. 1974). These could be important sources of bias in estimating mean cub production in a population from which data are available for less than one full "cycle". Substantially different estimates might be obtained according to which years were sampled. So some of the differences between population sample means could be attributable to this. Ideally, litter sizes should be measured over at least two or three times the length of the mean inter-litter interval. Where that has not been possible, inter-population comparison of combined data for cubs, yearlings and other immatures might help avoid this bias (e.g., in EBR), despite the possibility of another bias: inter-population differences in age-sex specific mortality and migration rates. Due to lack of detail in some published findings, one cannot fully analyze litter size variance within vs. between populations. But when we compare the distribution of mean litter sizes between populations with that from year to year in YNP, neither the (unweighted or sample-size weighted) means nor the variances differ significantly. (Unless otherwise stated, all means given are unweighted; when sample size figures are unavailable, weighting cannot be done even if appropriate). Comparison of litter sizes can also be biased by inter-population differences in infant mortality, since censusing is not done until the cubs are at least 0.5 years old.

Mortality and Survivorship

The most reliable data on cub mortality are for MF and YNP 1959-70 (Table 3), where individually known litters could be compared from week to week and year to year. Among those litters, loss, but not necessarily death, of young were 38 percent and 31 percent, respectively (Glenn et al. 1976, Craighead et al. 1974). This included the loss of all cubs from some litters — a decrement not detectable merely by comparing mean sizes of cub vs. yearling litters. Thus, figures obtained by the latter method could substantially underestimate the number of cubs separated from their mothers between ages 0.5 and 1.5 years (Glenn et al. 1976). If complete yearling litters are easier to observe than complete cub litters, this would also promote underestimation — as Martinka (1974) suggested to help account for the fact that observed yearling litters averaged larger than cub litters seen in Glacier National Park of Montana. These two sources of bias might largely explain why Glenn et al. found only a 13 percent net decline at MRSGS when they also took into account an additional 41 cub litters and 69 yearling litters that were not individually identified. The known litters spent a greater amount of time at MF than the others; although they may have suffered a higher rate of mortality as a consequence (Glenn et al. 1976), most cub losses occurred *after* the bears had left MF for the

Table 3. Correlation matrix for density and reproduction parameters: simple Pearson Product-Moment Linear correlations, r = correlation coefficient; p = confidence level; ln = natural logarithm.

	Age at puberty females (A)	Cub litter size (L)	Interval between litters (I)	L/I	Potential Natality Index (PNI)	ln PNI	Percent in Population		Density of	
							cubs	yrlgs.	cubs	yrlgs.
% adult males in population	0.811 0.05	−0.694 0.13	0.775 0.07	−0.921 0.009	−0.945 0.004	−0.906 0.01	−0.877 0.05	−0.645 0.24	−0.587 0.42	−0.542 0.46
% adult females in population	0.383 0.45	−0.096 0.86	0.888 0.02	−0.599 0.21	−0.494 0.32	−0.500 0.31	−0.094 0.88	−0.902 0.04	−0.493 0.51	−0.539 0.46
% adults (M+F) in population	0.726 0.10	−0.528 0.28	0.902 0.01	−0.890 0.02	−0.864 0.03	−0.839 0.04	−0.695 0.19	−0.865 0.06	−0.746 0.25	−0.724 0.28
Adult sex ratio M/F	0.737 0.09	−0.831 0.04	0.340 0.51	−0.754 0.08	−0.861 0.03	−0.796 0.06	−0.954 0.01	−0.125 0.84	−0.527 0.47	−0.484 0.52
Density of population (D)	−0.552 0.83	0.537 0.35	−0.387 0.52	0.572 0.31	0.615 0.27	0.578 0.31	0.563 0.44	0.896 0.10		
lnD	−0.883 0.05	0.713 0.18	−0.813 0.09	0.896 0.04	0.864 0.06	0.883 0.05	−0.691 0.31	0.797 0.20		
Density of adult males	−0.553 0.33	0.512 0.38	−0.460 0.44	0.576 0.31	0.557 0.33	0.562 0.32	0.372 0.63	0.779 0.22		
Density of adult females	−0.579 0.31	0.568 0.32	−0.400 0.50	−0.598 0.29	0.642 0.24	0.605 0.28	0.590 0.41	0.882 0.12		
Density of Adults (M+ F)	−0.580 0.31	0.563 0.32	−0.418 0.48	0.601 0.28	0.613 0.25	0.603 0.28	0.553 0.45	0.872 0.13		
Density of yearlings	−0.494 0.51	0.427 0.57	−0.320 0.68	0.534 0.47	0.553 0.45	0.523 0.48	0.544 0.46	0.909 0.09		
Density of cubs	−0.540 0.46	0.474 0.53	−0.308 0.69	0.579 0.42	0.596 0.40	0.568 0.43	0.588 0.41	0.891 0.11		
Percent yearlings in population	−0.125 0.84	0.0000 1.000	−0.846 0.07	0.519 0.37	0.453 0.44	0.388 0.52	0.381 0.53			
Percent cubs in population	−0.953 0.01	0.893 0.04	−0.292 0.63	0.969 0.006	0.994 0.0005	0.999 0.0001				
ln PNI	−0.974 0.001	0.878 0.02	−0.753 0.08	0.990 0.0001	0.989 0.0002					
Potential Natality Index (PNI)	−0.938 0.006	0.877 0.02	−0.720 0.11	0.983 0.0005						
Annual unit natality rate (L/I)	−0.941 0.005	0.831 0.04	−0.811 0.05							
Interval between litters (I)	0.695 0.13	−0.360 0.48								
Cub litter size (L)	−0.882 0.02									

Correlations are between population means, not between individual observations. In most cases, $N=6$ populations. But as will be noted from Tables 1 and 2, certain data are missing from some populations. Corresponding correlations are based on only 5 or 4 populations. Hence, the relatively low confidence levels in some cases despite high correlation coefficients. Any association significant with N based on number of populations should still be significant when correlations are done on raw data; but some which are not yet known to be significant may be found significant when raw data become available for analysis.

year (Egbert and Stokes 1976). The larger sample size for the 110 unidentified litters suggests that those figures are more representative of cub vs. yearling litter sizes than are values for the 13 known litters; but that does not make the former a better estimate of cub loss. Annual fluctuation in mean litter size renders the cub vs. yearling litter size comparison method even less reliable as an estimator of mortality.

DISCUSSION

The fact that figures for maturation rate, inter-litter interval, litter sizes, and survivorship, may be seriously biased, certainly does not demonstrate that they are. The uncertainties restrict the confidence we can place in conclusions drawn from these data; but uncertainties should not preclude an interim face-value analysis of the data. We need to derive as much information as possible from past research as a basis for planning new investigations and evaluating current management practices. So a tentative picture of relationships should be much more heuristic than none at all. It is within these constraints that the following statistical analysis should be interpreted.

Potential vs. Realized Rates of Natality

Natality (birth) rate per unit number (N) of fertile females is a function of (a) age when the first litter is produced G (generation length) relative to age a puberty A, (b) interval between births of successive litters I, and (c) litter size L. In addition to considering each of these parameters separately, it is particularly revealing to examine inter-population differences in their combined effects. This is done using the summation formula given below. The following assumptions were made for the purposes of this paper: (1) 50:50 natal sex ratio; the mean number of female cubs produced per litter per year is thus $0.5(L/I)$; (b) the fraction of adult females producing cubs each year is $1/I$, (c) mean values of L, I, and G are stable through the index period; (d) rates of breeding, fertility, and survivorship for females are 100 percent; every female produces young when mature, none dies within the index period; and (e) there is no migration in or out of the population. This provides an index of *potential*, as proposed to *realized*, natality. Starting with N (e.g. 1,000) adult females at made for the purposes of this paper: (a) 50:50 natal sex descendents born during the index period were computed. The index period used is 1 generation — the mean length of time it takes females born in year t_1 to produce their own first litters (year t_{G+1}) — in the slowest reproducing population. That is EBR, where females don't bear until age 10 years (t_{11}) on the average; so the index period is 11 years. This computation yields the coefficients for the Potential Natality Index (PNI) given in Table 3(e.g., 7.04 N for KI) — indicators of total female descendents born between years T_1 to t_i:

$$\text{PNI}\ (t_i) = \text{daughters} + \underset{\text{daughters}}{\text{grand-}} + \underset{\text{daughters}}{\text{great-grand}} + \ldots$$

$$= N\left[\ (t_i)R + \sum_{i-1}^{k}(t_i\text{-}G)R^2 + \sum_{j=1}^{k}\sum_{i=1}^{j}(t_i - 2G)\ R^3 + \ \ldots\right]$$

Note that the natural logarithm (ln) of PNI, rather than PNI as such, will be used for comparing populations. This is done to minimize geometric exaggeration of errors in estimating differences in A, L, and I. Such exaggeration might otherwise occur since PNI is based on geometric population growth.

Realized natality is the actual number of cubs born each year, a value estimated by censusing at age 0.5 year (so, as with L values for 0.5 year, bias by inter-population differences in rates of infant mortality and migration cannot be ruled out). This index is symbolized by *RNI*.

$$\text{RNI} = \left[\left[\begin{matrix}\text{\# females}\\ \text{bearing cub}\\ \text{litters}\end{matrix} \times \begin{matrix}\text{mean natal}\\ \text{litter size}\end{matrix} \times \begin{matrix}\text{survivorship}\\ \text{to age 0.5 yr.}\end{matrix}\right] + \left[\begin{matrix}\text{net}\\ \text{immigration}\\ \text{of cubs}\end{matrix}\right]\right]$$

Correlations (Table 3) among A, I, and L, are only moderately strong; knowledge of one is not a precise predictor of the others. However, annual unit natality rate L/I is highly correlated ($r = -0.94$; $P < 0.005$) with A for females and with lnPNI. A is similarly correlated with lnPNI. Inter-population differences in L/I, A and lnPNI, are highly correlated with percent cubs at age 0.5 years (RNI) ($r = 0.95$ to 0.999; $P < 0.01$ to 0.0001). The very close association between PNI vs. RNI suggests that net inter-population differences in rates of impregnation, prenatal survivorship, natal sex ratio, etc. were minor. By contrast, within YNP (Craighead et al. 1974), annual differences in litter size L showed only moderate relationship with RNI, as measured by either percent ($r = 0.48$; $P < 0.11$; $N = 12$) or density/number ($r = 0.60$; $P < 0.02$; $N = 15$) of cubs at age 0.5 year (Stringham et al., in preparation). Now let us consider some of the factors which control reproductive rate.

Factors Affecting Natality

Inter-population differences in maturation rate, inter-litter interval, and litter size could all be genetically controlled. But in lieu of information on heritability, analysis will be confined to other endogenous and environmental influences. These include hunting pressure, social strife, population density and dispersal, nutrition, and age of the mother.

Hunting pressure, social strife, and population dispersal. — When maturation rate, inter-litter interval, cub litter size and lnPNI are compared between the hunted (KI, CBL, EBR) vs. protected (MRSGS, YNP, KGS) populations, significant differences are not found. The same is true when we compare populations having low (KI, CBL) vs. high (MRSGS, YNP, KGS, EBR) proportions of adult males, in terms of *A*, *I*, and *L;* only the difference in lnPNI is significant ($P < 0.03$). Nevertheless, all 4 reproductive parameters are strongly correlated with proportion of adult males (Table 3). Particularly striking are those for L/I, lnPNI ($r = -0.91$; $P < 0.01$) and percent cubs ($r = -0.88$; $P < 0.05$). Correlations involving just those populations with high proportions of adult males are comparable; so inclusion of depleted populations, despite lack of data from populations with intermediate proportions of adult males, has not appreciably biased the coefficients.

Note that significance figures given for correlation coefficients are based on the number of populations (6), rather than number of observations; some of the population means represent hundreds of observations. So if and when the investigators pool their raw data for statistical analysis, some of the correlations should attain much higher significance.

Re-analysis of the Craighead et al. (1974) data indicates that peak cub production would be achieved with about 65 adults (38 percent of the mean population size) (McCullough, in press). It is not clear what proportion of the adults should be males. Litter size, number of litters, and percent cubs were not significantly correlated with either the current density or percent of adult males, although there was a significant correlation between litter size at age 0.5 year vs. number of adult males during the previous year, when conception occurred ($r = -0.83$; $P < 0.02$; $N = 7$) (Stringham et al., in preparation). Thus, while findings are somewhat similar to those between populations, the relationships are not quite the same. Caution should be used in trying to draw conclusions about intrapopulation relationships from inter-population analysis.

The strong negative correlations for interpopulation differences in maturation rate, annual unit natality rate (L/I) and potential natality index vs. percent adult males are consistent with the hypothesis that adult males depress reproduction. Among grizzly/brown bears, they tend to dominate other age-sex classes. Many fully adult males are highly feared by subordinates (Hornocker 1962; Stonorov and Stokes 1972; Bledsoe 1975, personal communication; Egbert and Stokes 1976). They may restrict access by adult females to food at sites of feeding aggregations and through inducing psychologically mediated stress could disrupt their reproductive physiology.

It has been observed among a wide variety of vertebrates that social strife can stress an animal both through the physiological dimension of the emotions/states it arouses (e.g., fear) (Selye 1956, 1976; Davis 1964) and through the activities of strife (e.g., chasing and fighting), as well as any consequent injuries. If extreme enough and chronic, strife like any other stressor can arouse the Selye "General Adaptation Syndrome" (G.A.S.); at least the pre-acclimation and exhaustion phases can lower rates of reproduction, maturation, and survivorship. But is this true for bears? When captive black bears are reared in small groups, maturation of subordinates is not known to be retarded (Rogers 1976). But domination of subordinates does not necessarily stress them enough to arouse the G.A.S. appreciably. Domination by a constant companion in captivity may be less stressful than domination in the wild.

Nutrition, habitat quality and population density. — Nutrition can affect natal litter size evolutionarily or directly. It can select for genotypes promoting large litters in good habitat and small ones in poor habitat, which could result in geographic differences in mean litter size (e.g., coastal vs. inland bear habitat). It can maintain genetic polymorphism within a given habitat whose carrying capacity, and thus optimum litter size, fluctuate strongly from year to year (Lack 1954; Geist 1974). Nutrition can also influence natality through direct alterations of reproductive physiology (Sadlier 1969; Hafez 1974).

Among the ways in which malnutrition or starvation can proximally affect a female vertebrate is through arousal in her of the G.A.S. That, along with more specific effects of nutritional deficit, tends to impair reproduction and recruitment. Conception and prenatal survivorship may decline, maternal care and lactation can be inhibited. Rate of maturation by offspring can be retarded (Selye 1956, 1976; Davis 1964).

These symptoms of the G.A.S. are comparable to what Rogers (1976) observed about effects of restricted diet in black bear. He found that litter production or nonproduction by a mature female black bear and the cubs' rates of (a) weight gain, (b) survival, and (c) sexual maturation were all strongly related to nutrition, as evidenced primarily by body weight. His own well-fed captive black bears matured earlier than garbage-eating wild black bears, which in turn were better nourished and matured earlier than wild black bears with no access to garbage. Litter size also seems to have been positively correlated with nutrition, as a function of postnatal survivorship and perhaps birth rate.

This is consistent with observations by other biologists. Beecham (1980) compared 2 black bear populations in Idaho, 1 in good habitat that was hunted heavily and a second in somewhat poorer habitat that was hunted lightly. Densities and sex ratios (all ages combined) were comparable, but maturation rate [1/ (4.25 years) vs. 1/ (4.50 years)] and mean litter size (1.90 vs. 1.65) were higher in the former. He attributes the greater natality per female not to hunting but to a better habitat, as also evidenced by higher age-specific body weights. The direct relationship between nutritional status and speed of maturation to puberty has previously been documented for bears by several investigators (Baker 1912, Rausch 1961, Jonkel and Cowan 1971; summarized by Pearson 1975) and for many other mammals (Sadlier 1969, Giest 1971, Hafez 1974). In numerous species, weaning is partly governed by loss of juvenile appearance and behavior as the young mature (Ewer 1968, Lent 1974), so age at weaning tends to be directly related to age at puberty. Growth and rate of maturation are in turn functions of nutrition. Jonkel and Cowan (1971) reported 1 case where a poorly nourished cub was nursed at least 9 months longer than was typical in a northern Montana population. A female typically mates again during the same spring-summer that she weans her previous litter, and if adequately nourished (Rogers 1976), gives birth about 7 months later. However, if she is too depleted after rearing a litter, 1 or more additional years may pass before she can produce another.

So far, we have no physiological evidence on nutritional status from the 6 grizzly/brown bear populations. While clues might eventually be gotten from data on body weight, stature, and fat deposits, those data were not collected consistently for all the populations; nor are all the data published yet. We also lack detailed comparisons of habitat quality. At best, we have rough impressions that good quality food has been abundant (a) on the coasts of KI and the Alaska Peninsula (CBL, MRSGS), where salmon and berries are plentiful during part of the year, and (b) at YNP 1959-68 (J. Craighead, personal communication). Apparently, garbage is a good supplimental source of nutrition for bears (J. Craighead, personal communication; Rogers 1976). KGS and EBR have been described as having very poor sources of food (Pearson 1975, Reynolds 1976).

Splitting these 6 populations into 2 classes according to food supply, good vs. poor, reproductive rates in the 2 classes can be contrasted (Table 3). Mean age at puberty was lower ($4.5 < 8+$; $P < 0.03$), cub litters were larger ($2.29 > 1.75$; $P < 0.03$), and thus reproductive potential (lnPNI) was higher ($1.805N > 1.103N$; $P < 0.03$) in the 4 best habitats KI, CBL, MRSGS, and YNP 1959-68, compared with KGS and EBR. Furthermore, following closure of the garbage dumps in YNP, the size of cub litters dropped 24 percent from the 1959-68 mean of 2.23 to a low of 1.7 in 1974 (Knight et al. 1975). The difference between the two periods 1959-68 vs. 1969-74 is highly significant ($2.33 > 1.87$; $P < 0.001$).

Of course, the assumed drop in food supply may not have been the only influence retarding reproduction. When black or grizzly/brown bears concentrate at feeding sites, aggression between these normally dispersed animals can become intense. This aggression has been documented at the YNP garbage dumps and at salmon streams, including the McNeil River (Hornocker 1962, Stonorov and Stokes 1972, Frame 1974, Egbert and Stokes 1976). While the YNP dumps were being closed (1968-71), the progressive reduction in available garbage supposedly (Cole 1975) accentuated competition and strife at those dumps still open. Intensification of strife, alone or in combination with reduction in food supply, may have elevated physiological stress and the G.A.S., thereby lowering rates of conception or raising prenatal and postnatal mortality — accounting at least in part for the drop in mean size of litters censused at age 0.5 year. Conversely, closure of dumps and consequent dispersal of the bears may have eventually lowered the vulnerability of cubs (mostly over 0.5 years old during the tourist-garbage season) to murder; there was an apparent increase in rate of survivorship between ages 0.5 and 1.5 years from 61 percent (1959-68) to 69 percent (1959-70) to 93 percent (1974) (Craighead et al. 1969, 1974; Knight et al. 1975). But as mentioned above, this trend may be exaggerated or spurious because whole-litter losses may have gone undetected after 1970.

We have no evidence that nutrient supplies at MRSGS or YNP (1959-68) were poorer than at KI and CBL. MRSGS is rich in salmon, berries, sedges, and other natural forage; YNP offered spring carrion in addition to natural vegetation and garbage. So the fact that rates of maturation by females to puberty averaged 1 year slower at MRSGS and YNP than at KI and CBL, despite seemingly abundant food, may indeed be due to effects of strife at feeding aggregations (see also Stokes 1970, Cole 1975). In other words, maturation rate is hypothesized to be a function of both strife (as related to dispersal and other factors) and nutrition. At KI and CBL dispersal is at least moderate; at KGS and EBR it is high. Hence, now that the YNP dumps have been closed and the bears dispersed, we would have expected maturation rate to increase there, all other factors being equal; however, the loss of garbage as a substantial source of food may have counteracted this effect of dispersal.

As Glenn (personal communication) has also noted, contrasting density figures between populations can be misleading since they are calculated per unit land area, rather than per unit habitat or resource (e.g., food). They were determined by a variety of methods whose results are only roughly comparable. The bears travel so widely that it is extremely difficult, for instance on the Alaska Peninsula, to obtain a meaningful estimate of density for any subunit. Lastly, the fact that data on only five populations spans two orders of magnitude ($1/1.6\ km^2$ to $1/260\ km^2$), with three of the values clustered centrally ($1/15\ km^2$ to $1/27\ km^2$), prevents us from making meaningful correlations between densities (as opposed to percents or numbers) within each age-sex class (e.g., cubs vs. adult males); interpopulation differences in density are so great that the density-density autocorrelation overwhelms differences in population structure. Nevertheless, even with this limitation in mind, it is interesting to note that density (D) is significantly correlated with reproductive potential ($\ln D$ vs. $\ln PNI$:$r = 0.88$; $P < 0.05$). Not only is density a function of natality, but both density and natality are presumably functions of nutrition.

Productivity of females as a function of age. — On the basis of data published by Craighead et al. (1969, 1974), intervals between successful matings and between litters did not differ as a function of age in females 4.5 to 9.5 years old. However, there was an age-related difference in mean litter size. The 5.5- and 6.5-year-old mothers ($N = 7$) had 2 cubs each, whereas 7.5- to 9.5-year olds averaged 1.8 ($N = 8$), or 1.4 if we exclude an a typical litter of 4 cubs (perhaps enlarged by adoption). Whether the decline in litter size ($P < 0.01$) as a female ages in typical of North American *Ursus arctos* is unknown. It may be that females which reach maturity latest also produce smaller litters. Couturier (1954, cited by Mundy and Flook 1973) reported that female European brown bears 5-7 years old usually had only 1 cub, those at their reproductive peak had 2 or 3, and old females had 1 or 2.

MORTALITY vs. SURVIVORSHIP AND MIGRATION

Mortality Induced by Adult Males

Sexually mature males, especially full adults — those that have completed puberty and are also mature in most other socially important morpho-physiological and behavioral traits (for ungulates see Bubenik 1971, Geist 1971, and Stringham and Bubenik 1975; for *U. arctos,* Egbert and Stokes 1976) — seem to be dangerous to juveniles at least when not protected by their mothers. Adults force egress of subadults; full adults may eject adolescent adults. If the emigrants have to live in marginal habitat, their chances of survival and reproduction are diminished accordingly. So it has been suggested that removal of large males through trophy hunting would increase survivorship of juveniles and subadults (Glenn, cited by Egbert and Luque 1975; Kemp 1976).

That assertion is plausible, but available data on grizzly/brown bears provide little support for it. I have found reference to less than 2 dozen confirmed murders (J. Craighead, personal communication; Murie 1961; Glenn et al. 1976). The aggressor is rarely known to have been an adult male. Murie saw an adult female kill cubs of another mother after the two litters had mixed and the former sow was trying to recover her own young. Nor has definitive evidence yet been published that survivorship of cubs between ages 0.5 to 1.5 years is higher in the 2 populations with few adult males than in the 4 with many, hunted (EBR) or not.

Litter Size Declines

Recall that figures solely on loss of cubs from known litters are available only from YNP (31 percent) and McNeil Falls (38 percent). These are also the only habitats of the 6 with sites where the grizzly/brown bears aggregated in large numbers to feed — sites where aggression between these normally dispersed animals was very high. Hence, because of differences in both methods and dispersal, these mortality estimates cannot be compared directly with figures from other populations based strictly on contrasting mean sizes of mostly unidentified cub vs. yearling litters. The only data from MRSGS which can be used are for the 110 unidentified litters.

Comparative data on cub and yearling litter sizes are thus available from 9 populations (Table 3). Lacking sample size figures for Lake Becharof (hunted) and Katmai National Monument (protected), these two populations cannot be included in the comparison of cub to yearling litter size declines. Among the others (using the 13 percent figure for MRSGS), the decline averaged 8.7 percent ($s^2 = 127$; $N = 3$)* in hunted

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*sample-size weighted means

populations, contrasted to 3.1 percent ($s^2 = 78$; $N = 4$) in the protected ones. Comparing litter size declines between populations with few adult males (KI and CBL: 9.4 percent; $s^2 = 0.5$) vs. those with many (MRSGS, KGS, and ERB: 9.9 percent; $s^2 = 136$), the difference is not significant. These comparisons provide no basis for concluding that cub mortality rates between ages 0.5 and 1.5 years could be reduced by hunting adult males. Under some conditions, hunting adult males may even increase cub mortality, as will be discussed later.

We also do not know the extent to which these declines in litter size between ages 0.5 and 1.5 years reflect mortality. Some young may become independent before they can be censused as yearlings. Johnson and LeRoux (1973) reported that a cub orphaned at age 7 months survived at least until the next year. Others are adopted, at least temporarily. Adoption is a well documented and fairly common phenomenon at MRSGS and YNP (1959-70) (e.g., Erickson and Miller 1963, Craighead et al. 1969, Bledsoe 1975). Indeed, yearling litters at EBR averaged 10 percent larger than cub litters. Whether this finding represents sampling error (e.g., due to annual fluctuations in cub litter size), migration or adoption remains to be determined.

In view of these considerations, we cannot be sure that mortality rates at YNP before dumps were closed and at MRSGS were significantly higher than for other populations or for YNP after 1970. Nor is there yet any basis for claiming that juvenile mortality is higher in populations with many adult males than in those with few. Even where adult males do induce mortality, we do not yet know to what extent this is due to strife-induced, psychologically-mediated stress disrupting fetal development or inhibiting lactation and maternal care, for instance via the General Adaptation Syndrome, rather than to direct murder. Re-analysis of the Craighead et al. (1969, 1974) data shows that the ratios of yearlings or 2-year-olds to adults are more highly correlated with number of adults in the year each cohort was born than in subsequent years (McCullough, in press); correlations with year of conception are comparable (Stringham et al., in preparation).

Evidence on juvenile mortality relative to percentage of adult males is also provided by Kemp's (1976) simulation of trophy hunting for black bears at Cold Lake, Alberta. After removal of most mature males, population density doubled within 2 years — a result that some sportsmen construe as experimental confirmation that trophy hunting is beneficial. But no evidence has been presented that increased density cannot be explained by enhanced immigration and lower egress. No increase in reproduction was demonstrated. We have no data on murder rate. However, *if* a "territorial" matrix was intact before the simulated hunting, there is reason to expect (Rogers 1976) that murders would have *increased* after removal of resident males disrupted the matrix, allowing a consequent influx of other males. Furthermore, after the peak, density declined over the next 3 years to a level only 25 percent above the original (G. Kemp and R. Ruff, personal communication). I do not know whether the decline continued beyond that time; nor had its cause yet been established. The decline is consistent with what would be expected if (a) the initial density rise had led to overpopulation and deterioration of the habitat, and/or (b) if a "territorial" matrix was reestablished, forcing egress of "surplus" males.

The Roles of Social Organization in Enhancing Survivorship

Social organization is, in general, evolutionarily specialized for optimizing resource income while minimizing the costs of living and reproducing. This capability elevates the number of individuals that can be sustained by a given amount of resource. While social behavior may limit density below the highest level that it could attain temporarily, it can substantially raise (maximize?) the long-term average (Rogers 1976), which is equivalent to increasing the carrying-capacity (K) of the habitat.

Hence, a distinction is drawn between *potential* vs. *realized* carrying capacity (PK vs. RK). PK represents the theoretical maximum number of animals that can be sustained by a given supply of resources — a maximum that can be approached only more or less asymptotically in practice. By contrast, RK represents the actual number that can be supported. RK is a function of (a) available resources and efficiency in (b) obtaining and (c) utilizing them, which in turn influences *per capita* requirements. RK is also a function of (d) efficiency in, and effectiveness of, stress avoidance.

In the mountain sheep (*Ovis* spp.) of North American and Iran and in the ecologically similar chamois (*Rupicapra rupicapra*) of Europe, fully adult rams play a number of vital roles besides impregnation. Limiting aggression by adolescent adults is 1 of the most important roles; so depletion of fully adult males through hunting can markedly lower viability of a population (Grubb, personal communication to Sadlier 1969:34; Bubenik 1971, Geist 1971, Schröder 1971, Stringham and Bubenik 1975, Valdez and Stringham, in preparation). Do adult male bears also play this role? Apparently not. The limited data available on grizzly/brown bear social behavior (Murie 1961, Hornocker 1962, Craighead et al. 1969) provide no evidence that adult males enhance the viability of a population other than by siring offspring. The same may be said of black bears, except perhaps in cases where a resident male excludes transient males from his home range. This inadvertently prevents them from endangering the cubs of females which share his home range — cubs likely to be his own offspring (Rogers 1976).

SUMMARY AND CONCLUSIONS

Limitations in quality and detail of published data preclude rigorous analysis. However, preliminary analysis leads to the following tentative interpretations: Differences in reproductive potential between six North American grizzly/brown bear populations are directly related to differences in food supply and density, but negatively correlated with differences in proportions of adult males; there is also evidence of a negative correlation within YNP. Whether adult males actually depress birth rate and survivorship by disrupting reproductive physiology of mothers, perhaps via social strife, or whether lowered reproductive potential is a co-effect of other variables, remains uncertain. The interpopulation correlation between natality vs. deficit of adult males could arise because harvests reduce population density below realized carrying capacity of the habitat and elevate access to prime food by females and young, thereby increasing *per capita* nutrition. Alternatively, the correlation could be spurious, arising from the concentration of harvest in areas of peak carrying capacity where bears are largest, most numerous, and easiest to find. Beecham (1980) likewise attributed to nutrition, rather than to hunting, differences between his 2 black bear populations, 1 in good habitat that was hunted heavily, and a second in poorer habitat that was lightly exploited. When Kemp (1976) simulated trophy hunting on a formerly little-exploited population of black bears, the natality rate was not noticably altered.

There is no solid evidence that removing adult males raises the survivorship of juveniles. Although such enhancement probably does occur under certain circumstances, under others the reverse may be true. According to Rogers (1976), in dispersed populations, a resident male black bear inadvertently protects his offspring by excluding transient males from his home range. Removal of a resident male would permit an influx of subadult and adult males from the periphery of his range, which could result in increased murder of resident young. The same situation may arise among dispersed grizzly/brown bear populations where individuals have stable home ranges. However, it can be hypothesized that where either species is nomadic or hierarchial, natality and survivorship of offspring may be enhanced by depletion of adult males — providing the number remaining are sufficient to breed most of the fertile females. This critical minimum adult sex ratio has yet to be determined but is probably proportional to dispersal of the population. The more widely females are scattered, the more adult males will be necessary to assure maximum impregnation without excessively taxing individual males. Within any population there might be an optimum proportion of adult males at which reproduction and recruitment are maximized.

Thus, despite some preliminary evidence, utmost caution should be exercised in removing adult males to stimulate recovery of an endangered population. Not only do data limitations weaken the analysis, but there is no *proof* that aggression by adult males significantly lowers either natality or survivorship. Less than 2 dozen murders have been confirmed, and the aggressor is rarely known to have been an adult male. Adult females also kill cubs. Nor do we know what determines *which* adult males kill a significant number of young; perhaps most of the killers are the highest-ranking and/or transient males. If so, they alone should be removed. We know little about variations in intensity and amount of male-induced strife under different ecological and social conditions, except that it may be greater amidst feeding aggregations. We also need to learn the extent to which trophy hunting is detrimental — by biological and trophy criteria — to a population's gene pool, via selection against the qualities that make for trophy animals and consequent reduction in the number of cubs produced by trophy-quality bears. For this calculation, we need data on heritability and selection coefficients. Lastly, trends found between populations do not necessarily hold within them.

Removal of adult males from a population seems to decrease emigration of subadults. Decreased emigration would benefit hunters to the extent that it increases the number of potential emigrants that could be harvested within a core area on a sustained-yield basis. Conversely, decreasing egress could eventually reduce harvestable yield in cases where (a) hunting is concentrated on the periphery of a core area (for instance a wilderness) and emigrants are the most available class of bears to harvest, and where (b) emigration serves to prevent overpopulation in the core area or to (c) repopulate peripheral areas depleted by hunting. In such cases, it would be advantageous to maintain adult males in the core area. Note that dispersal of subadults from an area does not necessarily indicate that the area has reached carrying capacity, even from a long-term standpoint. Dispersal is not a reliable indicator that density should be reduced. Harvest should be governed by more reliable evidence on how closely a population has approached the realized carrying capacity of its habitat.

If adult males are to be removed from a protected population (for instance, YNP) in an effort to enhance reproduction and survivorship, sport hunting should not be the means of removal. Bears may already discriminate too little between hunter vs. visitors in parks where hunting occurs only along the boundaries. Permitting hunting within a park could tend to reduce discrimination even further, increasing danger to hikers and campers. Greater wariness by bears would also reduce opportunities for visitors to view them.

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FACTORS INFLUENCING HUMAN-GRIZZLY BEAR INTERACTIONS IN A BACKCOUNTRY SETTING

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Abstract: Interactions between humans and 7 species of wildlife, including grizzly bears (*Ursus arctos horribilis*), were investigated in backcountry areas of the Gallatin Range, Yellowstone National Park, during the summers of 1973 and 1974. Grizzly bear distribution, movements, and behavior and human behavior were examined. Because grizzlies utilized areas with elevations much in excess of the study area's average trail elevation, the likelihood of the off-trail party observing a grizzly bear was 3-4 times greater than that of a trail-traveling party. During the hiking season, grizzlies exhibited an elevational migration. The frequencies of on-trail and combined on- and off-trail observations and sign discoveries per party tended to peak during those periods that grizzlies were found at low elevations. Activity patterns of grizzlies at the point of first observation or after the bears had become aware of the human presence did not indicate behavioral traits likely to accentuate the possibilities of human-bear confrontations. Some backcountry travelers engaged in activities that could increase detrimental encounters with grizzly bears.

Little research has been done on human-wildlife interactions in backcountry settings.

In 1973-74, the National Park Service in cooperation with Montana State University undertook a study of human-wildlife interactions in the Gallatin Range of Yellowstone National Park. Specific objectives were (1) to gather quantitative data on the intensity and kinds of human use in the study area; (2) to gather quantitative data on the distribution, movements, and behavior of wildlife in the study area; (3) to analyze the relationship among these factors to determine the cause and predictability of human-wildlife interactions; and (4) to make recommendations consistent with Park goals concerning humans and wildlife in the backcountry setting. Although 7 species were studied, this paper is primarily concerned with interactions between humans and grizzlies.

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STUDY AREA

The study area of roughly 1,036 km^2 includes the Gallatin Range in northwestern Yellowstone National Park (Fig. 1). The area consists of a north-south ridge of mountains, with an average crest elevation of 2,876 m. Stream valleys of the Gallatin, Gardner, and Madison River drainages dissect the range. Area elevations vary from 2,049 m to 3,330 m.

The climate of the Gallatin Range is severe with ong winters, heavy snowfall, and short summers. Snow depths dictate the beginning and end of the hiking season (late June to October).

A complex of herbivores and carnivores exist in the area. The most abundant herbivore species is the elk (*Cervus canadensis nelsoni*). Others commonly found include moose (*Alces alces shirasi*), mule deer (*Odocoileus hemionus hemionus*), and bighorn sheep (*Ovis canadensis canadensis*). Major carnivores in the area are coyotes (*Canis latrans*), black bears (*Ursus americanus*), and grizzly bears.

The spruce-fir zone, dominated at climax by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*), is the predominant vegetation zone within the study area (Despain 1973). According to Despain (1973), this zone lies at an elevation of 2,560 to 3,048 m. An alpine tundra zone, dominated by dense matlike vegetation, occurs above 3,048 m, and a lodgepole pine zone lies between 2,316 m and 2,560 m (Despain 1973). The latter zone consists of dense stands of lodgepole pine (*Pinus contorta*) interrupted by large open areas with sagebrush (*Artemisia* spp.)-grass communities.

The study area is traversed by 4 major east-west trails (Fig. 1). The trails follow stream drainages with the exception of the upper portions of the Fawn Pass west trail. Consequently, they are lower than the surrounding terrain. Twenty-nine wilderness campsites were scattered throughout the area.

METHODS

Data on the kinds, intensity, and distribution of human use were obtained from backcountry use records of the National Park Service, questionnaires, and personal observations and interviews. Data on bear distribution and behavior were gathered through the return of 258 questionnaires sent to backcountry visitors and by systematically traversing the study area, either on

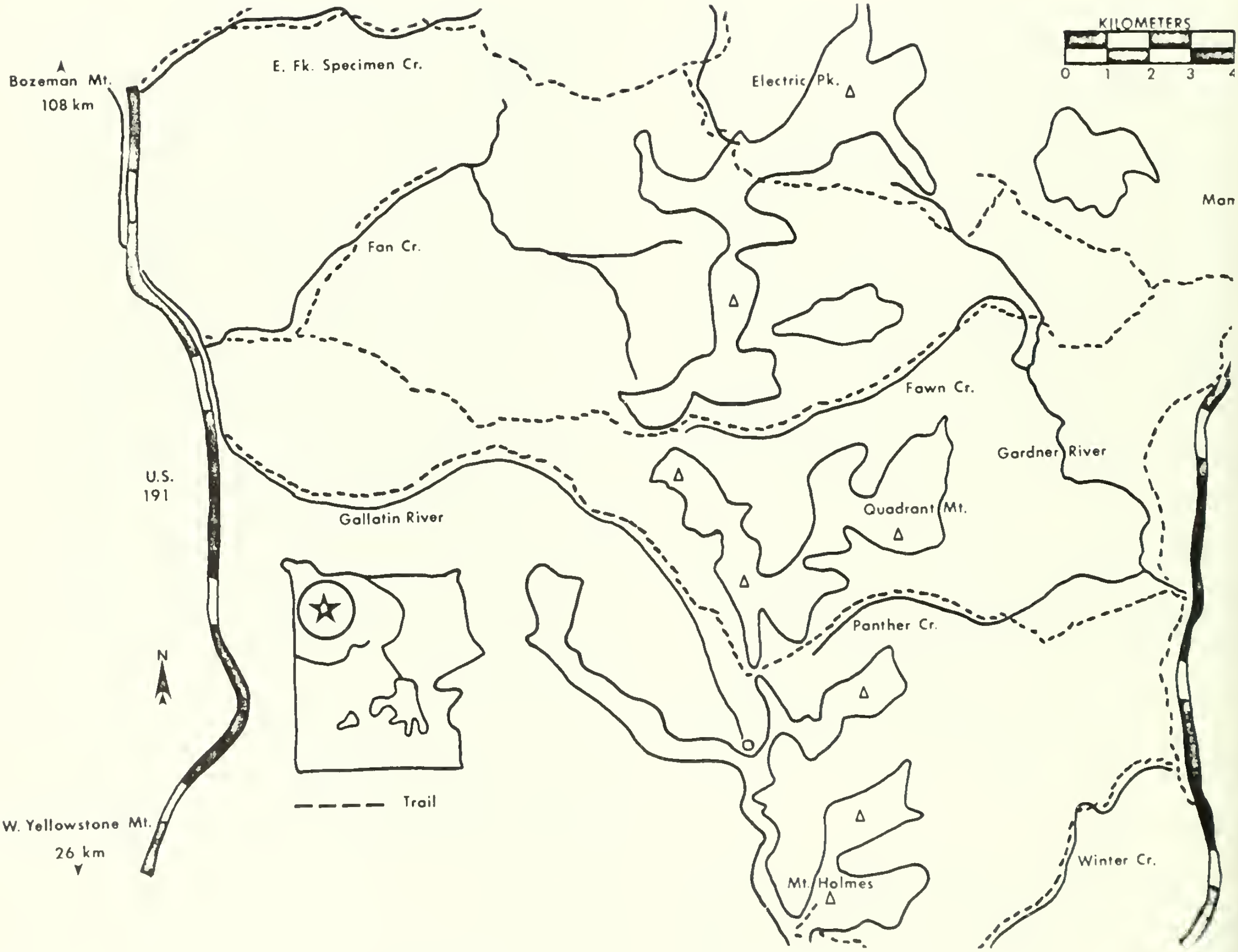

Fig. 1. The Gallatin Range, Yellowstone National Park.

foot or horseback (Chester 1976). The area was traversed 6 times at 2-week intervals in 1973 (30 June-29 September) and 1974 (4 July-7October) for a total of 127 field days. Circuits consisted of relatively fixed routes that included established trails as well as areas seldom visited by humans. In 1974, supplemental information was obtained during 3 aerial flights.

In 1974, a record was maintained of all bear sign, following procedures used by Knight (1974). Species determinations from scats and tracks were made by a combined evaluation of the locality where the sign was found and of the measurements of the sign (Murie 1954, Greer and Craig 1971). Ages of scats were estimated by moisture content, freshness of constituents, and decomposer activity. Tracks were aged by the clarity and sharpness of impression in relation to the substrate. It was often possible to calculate a maximum age of sign since it had been left subsequent to the last trip through the study area. To calculate discovery frequencies, only sign left within 2 weeks of discovery was used.

RESULTS

Elevation of Human-Grizzly Bear Interactions

In the Gallatin Range, trail elevations, elevation of the area as a whole, and elevational distribution of wildlife combined to influence the nature of actual or potential human-wildlife interactions. Since the trails follow stream drainages, most sections of the trails lie far below the average Gallatin crest elevation (2,876 m), and the average elevation of the trails, 2,419 m, is nearly 61 m less than that of the area as a whole. Consequently, off-trail travel in a given area usually involves higher-elevation travel than does on-trail travel.

Average observation elevations for all species studies except moose exceeded the area's average trail elevation, indicating the need for off-trail travel if frequent observations of most area species are to occur (Table 1). Those species occupying the highest elevations generally had the lowest ratios of on- to off-trail observation frequencies (Table 1). Since the average observation elevations of grizzly bears exceeded those of all other species, except bighorn sheep, the ratio of on- to off-trail observation frequency for this species was among the lowest of any studied. Off-trail travelers observed grizzlies 3-4 times as frequently as on-trail travelers (Table 1).

During the course of the hiking season, grizzlies exhibited an elevation migration, moving from low (May-June) to high elevations and back to low elevations (September-October) (Table 2). This migration was also observed by Mealey (1975). The average observation and discovery elevations exceeded the average trail elevation during all phases of the migration, resulting in frequencies of off-trail observation and sign discovery generally exceeding the corresponding on-trail frequencies throughout the study period (Tables 2, 3). However, during those periods when grizzlies were at relatively low elevations, the frequencies of on-trail and combined on- and off-trail observations and sign discoveries tended to peak, indicating a convergence in

Table 1. The relationship between the average observation elevation of each species and the frequency of on- and off-trail observations of these species in the Gallatin Range, Yellowstone National Park, 1973-74. Average observation elevations are based upon personal ground and aerial observations.

Species	Average observation elevations (*N*)	Personal observations			Questionnaire observations		
		On-trail observations per hour	Off-trail observations per hour	On/off-trail ratio	On-trail observations per hour	Off-trail observations per hour	On/off-trail ratio
Bighorn sheep	2,833 m (14)	<0.002	0.015	0.13	0.002	0.013	0.15
Grizzly bear	2,824 m (13)	0.005	0.021	0.24	0.003	0.011	0.27
Elk	2,642 m (421)	0.220	0.501	0.44	0.046	0.099	0.46
Black bear	2,637 m (10)	0.007	0.015	0.47	0.004	0.009	0.44
Mule deer	2,590 m (46)	0.047	0.067	0.70	0.011	0.019	0.58
Coyote	2,539 m (19)	0.021	0.024	0.88	0.008	0.028	0.29
Moose	2,386 m (42)	0.073	0.028	2.61	0.035	0.026	1.35

Table 2. Average elevations, by month, of observations and sign discoveries of grizzly bears in the Gallatin Range, Yellowstone National Park, 1973-74. Average elevations are based upon personal ground and aerial observations.

	Month			
	May-June (*N*)	July (*N*)	August (*N*)	September-October (*N*)
Observation	2,979 m (1)	2,819 m (5)	2,846 m (5)	2,703 m (2)
Sign discovery	2,562 m (9)	2,780 m (39)	2,601 m (45)	2,560 m (36)

Table 4. Species comparison of the percentages of occurrence of alert flight and stationary alert responses to the presence of humans, Gallatin Range, Yellowstone National Park, 1973-74. Percentages for moose, coyote, elk, mule deer, and bighorn sheep are based only upon backcountry visitor results.

Species	Total number	Percentage of occurrence		Stationary-flight ratio
		Stationary alert (%)	Alert flight (%)	
Grizzly bear				
Visitor	7[a]	0.0	85.7	0.00
Personal	6	0.0	100.0	0.00
Black bear				
Visitor	17	5.9	94.1	0.06
Personal	3	0.0	100.0	0.00
Coyote	32	9.4	90.6	0.10
Mule deer	39	12.8	87.2	0.15
Bighorn sheep	12	16.7	83.3	0.20
Elk	121	28.1	71.9	0.39
Moose	96	41.7	58.3	0.72

[a] One visitor group encountering a grizzly bear failed to report the bear's response.

the areas of human and grizzly bear activity (Tables 2, 3). Notable exceptions to the above statement are observation frequencies by the writer, which were highest during the period when grizzly bears were using the highest elevations. This exception probably reflects the combination of personal off-trail travel at high elevations and the increased high-elevation observability of grizzly bears because of sparse vegetation.

Bear Activity Patterns

To examine the nature of human-grizzly encounters, data were gathered on bear encounter distances, initial bear activity upon observation or encounter, and bear response to the human presence. Encounters are defined as an interaction between humans and bears; an observation did not necessarily involve interaction. The average personal encounter distance for 6 grizzlies was 119 m, which was exceeded only by the average for black bears. One-third of the encounters occurred at distances greater than 152 m. The most commonly observed grizzly bear activity immediately upon observation or encounter was feeding (Fig. 2). No grizzlies were observed while resting. The level of alertness (including stationary alert and running reactions) was comparable to or exceeded that of 4 of the other species studies (Fig. 2). In examining wildlife response to the human presence, the ratio of the percent of occurrence of alert stationary response to alert flight response is lowest for the grizzly bear, suggesting that the grizzly is more wary of the human presence than most other species (Table 4).

Backcountry Traveler Activities

Backcountry travelers were observed in, or reported, activities that could increase confrontations with grizzly bears. The percentages given below are based upon numbers of groups responding to a given question rather than on numbers of questionnaires returned. Twenty-one percent of the parties ($N=197$) reported their groups were fragmented into subgroups of 1-2 persons during at least part of their trip. Table 5 suggests that groups of this size are more prone to observe wildlife than are larger parties. One hundred percent of the grizzly bear encounters reported by backcountry visitors ($N=7$) involved 1-2 persons.

In grizzly country, proper handling of food is important. Herrero (1976) tentatively holds poor management of garbage and food responsible for 49 of the

Table 3. Frequencies of on- and off-trail and combined on- and off-trail grizzly bear observations and sign discoveries during the course of the field period, Gallatin Range, Yellowstone National Park, 1973-74. Sign discovery frequencies are for 1974 only.

Form of interaction	Observations or discoveries per hour											
	Combined on- and off-trail				On-trail				Off-trail			
	May-June	July	August	September-October	May-June	July	August	September-October	May-June	July	August	September-October
Personal observation	-	0.017	0.008	0.009	-	<0.007	0.007	0.008	-	0.036	0.011	0.010
Sign discovery	-	0.201	0.260	0.281	-	0.132	0.306	0.235	-	0.289	0.181	0.343
Visitor observation	0.009	0.003	0.003	0.005	0.010	0.003	<0.001	0.004	<0.014	0.006	0.024	0.010

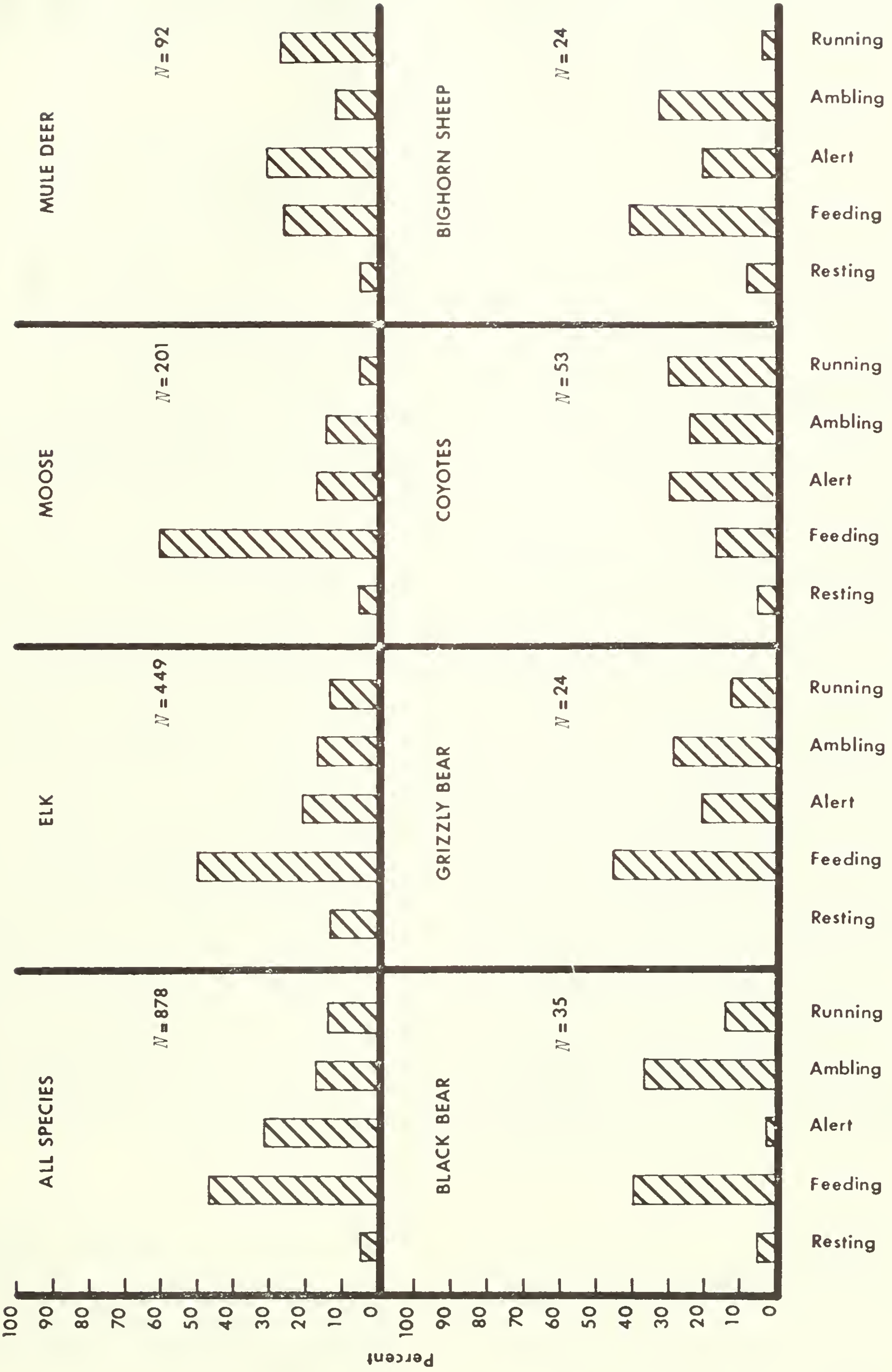

Fig. 2. The initial activities of all species combined and of each species upon encounter or observation by the investigator and the backcountry visitor.

Table 5. Frequencies of wildlife observations by parties of various sizes, Gallatin Range, Yellowstone National Park, 1973-74.

	Party size					
	1 (*N*)	2 (*N*)	3 (*N*)	4 (*N*)	5 (*N*)	(*N*)
Observations per hour	0.11 (50)	0.14 (91)	0.15 (27)	0.09 (19)	0.02 (3)	0.06 (6)

54 camping-related human-grizzly bear incidents that occurred from 1872 to 1973 in North America's national parks. Relevant factors are the types of food used, ultimate disposition of excess food, and methods used for securing food. The use of fresh and canned food as opposed to dried food probably increases the potential for attracting grizzly bears into camps. The fact that nearly 60 percent ($N=248$) used fresh and/or canned food at one time or another points out a potential problem.

Less than 5 percent of the parties ($N=170$) reported dumping or burial of excess food. Thus, there seemed to be general knowledge of the correct procedures for handling leftover food. Whether this knowledge is translated into action is questionable. Seventy-five searches of camps for food and food-related items were made. Food was found in 21 percent of the searches and major food items in 8 percent.

On a number of occasions, backcountry parties were encountered who either had not secured their food or secured it in or very near their camps. Ninety-one percent ($N=249$) of the groups stated that they secured their food before sleeping. Only 83 percent ($N=246$) secured food before absences from camp. Although most groups were aware of the necessity for securing their food, the distances from camp at which they did so seem to indicate naiveté toward the potential danger of bear encounters. Eighty-two percent ($N=225$) secured their food within 92 m of camp and over 90 percent ($N=225$) within 137 m. Because of short-distance speed of bears, food cached at these distances may invite problems. Herrero (1970:596) pointed out that "Even at 100 yards [92 m] a person has little time to think or maneuver if a grizzly suddenly finds its individual distance violated and is startled into making an attack."

DISCUSSION

Backcountry use in the Gallatin Range was highest during July and August (1973-74), totaling 76 percent of the May-through-October use. During periods of peak human use, grizzly bears were using high-elevation off-trail areas. During those periods when the bears were found in the lower-elevation trail areas, human use was minimal. Thus, there appear to be natural checks to human-grizzly bear confrontations in the Gallatin Range provided that the numbers of people in the backcountry areas remain low in May-June and September-October and that people remain on the trails. Since the grizzly bear is a high-elevation species in these areas, campsite confrontations can probably be minimized by limiting camping to areas below 2,591 m.

Activity patterns of grizzlies at the point of first observation and after bears had become aware of the human presence did not suggest aggressive behavioral traits likely to increase the possibilities of human-bear encounters. Grizzlies were encountered at greater distances than most other species (possibily because they use areas of open vegetation). They are an alert species, and there was no indication of innate aggressiveness in those cases where bears were able to flee without molestation.

A considerable number of backcountry travelers reported engaging in activities that could increase detrimental encounters with grizzly bears. The reported figures are probably conservative since some visitors would not report activities considered unsafe. Some unsafe activities can be eliminated by better education of the backcountry traveler. In areas where there are permit systems, the permit briefings should be used to refresh the visitor's knowledge of camping and traveling procedures in grizzly bear country, and the information system should be extended into backcountry areas by backcountry rangers.

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MOVEMENTS OF RADIO-INSTRUMENTED GRIZZLY BEARS WITHIN THE YELLOWSTONE AREA

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Abstract: Grizzly bear (*Ursus arctos horribilis*) movement patterns were studied with the aid of 18 radio-instrumented grizzly bears in 1975 and 1976. Five bears gave minimal information because of death, transmitter failure, or loss of transmitters. Seasonal home range information is presented for 13 bears. Two bears, trapped inside Yellowstone National Park, included areas outside of the park in their home ranges. Twelve bears trapped outside included parts of the park in their home ranges. Three females with young gave no indication of having smaller home ranges than other individuals. Movement patterns prior to denning and dates of denning varied among individual bears.

Grizzly bears in and around Yellowstone National Park are under the jurisdiction of several state and federal agencies. The states of Idaho, Montana, and Wyoming, and the National Park Service all have direct responsibilities for bear management. The U.S. Forest Service has direct responsibility for most bear habitat outside of Yellowstone National Park, and the U.S. Fish and Wildlife Service has jurisdiction over the entire population under the Endangered Species Act. The philosophies and management objectives of most of these agencies differ with respect to grizzly bears.

Knowledge of movement patterns across political boundaries is desirable for the formulation of management plans by each agency involved. Information on use of habitat types, especially those where physical modification or other human encroachment has occurred or may occur, is essential in light of the Endangered Species Act. Previous research was carried out by Craighead and Craighead (1970), but no radiotracking has been conducted since major garbage dumps within Yellowstone National Park were closed in 1971. Bear movement patterns since that time are largely unkown.

In 1975, the Interagency Grizzly Bear Study Team began to radio-instrument grizzly bears in and around Yellowstone National Park with the following objectives: (1) to obtain data on bear use of various habitat types; (2) to determine movement patterns of bears with repsect to various political boundaries; and (3) to document reactions of grizzly bears to other activities within their habitat, especially logging, livestock grazing, and recreational development. This paper reports on movement patterns observed during the 1975 and 1976 field seasons.

STUDY AREA

The study area lies in the junction of the states of Montana, Idaho, and Wyoming. Yellowstone National Park forms the center and covers approximately half of the more than 20,720-km^2 area. The remaining half falls mainly on National Forest lands surrounding the park (Fig. 1). The area is essentially a very large high-elevation basin encircled by mountain ranges. Elevational extremes range from 4,196 m on Grand Teton Peak to 1,610 m around Gardiner, Montana, with most of the area lying between 2,134 and 2,438 m.

The basic geology of the area was extensively studied and described by Hague (1899). Considerable uplifting and faulting of sedimentary strata and volcanic activity within the more recent geologic past have elevated the surrounding mountains. Present geothermal activity is a persisting indicator of recent geologic instability. Former glacial activity is much in evidence in many of the surrounding high-relief areas, especially on the north and east sides. Much of the area is forest interspersed with marshes, meadows, steppes, and shrub steppes. This variation in cover type is due in part to the diverse topography with its inherent microclimates that foster a range of vegetative communities from cold-desert to alpine.

The forest habitat types have been extensively described by Pfister et al. (1974) and Cooper (1975). Periodic wildfires have played a key role in many plant communities in the Yellowstone system. Though fire suppression by man over the past 80 years is now allowing many areas to reach or approach climatic climax (Houston 1973), many of the forest habitat types are presently in seral stands of lodgepole pine (*Pinus contorta*) because of these fires.

The nonforest habitat types have not been as intensively classified. Many, however, will fall into the tentative habitat types that have been delineated in grasslands and shrublands below the alpine zone in western Montana by Mueggler and Handl (1974).

The mean annual temperature at Mammoth, Wyoming, is 4.3C. January is generally the coldest month, averaging -7.7C, and July is the warmest, averaging 16.9C. Annual precipitation ranges from about 34.8 cm in the northeast to 97.2 cm in the southwest. A

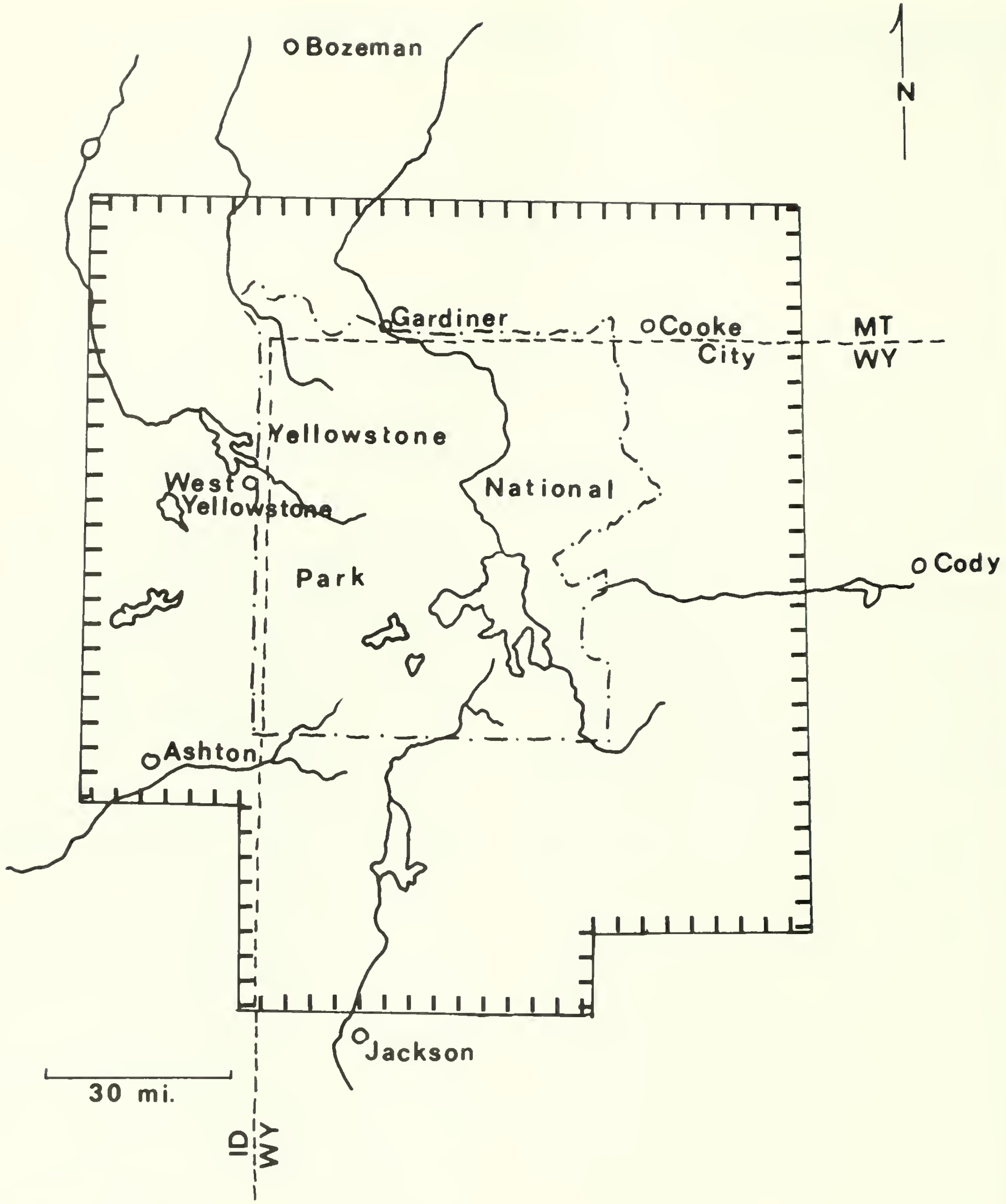

Fig. 1. Interagency Study Area.

rain shadow effect causes xeric conditions in the central and eastern portions of the study area. Most precipitation occurs as snow, with areas above 2,134 m receiving an average in excess of 3.8 m.

Populations of large ungulates share the area with grizzly bears. These animals at times become a food source for the bears, especially as carrion during the spring months. Populations of black bears (*Ursus americanus*) and other large carnivores also inhabit the study area. Pocket gophers (*Thomomys nuttalli*) are abundant in many meadow areas and are at times sought by grizzly bears for food.

Until recent years, this area remained a virtual wilderness. Although forested, access was too difficult for logging, and the timber was of the type and quality that was not in great demand. Climate and terrain prevented extensive agriculture. Hunters and stockmen were the main users of the area, and neither made many apparent major changes in the grizzly bear habitat.

Since 1960, changes in logging needs and practices have opened up many formerly inaccessible areas. Increased recreational demands and developments have opened still more. How these changes will ultimately affect the grizzly bears and their habitat remains to be seen.

METHODS

Radiotelemetry was used to determine bear movements and habitat use. Transmitters used were in the 164-MHz range. Transmitter failure due largely to improper packaging caused some difficulty early in the summer of 1975.

Most radiotracking was done from the air. A Piper Supercub equipped with a rotatable 3-element yagi antenna was used for most of the work. Stacked yagi antennas mounted on wing struts were available when additional range was required. Weather permitting, flights were made 3 times a week.

The extent of movements of radio-instrumented bears was found by using a center of activity (Harrison 1958, White 1964). Relocation of each animal was plotted on a map, and a geometric center (center of activity) was calculated by superimposing the relocations on a grid system described by Haynes (1949). Standard diameters (SD) for each animal were then calculated by using Harrison's (1958:198) formula:

$$\mathrm{SD} = \sqrt{\sum d^2 / N}$$

where d is twice the distance from the center of activity to each relocation and N is the total number of relocations. The standard diameter describes the diameter of a circle that has the center of activity as its center; this circle contains 68.26 percent of all the relocations and thus 68.26 percent of the animal's activity during the period considered. We use the standard diameters as an index for comparison of movements among bears in different areas and different years. We do not ascribe any biological significance to them.

Minimum home range of each bear was calculated by using the minimum polygon that enclosed the bear's known movements (Stickel 1954). We feel that this method presently gives the best biological interpretation of radiotracking data.

RESULTS

Eighteen grizzly bears were captured and instrumented. Twelve of these furnished sufficient data to make some interpretations of seasonal movements. Five bears furnished data for 2 consecutive years. Two bears were trapped inside Yellowstone National Park near Yellowstone Lake, and the rest were trapped in areas surrounding the park.

Both 1975 and 1976 were years of exceptionally high precipitation resulting in lush growth of herbaceous vegetation throughout the study area. We are not sure what effect this had on bear movements but do believe it contributed to relatively poor trapping success. Most bears were trapped in July and August, when they began to concentrate in areas of high food availability.

Grizzly bears in our study area exhibited a variety of habitat use and movement patterns as well as home range sizes. We use Calhoun's (1963) definition of home range. On 27 August 1976, 11 single bears and 3 family groups were located. Elevational differences among bears ranged from a low of 1,920 m to a high of 2,999 m on this day. Habitat types being used included wet meadows, dense lodgepole pine stands, subalpine fir (*Abies lasiocarpa*), and spruce (*Picea engelmannii*).

The movements of any individual bear were apparently influenced by the habitat types available to it, the amount of forage available, and prior experience. Data on 2 bears immediately after emergence from the den illustrate the difference between available habitats. A 5-year-old male (No. 7) that denned in northern Yellowstone Park moved from his denning area to an elk winter concentration area where he partially consumed a winter-killed elk and then killed and consumed an adult elk. Six days later, he killed an elk calf and consumed it. A 4-year-old female (No. 4) that denned west of Yellowstone Park was 26 airline km and over one mountain range from the nearest ungulate winter range when she emerged from her den. Her early spring movements were between her den site and areas where she could find squirrel caches, insect larvae, and grass, which were essentially the only forages available at the time.

A female (No. 16) with 2 cubs of the year appeared to be highly motivated by previous experience in her movements. Trapped near Hebgen Lake in August, she moved to Yellowstone Park for 10 days where she apparently spent most of her time digging for roots on the periphery of small ponds and swamps. She then returned to the vicinity of Hebgen Lake where she fed on the carcass of a dead horse and spent some time in close proximity to the West Yellowstone dump, which had been bearproofed for 4 years. The bear then returned to Yellowstone Park where she resumed digging around ponds and swamps until she denned. This bear's movements from Yellowstone Park to Hebgen Lake were probably influenced by prior experience of finding carrion in that vicinity and feeding at the West Yellowstone dump before it was bearproofed.

Minimum home range sizes for 4 bears trapped at Cooke City dump in 1975 are shown in Fig. 2. Minimum home range sizes in km² are given in Table 1. Somewhat comparable information for 3 of these bears appears in Table 2 and Fig. 3, as well as information on 3 additional bears.

Movement patterns of these bears were diverse although their ranges overlapped. Two, a 15-year-old male (No. 9) and a 5-year-old female (No. 10), concentrated their activities around and near the Cooke City dump.

An 8-year-old male (No. 5) divided his time almost equally between the Cooke City dump and some natural range centered 23 airline km to the west. He used the same basic movement patterns and general range area and even denned in the same natural cave for 2 successive years.

Table 1. Minimum home ranges of 5 radio-instrumented grizzly bears. Interagency Study Area, 1975. Bears were in dens by last date of respective tracking periods. Home range sizes approximated areas used during tracking periods and do not necessarily represent total home range size.

Bear no.	Sex	Age (years)	Tracking period	Minimum home range (km²)	Number of locations
4	F	3	Jul 75 to 22 Dec 75	324	41
5	M	7	Jul 75 to 14 Nov 75	158	34
7	M	4	Aug 75 to 22 Dec 75	262	34
8	F	9	Aug 75 to 14 Nov 75	62	25
10	F	4	Sep 75 to 14 Nov 75	18	9

A 10-year-old female (No. 8) used the same general area for 2 years. In 1975, she spent some time at the Cooke City dump, but more of her time was spent on

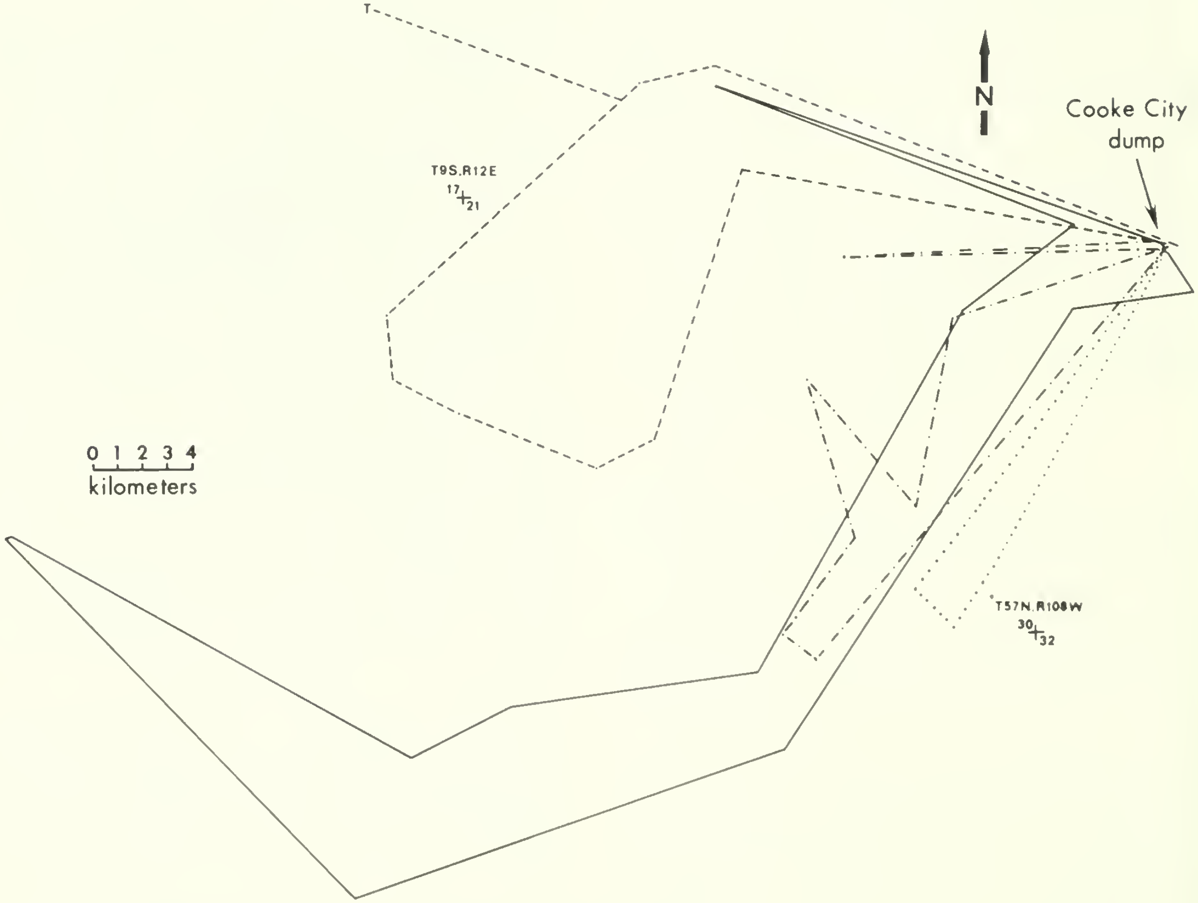

Fig. 2. Minimum home range areas of 4 instrumented grizzly bears: summer to denning, 1975.

Table 2. Minimum home ranges of 12 radio-instrumented grizzly bears. Interagency Study Area, 1976. Bears were at dens by last date of respective tracking periods except for bears No. 8 and No. 14. Home range size approximate areas used during tracking periods and do not necessarily represent total home range size.

Bear no.	Sex	Age (years)	Tracking period	Minimum home range (km^2)	Number of locations
4	F	4	3 Apr 76 to 29 Oct 76	194	51
5	M	8	28 Jul 76 to 3 Nov 76	212	24
6	F	7	14 Jul 76 to 22 Nov 76	523	39
8	F	10	10 Apr 76 to 19 Oct 76	150	27
9	M	15	9 Aug 76 to 5 Nov 76	117	28
10	F	5	4 Aug 76 to 5 Oct 76	26	18
11	M	6	18 Jun 76 to 20 Oct 76	255	35
12	F	Adult	9 Jul 76 to 3 Nov 76	174	38
13	F	7	11 Aug 76 to 5 Nov 76	741	28
14	M	9	13 Aug 76 to 15 Sep 76	98	13
15	M	5	16 Aug 76 to 8 Nov 76	93	23
16	F	10	18 Aug 76 to 11 Nov 76	350	29

natural range. In 1976, she was accompanied by a cub-of-the-year and again spent most of her time on natural range. She may have made 1 or 2 trips to the Cooke City dump.

A 4-year-old male (No. 7) used the Cooke City dump from summer into early fall in 1975. He moved west from the dump to a fall range, then on to a denning area about 40 airline km from Cooke City. His transmitter failed in early April and he was not relocated.

An adult female (No. 13) accompanied by a cub-of-the-year was trapped on 11 August 1976 at the Cooke City dump. She was not relocated at the dump after this date. Her movements were characterized by long-distance traveling. During the tracking period, she and her offspring used the largest minimum home range, about 741 km^2, that we documented. This home range is about 63 km long east to west, with the park boundary at the center of its east-west axis.

An adult male (No. 11) trapped east of the park area did not use or even approach the Cooke City dump. His home range was fairly well defined and randomly used (Fig. 3).

Two grizzly bear home ranges (Fig. 4) were apparently associated with spawning runs of cutthroat trout (*Salmo clarki*) from Yellowstone Lake. One adult female (No. 12) trapped in July 1976 had a distinct summer range separated by a migration corridor from her spring-fall range. These areas lie about 14.5 airline km apart. The other (No. 6), a 5-year-old female, apparently used the same spawning area, but there the resemblance ended. This bear was trapped in July 1975 while working spawning trout, but her radio failed before much information could be collected. We determined that she ranged several kilometers west-northwest of the trap site on Yellowstone Lake to the Old Faithful area. She was retrapped in July 1976 at the

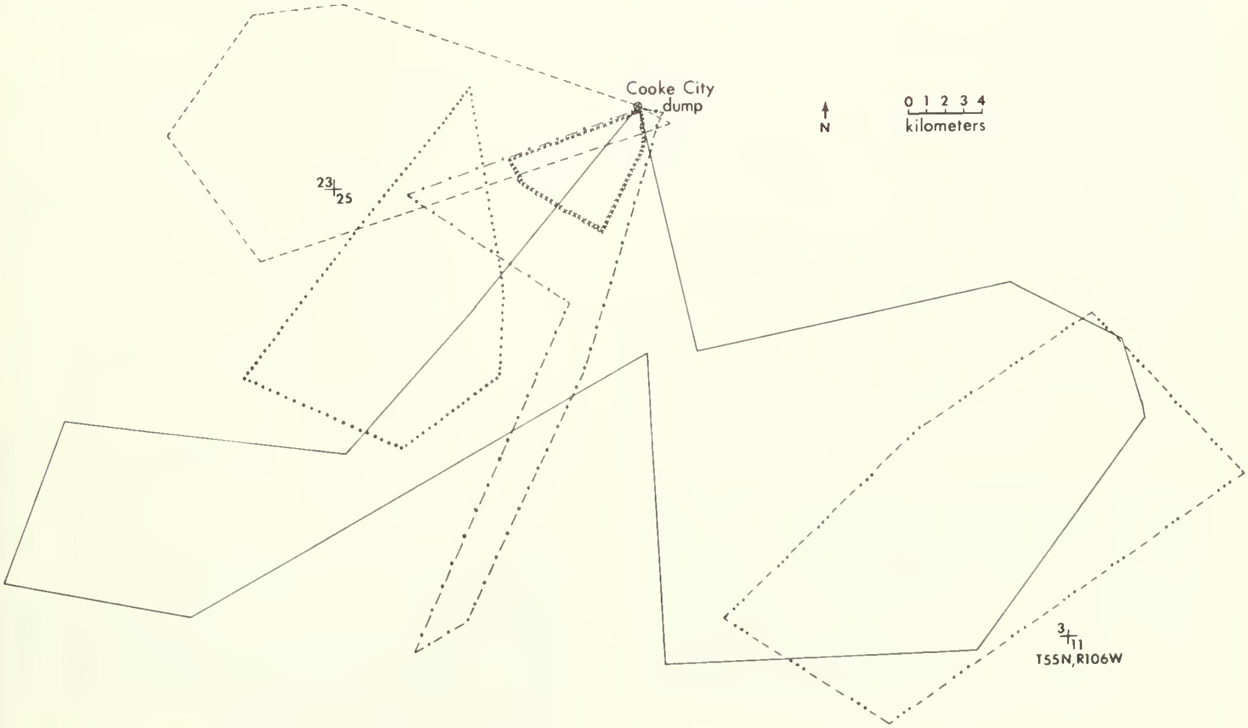

Fig. 3. Minimum home range areas of 6 instrumented grizzly bears, 1976.

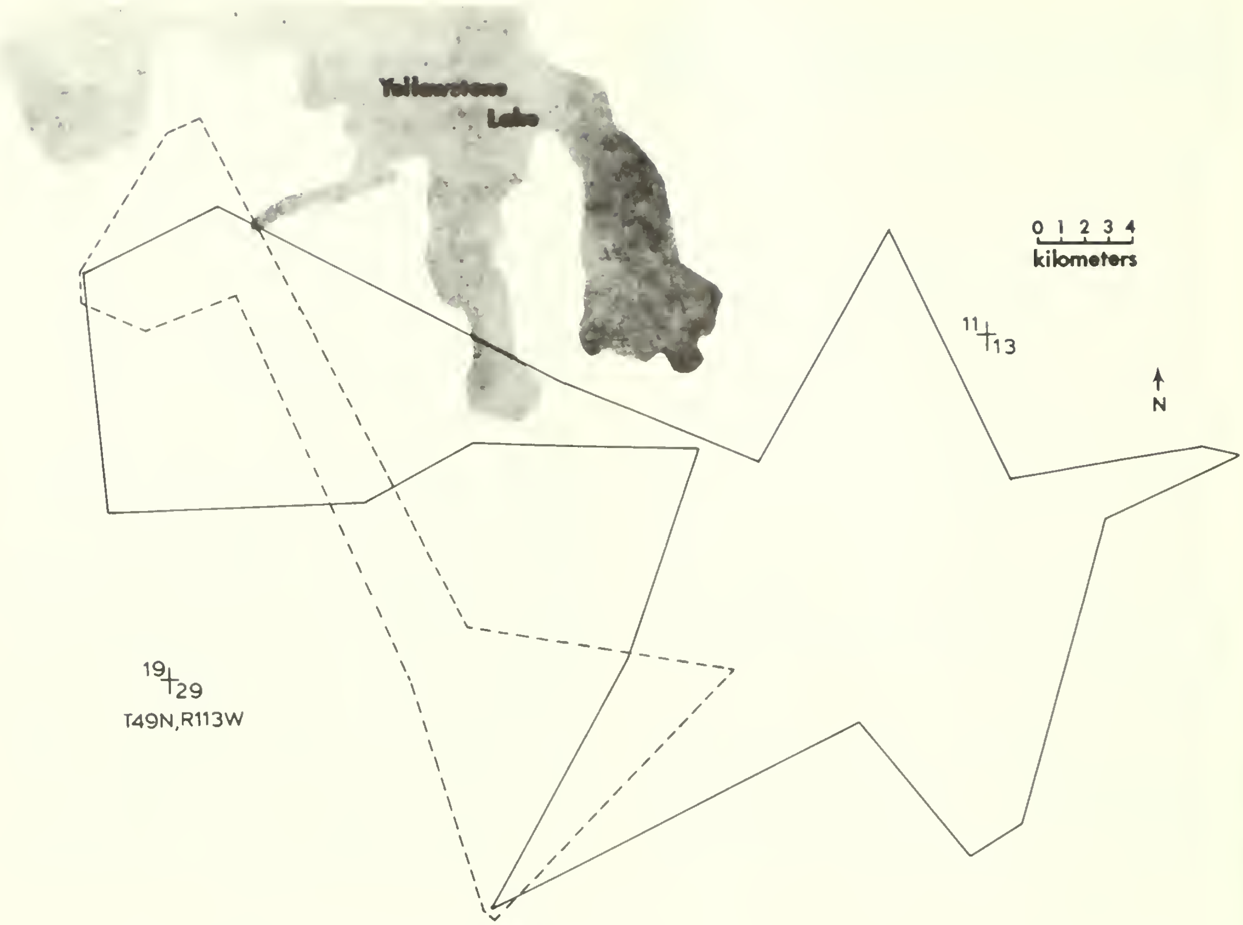

Fig. 4. Minimum home range areas of 2 instrumented grizzly bears, 1976.

same trap site and moved opposite to her previous year's range. She traveled east and south-southeast from Yellowstone Lake and eventually out of the park. The only known area of home range overlap between the 2 years was on the trout spawning area. She returned to an area near Heart Lake to den, and it is possible that she denned in this vicinity in 1975-76. In all, she used a minimum home range of 523 km² in 1976.

Minimum home ranges of a young female, an adult female with 2 cubs-of-the-year, and an adult male are presented in Fig. 5. The young female (No. 4), 4 years old in 1976, was tracked for portions of 2 years. She used a minimum home range of 324 km² in 1975. During 1976, she used only the northern 194 km² of her previous range. A partial explanation of this decreased range use may lie in the fact that she was traveling with a large bear throughout 1975. She either denned with or in close proximity to the other bear in 1975. However, they were not observed together again after a few days following emergence from the den, between 3 and 6 April 1976. She remained at or in the vicinity of the den site at least until 6 July.

The adult female (No. 16) with 2 cubs-of-the-year used 2 summer-fall range areas lying about 29 airline km apart. One was a natural forage area; the other appeared linked to garbage and livestock carrion. This family group was highly mobile at times; they once moved about 23 airline km in about 23 hours.

The 5-year-old male (No. 15) was trapped in West Yellowstone, Montana, in August 1976. He used a deceptively small, 93-km² summer-fall range. This male was originally trapped in August 1974 at West Yellowstone and by agreement between Montana and Wyoming Game Departments was transplanted into Wyoming. He denned just west of Cody, Wyoming, in 1974 and remained in the transplant area at least through mid-June of 1975. It is not known by what route he returned to West Yellowstone, but the minimum distance between his 1974 den site and the recapture site is 153 airline km.

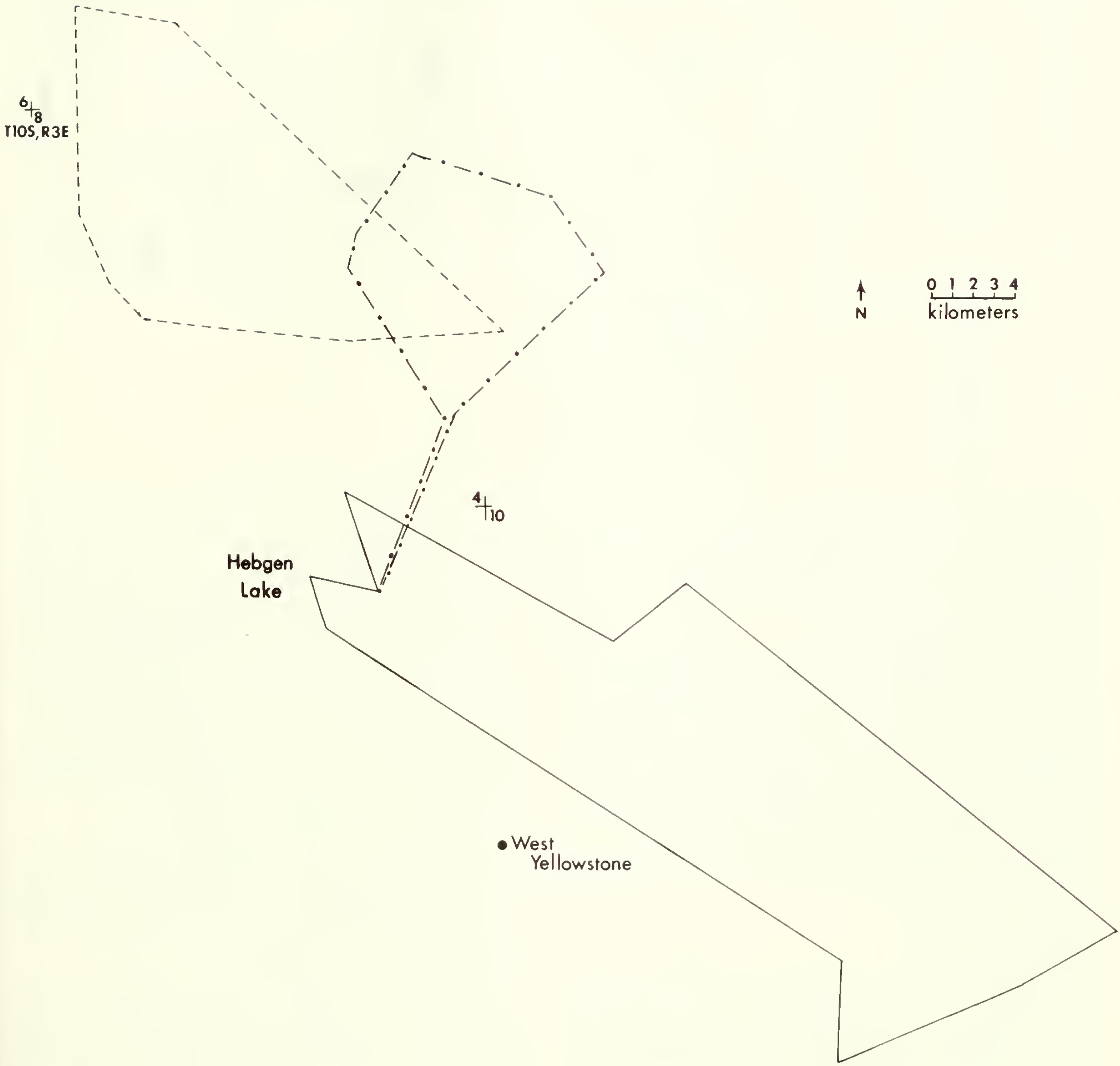

Fig. 5. Minimum home range areas of 3 instrumented grizzly bears, 1976.

DISCUSSION

Use of standard diameters was a poor method of measuring year-long movements and home ranges of grizzly bears. Only 3 bears used their entire home ranges in a uniform enough manner to permit the establishment of year-long activity centers (Table 3). Most of the bears made relatively long movements between seasonal foraging areas or to den areas. For those bears, we calculated geometric centers and standard diameters on areas of more concentrated use rather than include all of the movements in one figure, which, in most instances, would have given an unrealistically expanded movement index.

Similar data gathered by Joslin (personal communication) for grizzly bears west of the Continental Divide

Table 3. Ranges of activity of radio-instrumented grizzly bears, Interagency Study Area, 1975-76, as indicated by standard diameters of areas of activity. Numbers of observations do not include location checks when bears were in dens. Numbers of days indicate minimum time spent in areas and include time in dens where applicable.

	1976				1975			
Bear no.	Standard diameter (km)	No. of observations	Season(s) of use	No. of days	Standard diameter (km)	No. of observations	Season(s) of use	No. of days
4	13.15	52	All	315	17.65	41	Summer-fall	156
5	20.18	23	Summer	79	14.34	28	Summer-fall	84
	0	1	Predenning	58+	1.88	6	Predenning	26
6	20.44	27	Summer-fall	89	-	-0-	-	
8	-	-	-	-	11.00	5	Summer	15
	11.18	26	All	196+	5.30	20	Fall to denning	67
9	9.66	18	Summer-fall	67	-	-0-	-	
	3.09	3	Predenning	74	-	-	-	-
11	15.90	35	Summer-fall	125+	-	-	-	-
12	11.43	16	Summer	46	-	-	-	-
	6.97	22	Spring-fall	125	-	-	-	-
13	28.94	20	Summer-fall	63	-	-	-	-
	0.89	3	Predenning	66	-	-	-	-
16	12.70	18	Summer-fall	60	-	-	-	-
	8.26	11	Summer-fall	66	-	-	-	-

indicate that standard diameters for entire home ranges in that area may be comparable in size to diameters of seasonal use areas in the Yellowstone vicinity. In only 4 instances associated with predenning were movements concentrated in small areas.

Grizzly bears within the study area do not observe political or management agency boundaries, and movements across these were not restricted to any given area. Two of the 18 grizzly bears radio-instrumented in 1975-76 died before much information could be collected on them. Fourteen of the bears freely crossed into and out of Yellowstone National Park. Only 2 instrumented bears are not known to have ranged into the park.

CONCLUSIONS

Information gathered to date indicates that grizzly bear movements in the Yellowstone area are not typical of those found in other areas. Our movement data, especially of females with young, show much larger home ranges than those reported by Pearson (1975) for the Yukon Territory or by Berns and Hensel (1972) for Kodiak Island. Craighead and Craighead (1969) show ranges smaller than ours for most of their animals, but the movements of their radiocollared bears may have been influenced by abundant food sources at the Trout Creek dump, which was still in operation at that time.

Much of the difference between the movement patterns of bears in our study and those reported for bears in Alaska and Canada can probably be explained by wide differences in habitats and available foods. Differences from bears west of the Continental Divide in northern Montana may also be explained this way. Mealey (personal communication) has found approximately twice as many forested habitat types of apparent importance to grizzly bears in northwestern Montana than occur in the Yellowstone area.

The topography of Yellowstone Park may promote long movements. Although most of the area lies above 2,134 m, it is relatively flat. A grizzly bear on Yellowstone's Central Plateau may have to travel over 32 km to gain 305 m in elevation.

Prior experience appears to play an important part in the use of seasonal ranges by some bears. Bears that formerly fed at garbage dumps in Yellowstone National Park were probably forced into relatively long movements at times of the year when dumps were not in operation. Some of the movements of our radio-instrumented bears indicate that they periodically check the West Yellowstone dump even though it has been bearproofed for about 4 years.

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THE REINTRODUCTION OF ORPHANED GRIZZLY BEAR CUBS INTO THE WILD

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Abstract: Several techniques can be used to return captured orphaned bear cubs to the wild. They can be released immediately in suitable habitat, be adopted by another female with young, or be fattened and then released. The last technique was used successfully to return to the wild an orphaned cub obtained by the Border Grizzly Project of the University of Montana in 1975. The cub was fattened in captivity and released into an artificial den after being fitted with a radiocollar. She denned successfully nearby and survived the winter and early spring with no known problems.

Orphaned grizzly cubs (*Ursus arctos horribilis*) are becoming more common because of the increasing interactions and confrontations between people and bears. Intensive oil and gas exploration, subdivisions in grizzly habitat, increased backcountry recreational use, logging, and similar activities will undoubtedly result in greater bear mortality in the future. Unfortunately, much of the mortality may involve females with cubs because of their aggressive nature in enounters with people. In instances of female mortality, young cubs either have to be destroyed or must be sent to zoos or other facilities, which constitutes mortality so far as the wild population is concerned. With the grizzly now listed as a threatened species south of Canada under the U.S. Endangered Species Act of 1973, and because of the uncertain status of the various populations, there is a need to limit such grizzly mortality.

Because of these concerns and the low reproductive potential of grizzlies (Craighead et al. 1974), the survival of orphaned cubs, especially females, is increasingly important (Stirling et al. 1976). Concepts and techniques for the reintroduction of orphaned cubs include:

> (1) Immediate release of the cubs into suitable habitat. If orphaned late in the year, after they have acquired sufficient fat reserves and a familiarity with bear habitat, they may survive on their own. Erickson (1959) in Michigan and Payne (1975) in Newfoundland found that black bear cubs (*U. americanus*) were self-sufficient if orphaned after August. In Glacier National Park, 2 grizzly cubs orphaned in late autumn were known to have denned. One of these bears was observed the next year (Martinka, personal communication). Russell observed 3 grizzly cubs that survived in the wild after their mother was shot in Jasper National Park, Canada, on 4 July 1975. The 3 cubs seemed very dependent on each other for security and panicked when they became separated.
>
> (2) Adoption of orphaned cubs by females that have cubs or that have recently lost cubs. Hornocker (1962), Erickson and Miller (1963), Bledsoe (1975), Vibe (1975), and Sumner and Craighead (personal communication) have documented the natural adoption of black, grizzly, and polar bear (*U. maritimus*) cubs in the wild. The cubs adopted by a female polar bear with 2 cubs of her own did not fare well, however, as 1 was found dead the next year and the other, wandering into a settlement, was in an emaciated condition (Vibe 1975).

We know of 2 attempts at planned adoption of orphaned cubs by free-ranging females. Lentfer (personal communication) successfully facilitated the adoption of an orphaned polar bear cub in northern Alaska. The female, which had 1 cub of her own, was immobilized and the orphan began nursing soon after being placed with her. Scents (body oils) of the orphaned cub, female, and natural cub were mixed together by hand to help prevent rejection of the new cub.

Hugie (personal communication), working on black bears in Baxter State Park, Maine, reported the possible adoption of 2 orphaned cubs by a female black bear with 2 cubs:

> The cubs were captured and held for several days. Park personnel found that another female with 2 cubs was utilizing a garbage dump near the area where the first female was killed. The 2 orphaned cubs were taken to the dump and released in the presence of the second female and her cubs. Later, a female with 4 cubs was observed in the same area.

A similar method designed for the adoption of grizzly cubs would involve keeping an inventory each year of the locations of female grizzlies with young, especially in areas where the females could be easily captured. Whenever orphaned cubs were obtained, immediate efforts would be made to capture a female with young, and to put the orphans with her. To ensure adoption, the cubs should be allowed to nurse, possible by using Oxytocin to stimulate lactation (Bowes and Jonkel 1975), and the female should be injected with a tranquilizer before she recovers. Saturating the orphaned cubs with scent from the female and her natural cubs (i.e., urine, saliva, body oil) may also encourage the female to accept the orphans. Additional techniques include:

(a) Hold the group in confinement for a short period to increase the exposure of the foster mother to the orphans.

(b) Spray a strong deodorant directly onto the nose of the female and on the orphan cubs to help prevent rejection. This practice is common on commercial mink ranches, where it is desirable to raise orphaned litters. The technique has not been tried on bears, however.

(c) Place food near the release area to encourage the family group to remain together and build stronger ties, thus reducing competition between the cubs, and perhaps to hold the orphans at the site to give the investigator a second chance to reintroduce them to the wild should the adoption fail.

(3) Reintroduction of orphaned grizzly cubs to the wild after holding the cubs in captivity, feeding them for maximum weight gain, and releasing them during periods of food abundance or during the denning season. Greer (personal communication) has released orphaned black bear cubs in the Yellowstone Park area in this way, and Krott and Krott (1962) were able to release 0.8-year-old orphaned European brown bear cubs by taking them to suitable habitat and walking with them to various feeding and denning areas. At Churchill, Manitoba, polar bears of various ages have been released into the wild successfully (i.e., have been seen or recaptured in later years) after being held 3-4 months in captivity for physiological studies (Jonkel et al. 1976). Beecham has held 10 orphaned black bear cubs in captivity in Idaho and released them at various times of the year with total success. He considers fattening the cubs in captivity and releasing them during periods of food abundance to be key factors in successful reintroductions.

The University of Montana Border Grizzly Project (BGP) obtained 2 orphaned grizzly cubs on 31 July 1975, when a female was illegally killed near Ford Station, Montana, west of Glacier National Park. The remainder of this paper reports the techniques used to return 1 of these cubs to the wild.

METHODS

Care of Cubs in Captivity

Two orphaned cubs were captured alive by Montana Fish and Game Department personnel and were moved to the State Animal Shelter in Helena. They were approximately 6.5 months old when orphaned and were in good condition, although somewhat small for their age (approximately 9.0 and 13.5 kg).

The cubs were fed a mixture of evaporated milk and water during their first 3 weeks in captivity. As the milk ration was phased out, increasing amounts of fruit and dry dog food were supplied.

On 9 September 1975, the cubs were transferred to facilities at the University of Montana. The female cub was maintained at the University of Montana and was prepared for release into the wild. The cub was fed for maximum weight gain by providing all she would consume of fruit, vegetables, dry dog food, and evaporated milk. She was weighed at weekly intervals during this period of maximum weight gain (Table 1).

Table 1. Weights of a female grizzly bear cub taken weekly prior to feeding, 7 October-7 November 1975.

Date	Weight (kg)
7 October	38.1
14 October	43.5
21 October	46.3
28 October	48.5
4 November	48.1
7 November	50.8

The Den Site

An artificial den was constructed to increase the cub's chances of survival in the wild. The den site, selected on the basis of published descriptions of grizzly dens (Craighead and Craighead 1972, Pearson 1975), was located in the Shorty Creek area of the Whitefish Range, approximately 17 km from the site where the cub was orphaned. The den was dug under a large spruce (*Picea engelmannii*) so that the entrance was between the roots on the downhill side. The floor of the den consisted of gravel but was covered with leaves and straw before the cub was released. The form and dimensions of the den are shown in Fig. 1.

Vegetation in the den site area consisted of a mature spruce-fir *(Picea-Abies)* overstory that was previously logged for mature western larch *(Larix occidentalis)*. The den was at an elevation of 1,380 m on an east-facing slope about 5 m from the bottom of a steep draw. The slope of the hillside was approximately 30°.

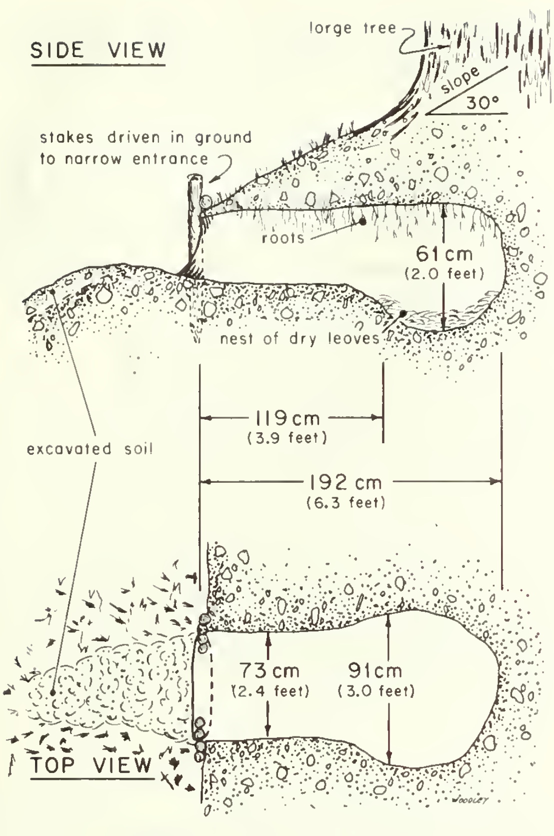

Fig. 1. Diagrammatic views of artificial grizzly den, Shorty Creek, 1975.

The cub was ear-tagged, fitted with a radiocollar, and transported to the site of release. Succinylcholine chloride and acepromazine were used as immobilizers. After release, her movements were monitored by radiotracking, visual sightings, and track observations.

RESULTS

Prerelease Preparation

During the period from 7 October through 7 November, when the cub was being fed for maximum weight gain, she gained 12.7 kg (Table 1), a gain of 0.41 kg/day, which is slightly less than the 0.635 kg/day gained by a free-ranging subadult female grizzly in the Yukon as reported by Pearson (1975). From 21 October through 7 November, the cub's food intake decreased, possibly due to physiological changes associated with the urge to den. She displayed signs of lethargy during this latter period and was often engaged in digging activities in the bedding of her cage.

Introduction to the Den

The cub was transported to the den on 11 November 1975. The temperature was −3.9 C and 15 cm of snow covered the ground. The cage in which she was transported was placed directly against the entrance to the den. Wooden stakes were driven into the ground on both sides of the den entrance to narrow it and to prevent the bear's escape as she moved into the den. The gate of the cage was opened at about 1500 hours, but the bear was reluctant to enter the den. After being coaxed with food and prodded unsuccessfully, the cub abruptly backed into the den 1.5 hours after the cage was opened.

The cage was removed once the cub was in the den and the den entrance was closed by placing more stakes across the tunnel. The animal was quiet in the den during this procedure. Although it was obvious that the cub could dig her way out through the stake barrier, we hoped that by confining her as long as possible in the den we could provide more time for adjustment to her new surroundings and thereby encourage her to stay in the den.

At 1700 hours, all personnel and equipment were withdrawn from the den area. A strong radio signal was received from the bear's transmitter at this time. At 2000 hours, we returned to the area and received a signal while standing approximately 40 m from the den. The cub had dug through the barricaded entrance but was still in the area of the den. In order to avoid scaring her from the den site, we again withdrew from the area.

The next morning, 12 November, the bear was standing above the den entrance at 0800 hours. Again that evening, a strong signal was detected from the den area and the cub was not in sight, indicating that she was probably in the den.

At 0800 hours on 13 November, we approached the den after receiving a strong radio signal. We observed the bear scraping leaves away from the den entrance. The cub saw us, walked downslope from the den, turned, and slowly approached us on an old skid road. The transmitter was gone from her neck. We left the area and returned in the early afternoon. The cub was nowhere in sight and the radiocollar was found inside the den. She had enlarged the den, making it wider and deeper. She had also dug 3 shallow excavations within 100 m and upslope of the original den. No good tracks could be found, but we left a box of fruit just above the den in hopes of keeping her in the area.

Some of the fruit had been eaten on 14 November, but heavy rain was now falling and her tracks were difficult to follow. On the evening of 15 November, the tracks of a grizzly cub coming from the release area were found on the Shorty Creek road, approximately 3 km from the release site. We followed the tracks on 16 November to a ridgetop at an elevation of approximately 2,370 m, where they were lost in drifting snow. Attempts to relocate the tracks and the cub failed, and no tracks were seen again that winter on any trails or roads in the area.

The released cub was seen by BGP personnel and various other people on 10 different occasions in spring 1976, in an area approximately 8 km from the artificial den site. She appeared to be in good condition and was feeding extensively on roadside and sidehill vegetation.

DISCUSSION

It has been reported that the final move to the den site is initiated by heavy snowfall and subfreezing temperatures (Craighead and Craighead 1972), but a combination of environmental and individual factors are probably responsible (Pearson 1975). The absence of a heavy, permanent snow cover at the artificial den site and the disturbance of the young bear by field crews may have accounted for her failure to stay in the release area and utilize the den.

To improve future chances that a bear will stay in the release area, several improvements should be made in the release techniques. The bear should be released into the artificial den when a heavy, permanent snow cover is on the ground. Heavy snow will make travel difficult and may encourage the bear to remain in the den. The bear should be monitored by its radio signal without approaching the release site to within visual or auditory range. Disturbance at the den site after the release should be kept to a minimum to prevent the bear from being frightened from the area.

The technique of returning an orphaned cub to the wild by releasing it during the denning season seems to have promise. It has advantages over adoption attempts in that a female with cubs does not have to be found and captured, and the orphan can be released when it is ready to go, not when and if a female with cubs can be captured. A possible disadvantage is that cubs may habituate to people during the feeding period. It is hoped that future releases of this type will be attempted, employing the improvements suggested, and that further data will thereby become available.

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