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A Primer on Wildlife Management Considerations for the Southern National Parks

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Southeast Region

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A PRIMER ON WILDLIFE MANAGEMENT CONSIDERATIONS FOR THE SOUTHERN NATIONAL PARKS

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This book has been influenced by many people in different ways. First, I am thankful for the influence of the late Dr. Henry S. Mosby who guided me into a philosophy of thinking about wildlife in a soil-plant-animal context and the basic principles which regulate wild systems. Part I is Dr. Mosby's philosophy expressed in my words and experiences.

This book would not have been possible without Dr. Jay Gogue's understanding of its need and his willingness to support my idea for addressing that need. His patience with me as I went from an original proposal for a 75-page manuscript to be prepared in two to three months to the present product, which has been drawn out over three years, is gratefully acknowledged.

The critical reviews, corrections, and helpful suggestions of Dr. David Guynn, Professor, Clemson University and Mr. James Wood, National Park Service editor, Southeastern Region, are also gratefully acknowledged. I am very thankful for the verbal contributions evaluating the manuscript's clarity and readability and which were made by: James Bessinger, Danny Cohan, Dr. Dominic Dotavio, Gene Parker, Bryan Woodward, and Larry Woodward.

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INTRODUCTION

This book is an introduction to the ecological bases for wildlife management. It is written for those who have a general interest, but not a professional background, in this art and science. It seeks to expand the understanding of ecosystem components and functions as they relate to wild animals. It also seeks to improve the technical communication skills of natural resource management generalists who work with wildlife management specialists.

Emphasis is placed on perspectives of ecological components and functions as well as the principles that describe their distribution and dynamics in time and space. Major assumptions that underlie ecosystem evaluation procedures are reviewed to sensitize the field worker to the need to critically assess any procedure that might be considered for application in a given situation.

Hopefully, after reading this book, the reader will have a heightened awareness of the multi-dimensional nature of wildlife management and science. He should understand that management is an art with a scientific basis. In addition, he should be aware that the selection and application of appropriate procedures in wildlife study is an art in itself. In particular, he should understand that management practices and study procedures cannot ever be applied without careful consideration of their ramifications and limitations.

While this book deals entirely with the ecological aspects of wildlife management, the practice of this art must also encompass social, political, and economic aspects. While I am keenly aware of the importance of these factors, this book was not the place to deal with them. Like most wildlife scientists, I firmly believe that everyone working with wildlife resources should have a basic knowledge of their ecology, and I have attempted to describe the rudiments of that subject area.

Finally, I must mention the influence of Leopoldian thinking on the goals of this book. Aldo Leopold (1887-1948), father of American wildlife management and land ethic essayist, had his greatest impact on my philosophy of the practice of wildlife management through his essay entitled, "Thinking Like a Mountain." The subject of that essay was predator control, but the message was far more catholic. His statement, "Only the mountain has lived long enough to listen objectively..." challenges wildlife managers to develop deep perspectives. Managers must strive constantly for heightened awareness, careful contemplation, and objective interpretation. Hopefully, this book will enhance one's efforts to meet the challenge.

PART I. WILDLIFE ECOLOGY

Chapter 1. HABITAT

The Ecological Meaning of Habitat

An ecosystem is a collection of inter-related plants and animals and associated abiotic factors which support plant and animal growth, maintenance, and reproduction. While ecosystem boundaries are arbitrarily set in the minds of men for convenience of study, discussion, or management, the ecosystems themselves may be as small as the gut of a termite which houses micro-organisms capable of converting cellulose to simple carbohydrates, or as large as the entire planet with its incomprehensible array of species and processes.

The plant components of an ecosystem are broken down into sub-groups called plant communities. The array of species present and the community's horizontal and vertical structure give it definition. These characteristics result from the interaction of the soil and the sun manifested in the process of photosynthesis and respiration. The nature of each interaction determines the types of communities which will occur at the interaction site on the landscape, as well as the direction and rate of change as communities mature or replace each other.

Replacement of one community by another is called succession. Successional stages are called seres and are characterized by species' presence, species abundance, and vertical structure. Succession results from growth and mortality. Mortality may result from competition for growing space, disease, comsumption by a herbivore, effects of weather, or the impacts of man's activities.

A wide array of communities gives diversity or complexity to the landscape. A highly diverse landscape has a high potential to offer habitat to a large number of wild animal species. Within a wide array of communities, many habitat components are available. Increases in component availability increase the probability that the habitat needs of a large number of species are likely to be met. This contrasts with a landscape of low diversity and small number of available habitat components.

The habitat for a species of wild animal is the array of community types which collectively meet the animal's requirements for food, cover, water and reproduction. Some species of animals are generalists, that is, they are highly flexible and adept at taking advantage of the multitude of opportunities offered by a broad array of communities. A premier example of such a species is the white-tailed deer (Odocoileus virginianus) which can thrive in the mountain forests, swamp forests, or agricultural lands bordered by forest or brush cover.

Some species require one or more habitat components. For example, the red-cockaded woodpecker (Picoides borealis) must have old-growth living pine trees in the southern pine forest for cavity excavation or it will not reproduce.

When reference is made to a species' habitat, it is usually to the general vegetative cover characteristics. For example, the natural habitat of the eastern gray squirrel (Sciurus carolinenisis) is the eastern hardwood and pine-hardwood forests, principally the older growth stands. The habitat of the eastern meadowlark (Sturnella magna) is agricultural and other open lands principally under low grass and herb cover.

Sometimes, when discussing habitat, it is necessary to consider the level of interaction with man. An example would be the contrast between wilderness habitat and urban habitat for the same species. It may also be important to give seasonal denotation to habitats. Seasonal denotations have two possible meanings. First, for resident species that are fairly sedentary, the animal remains at the same location while the plant communities change around it as seasonal changes redistribute the availability of food and cover. In the second case, the species is migratory and environmental changes cause it to move from one location to another, consequently moving from one set of habitat characteristics to another.

The habitat niche is the description of the combination of particular habitat components which a given species must have available for growth, maintenance and reproduction. Other aspects of the animal's habitat may change with little to no effect on its population so long as these changes have no significant side effects on the particular habitat niche components.

Niche component change can be critical. For example, in the days when farmers primarily used untreated wooden fence posts, the eastern bluebird (Sialia sialis) was thought of as a bird of the farmlands because holes in these posts offered ample opportunities for nesting. Today, however, the bluebird is far more abundant in forests with a good supply of dead snags than on farmlands. Standing dead wood with holes suitable for a nest site is a critical niche component for this species.

Another example of sensitivity to change in critical niche components is the rapid recovery of osprey (Pandion haliaetus) population following the ban on the use of DDT. Pesticide contamination of the foods of this bird had resulted in greatly lowered reproductive success because of weakened egg shells. As pesticide contamination has decreased in fish, the osprey population has recovered dramatically.

In summary, habitat can be viewed as that portion of the land that accommodates a species of animal. There are many attributes of the habitat which are relatively unimportant to the species. Those attributes that are critical to supplying the species with food, cover, water and an opportunity for reproduction are the habitat niche components. The species' flexibility in adjusting to habitat niche component change determines how important change many be in impacting growth, maintenance, and reproduction in the individual and consequently the health, productivity, size, and density of the population.

Food and the Factors Affecting It

The synthesis of plant tissue begins with the process of photosynthesis where carbon dioxide and water are combined to make a carbohydrate. The energy that drives this reaction is radiant energy from the sun. When this radiant energy strikes chlorophyl molecules in green plants, it is converted to chemical energy. This energy binds carbon, hydrogen, and oxygen into carbohydrate molecules and drives all of the metabolic processes required to synthesize tissue including the incorporation of nutrients and the synthesis of hormones necessary for tissue building and maintenance processes. When a herbivore ingests plant tissue, the process of digestion breaks down a portion of the tissue releasing nutrients and simple carbohydrates which, if absorbed through the wall of the gut and metabolized, will support the animal's growth, maintenance, and reproduction.

This chain of events and processes is awesome to contemplate. Energy in the form of light has come from a ball of fire 93 million miles away, struck a few chlorophyl molecules, and been transformed to chemical energy and now is the "fire of life" in the animal. Photosynthesis has been the foundation for the processes that began with the simplest of abiotic components and resulted in a complex animal.

Several aspects need to be considered when thinking about the food resources in an animal's habitat. When a habitat is evaluated, species or groups of species of foods or potential foods must be characterized according to their: (1) palatability, (2) availability, and (3) nutritional value. These considerations are most easily made when working with herbivores (primary consumers). They also apply to predators (secondary consumers), although behavioral interactions in predator/prey systems make this consideration somewhat more complicated.

First, we need to understand the basic aspects of food. Palatability is an attribute of a potential food indicating whether or not an animal testing it for taste will accept and ingest it. There is no way to assign any numerical value to palatability. We are simply left with subjective descriptions such as "highly palatable" because individuals of a species have been noted to utilize it in a manner suggesting that they enjoyed the taste greatly, or "non-palatable" when individuals obviously refused to ingest it, or some graduation in between these extremes.

The term preference is sometimes used interchangeably with palatability, but this is an error in understanding. Preference value can be calculated and is simply the ratio of the relative utilization of a food to its relative availability in the habitat. For example, if in evaluating deer forages, Species A accounted for 20% of all the plant stems available for browsing in a habitat and 20% of all the stems that had been found to be browsed were those of Species A, then Species A would have a preference value of 1.0. This means that the animals were neither avoiding Species A nor particularly seeking it out. It was being utilized in proportion to its availability.

On the other hand, if 60% of the browsed stems were of Species A, then we would say that it was a preferred species relative to the other plant species available. Conversely, if only 1% of the browsed stems were those of Species A, we would say that it had a low preference and conclude that it was low in palatability relative to the other species available. In summary, palatability indicates acceptability for ingestion, while preference indicates the appeal of a food relative to other potential foods in the habitat.

A highly palatable food may be relatively unimportant in its support of the processes of a wild animal population unless it has substantially high availability. Availability has two important aspects. First, a species of food can be present in the habitat, but it may be unimportant in the size of its contribution to an animal's diet. For example, the foliage of flowering dogwood (*Cornus florida*) is a highly palatable forage for deer. Considering that a deer can only forage to a height of about 1.5 meters above the ground, if very little of the dogwood foliage is located below this level, then the species is present but the palatable part of the plant is relatively unavailable. Thus the contribution of dogwood to the deer's diet in this situation may be quite small irrespective of its presence in the habitat and its palatability.

A second aspect of availability is its synchronization with the changing needs of the animal. For instance, just after coming through the ground, the fronds of bracken fern (Pterdium aquilinum) are palatable to deer and have high concentration levels of crude protein. They are present in the environment at a time when the pregnant does have a very high protein intake demand, but the time lapse from when they first became available in the spring to when the tissues harden and become relatively unpalatable, is only about one week. The length of time in which the plant is available in palatable form is so short that its contribution is not nearly as substantial as its crude protein value would suggest.

The third consideration for a food is its nutritional value. The food may be palatable and available, but what does the animal get out of it when he eats it? There are many aspects to nutrition all of which sum to the potential of the habitat to supply essential components of, or supply directly, the digestible energy, protein, minerals, and vitamins necessary for the support of an animal's life processes.

Unlike advertised breakfast cereals, there are no nutritionally complete foods in the wild animal's environment. The wild animal meets its nutritional requirements by ingesting an array of food items each of which is important to meeting one or more nutritional needs but not all of them. The food array changes in composition and size through the annual cycle as availability and palatability change. It also changes as the nutritional needs of the animal change.

In wild animal nutrition, the three most important aspects of diet items are dry matter digestibility, crude protein concentration, and concentration of minerals, principally calcium and phosphorus. The digestibility of a food refers to the extent to which it can be broken down in the gut of an animal and made available for metabolism. While the concept holds for all organisms, we most frequently see the term "digestible dry matter" applied to herbivore forages. A forage which is 50 percent digestible is one in which 50 percent of the ingested dry matter will be put into solution in the animal's gut. The other 50 percent passes through the gut in an insoluble form.

The most important aspect of the digestibility is that it can be applied to the total caloric value for the food to approximate its potentially metabolizable energy. A simple example is a plant forage which has a total caloric value of 5 Cal/g. If that forage is 50% digestible, then the potentially metabolizable energy content would be about 2.5 Cal/g. This is an approximation to the extent that it assumes that essentially all of the metabolizable energy is coming from soluble carbohydrates. The estimate is inaccurate in that the portion of the plant tissue that is protein is much lower and fats are much higher in metabolizable energy value. However, for most plant tissue, the percentage value for digestible dry matter is a reasonable approximation of the percent digestible energy.

Crude protein is a term describing the amount of actual protein plus all other nitrogen in the ammonia form in a tissue sample. The total amount of ammonia nitrogen present multiplied by a factor of 6.25 estimates the crude protein content of a food. The 6.25 factor is based on the assumption that the nitrogen concentration in proteins averages 16%. The fact that there is more ammoniacal nitrogen present than just that in actual protein molecules qualifies the estimate as one of crude protein. The additional ammoniacal nitrogen is included because the animal has the ability to metabolize it and synthesize proteins.

The principal minerals of interest in the diets of wild animals are calcium and phosphorus. Both nutrients are important for many physiological processes, but their main place of deposition is in bones and teeth. Inadequate levels of either of these nutrients will result in poor skeletal growth. In addition, these nutrients need to be properly balanced in the diet. At improper ratios, chemical reactions can occur that complex the two nutrients in an insoluble compound which preempts the availability of either one for metabolism.

Calcium is rarely, if ever, limiting in terms of its availability in the habitat. Conversely, few plant tissues have substantial levels of phosphorus at any time of year. Moreover, the high levels of calcium can pose the threat of complexing with phosphorus, ultimately causing phosphorus deficiencies. This situation is prevented usually by the wild herbivore feeding on a wide array of plant species and plant parts, each of which has a different chemical composition. Each species then makes its own contribution to the nutrition of the animal.

Water and Aspects of Its Importance

In the chemical sense, water is the universal solvent and is therefore essential to the metabolic processes of all living organisms. To some wild animals, it is the primary feature of their environment. The foods which they eat occur primarily, if not entirely, in an aquatic environment. It may also provide escape cover as well as a barrier to discourage invasion of den and nest sites by predators.

Many wild animals are able to get much of the water they require from the foods they eat. Their needs for free water in the environment are minimal in this respect. Some animals are physiologically adapted to maximize water conservation in their bodies which also reduces their needs for water intake.

The availability of free water depends on four primary factors: climate, weather, season, and physiography. Habitats in humid climates naturally have greater potential for free water than those in arid environments. Droughts obviously will decrease amounts of free water while rainy periods will increase them. During seasons when metabolic activities of plants are high, and transpiration of water through plant foliage is therefore high, moisture uptake by the vegetation will dramatically deplete soil moisture which might have fed springs and streams. Even swamps can be dried out rapidly by transpiration through the foliage in the forest overstory.

The factor of physiography is again a simple one. The coastal plains and flood plains of major river drainages are noted for their amounts of free water. Sandhill regions are noted for their droughty conditions, while the mountains are known for their wide variation in amounts of free water throughout the annual cycle.

The availability of water incorporated in plant tissue varies both with stage of maturity of the plant part and with the environmental conditions at the time of consideration. Young parts are highly succulent. Their percentage moisture may exceed 90. As the plant matures, however, the proportion of its dry matter increases greatly with a concomitant decrease in moisture. Also, if the plant is being stressed by inadequate soil moisture, its moisture content is going to be lower than when soil moisture levels are optimal.

Moisture level varies greatly among plant parts. Foliage has a higher moisture content than stem tissue. Fleshy fruits, of course, are very high in moisture. All seeds contain fairly high moisture levels in their cotyledon tissue. The relative amount of water obtained from a seed depends on whether the animal discards the seed coat and ingests only the cotyledon or if it ingests the whole item.

In summary, all animals have a physiological demand for water intake but the size of the demand and the sources needed by various species vary greatly. The demands for free water in the environment of some species is large and absolute, while for others it has minor importance.

Attributes of Cover

Cover is a term which applies to four basic needs in an animal's life: (1) opportunity for escape from am enemy, (2) opportunity for rest, (3) protection from elements of weather, and (4) opportunity to carry out the process of reproduction with low risk to parent and offspring. Escape cover is a vital need for most animals, although it is greatest for small herbivores and least for the larger predators. The purpose of escape cover is to provide an "obstacle course" which the predator must overcome in order to make contact with the prey. The best escape cover tests all of the sensory abilities of the predator as well as its ability for locomotion.

Resting cover may be any situation in which the animal feels sufficiently secure to relax. Acceptable resting cover varies greatly among species of animals, between day and night periods, seasonally, and changes in the animal itself, such as changes in its protective coloration.

Cover chosen because of its ability to protect the animal from the elements of weather substantially overlaps that which might be chosen for rest. It is a narrower array of situations within the habitat, however, because in addition to being a secure place, it must also function to prevent excessive loss or gain of body heat. Burrowing animals find dual purpose cover in their underground dens. Some other animals find protective cover through the selection of a desirable structure in the vegetation.

The attribute of cover to offer the opportunity for reproduction has primarily to do with the provision of a suitable site for birth and nurture of the young. The need for this resource is maximum among den and cavity nesting species. The young of these species are always helpless when born or hatched. They have little ability for locomotion and usually have no hair or feathers for protection from the elements of weather. Usually these species are restricted to single, small litters per annual cycle. Species which reproduce in situations where selection of cover for the site of birth and care of young is not exacting have one or more of the following characteristics: (1) the young are highly precocial, (2) protective coloration and behavior of the young is highly evolved, or (3) the species' reproductive capacity is large.

Combinations of cover requirements vary greatly among species. For example, the cottontail rabbit (Sylvilagus floridanus) which has minimal cover requirements for nesting is fairly demanding for good escape cover in its habitat. In contrast, the osprey is fairly exacting in its demand for a dead tree near water for nesting, but otherwise feeds and moves about in an environment almost totally lacking in escape cover. Still another set of circumstances exists for the white-tailed deer where the animal's sensory abilities, speed and agility, and the qualities of its coat for insulation and protective coloration minimize its needs for cover. However, the degree of success of a deer population is in part dependent upon these minimal needs being met. When its contact with man is likely to be frequent, the deer is going to be more successful with good cover than without it.

Changes in Habitat Resource Abundance

Habitat resource abundance changes temporally (with time) and spatially (across the landscape). Temporal changes are of two types. First, successional changes occur over time periods that may vary in length from a few years to a few centuries. Particular lines of successional change are called seres and each recognizable phase in this series of changes is called a seral stage. Each seral stage will have its own set of attributes in terms of the animal species to which it can offer niche components.

The second type of temporal change is seasonal change. Within a given seral stage, the seasonal changes are repeated in a general nature with each new annual cycle. Resource abundance changes drastically between seasons. These seasonal changes often cause shifts in levels of importance of different seral stages making up the habitat of an animal.

Spatial changes are the result of the occurrence of different environments at different locations on the landscape. Communities in different environments tend to have different species arrays and different structures. Spatial diversity indicates how habitat components are distributed across the landscape and consequently how species and populations of animals will be distributed.

Temporal Changes (Succession)

Time frames for succession and consequent habitat changes are determined primarily by three criteria: (1) the ability of the environment to support plant production, (2) the tenacity of a community in continuing to occupy a site, and (3) the competitive abilities of potential invader species that may create new communities. Succession continues until a community develops that is harmonized with the abiotic influences of the environment, e.g., rainfall, soils, exposure, etc. When this state of harmony is reached, the condition is called climax. In this condition the community has no net changes in biomass. That is, annual losses to death and decay equal net gains from reproduction and growth.

The most common type of succession with which the wildlife manager deals is secondary succession. Secondary succession begins when a site is drastically disturbed by either natural catastrophe or by man's actions but enough viable plant parts are left on the site to influence the composition of the first community to develop. This contrasts with primary succession which, in the strictest sense, begins with lichens and mosses on bare rock or at least on soils devoid of any living organisms.

In the eastern United States, one of the most obvious examples of secondary succession is that beginning with old fields on upland soils. Typically these areas go through a grass/herb stage to a stage in which seedlings of hardwoods and pines dominate the site. The third stage is the thicket stage in which the grasses and herbs have largely disappeared due to their being outcompeted for growing space by high shrubs and tree seedlings. The fourth stage is a pole stand of mixed pine and hardwoods. As the individual trees get larger, the short-lived hardwoods fade out, leaving the long-lived hardwoods and pine. The pines will die out in 100 to 200 years and the long-lived hardwoods will be the climax stand.

Think of how many times and in how many ways habitat components changed over the time period just described. In each recognizable stage there were changes in availability and distribution of energy and nutrients for ingestion by wild animals and cover for rest, protection, and reproduction. The most flexible species of birds and mammals were present in every stage, although their population densities probably oscillated over time. The most exacting species were found only in one stage.

Try the exercise of imagining yourself as a species of wild animal with specific food and cover requirements. Would you have been present throughout all of these stages? In which stages would your population density have been highest and in which would it have been lowest? What habitat factors might have been limiting you in each stage?

Temporal Changes (Annual)

Seasonal changes in habitats determine how animal utilization of a given location will fluctuate through the annual cycle. The distribution as well as total quantities of available energy, nutrients and cover will change as seasons change and wild animals must concomitantly redistribute themselves with these changes. For example, in summer, a mature oak stand with a light understory will offer forage to a few browsing species, species foraging on insects in wood, and species which glean insects from foliage. In years of a good acorn crop, fall utilization will include every species which can make use of acorns as forage and the predators that prey on them. Foliage gleaners may be absent or nearly so in fall and winter and populations of other insect feeders will be low.

Consider how the habitat components change through the year. If we begin with herbivore diets in spring, we find that, in general, protein concentrations in forages are at their highest levels of any time in the annual cycle. This is also true of forage digestibility. Herbivores are physiologically synchronized to take advantage of this habitat feature by having their young during this period. Thus, they match protein and energy demands for lactation and growth of the young with availability in the habitat.

Through the spring and summer, digestibility and nutrient levels (except for calcium) decrease in forages, although the total amounts of dry matter in forages steadily increase. By late summer to early fall, foliage tissue has become highly lignified and is at its lowest point in nutritional value. Hard masts are now becoming available. The cotyledon tissue of hard mast is composed primarily of simple carbohydrates which are highly digestible. Once again physiological synchronization with environmental changes becomes very important because this is an energy storing period for herbivores. Their appetities are ravenous and metabolic processes are adjusted so that large amounts of energy are being stored in the form of fat.

In the winter period, energy, nutrients, and cover will be at a premium for most species. Animal movements will be minimized and there will be a substantial loss of appetite, again synchronizing the annual low in demand with the annual low in availability. Energy for maintenance will come from catabolized fat stored during the high energy availability period. Young animals and unborn fetuses will grow very slowly during this period.

When the influences of spring once again begin to improve the habitat quality, appetites increase and there is a greater availability of high quality forage, particularly with respect to protein. Growing animals grow faster, fetuses grow faster, and females in the population are capable of extracting from the habitat those components necessary for their own maintenance and for the growth and maintenance of their dependent young.

The temporal changes within the annual cycle have caused certain species to redistribute their patterns of utilizations of the landscape. The reaction to these changes in some species was reflected by changes in population densities. Migratory species cope with these changes by alternate abandonment (emigration) and re-population (immigration) in each cycle.

Spatial Changes (Diversity)

Spatial changes in habitat are usually referred to by type and level of diversity. There are three main types of habitat diversity. Alpha diversity refers to the complexity of a given community or stand. It includes the factors of: (1) horizontal structure (patchiness), (2) vertical structure (layering), and (3) species and species group array. For animals whose habitat is made up of more than one community, alpha diversity describes the most basic unit when one considers habitat change. The second type of spatial diversity is beta diversity and is indicative of the array of community types within some defined area of the landscape. The area may be naturally defined as the boundries of an island or some given slope aspect on a mountain, or the area of movement of a given animal. The area may also be politically defined, as in the case of park boundaries.

The third type of diversity is referred to as gamma diversity and is used in a geographical region context. It tends to accent measure of gross change over very large areas and is primarily important in considering the potential of a region to support an array of species as opposed to the potential to support given population densities of a species.

When considering what diversity means, we must remember that highly diverse systems have higher probabilities of containing large arrays of wild animal species than those of low diversity simply because they contain larger numbers of habitat niche components. Large numbers of components mean that there is a large number of possible combinations of components. The habitat niche for a species is specified as the combination of components which it requires for growth, maintenance, and reproduction.

Alpha diversity is most important in indicating the size of the species array that might be accommodated in a given community within a given season. Beta diversity, however, will indicate the size of the species array that can be accommodated on the landscape throughout an annual cycle. High beta diversity accommodates the needs for shifts in habitat utilization patterns as temporal changes in given communities and animal species needs occur.

Chapter 2. SPECIES and POPULATIONS

Wildlife is the array of animal species living in a wild environment with no direct dependence on man for success in life processes. Discussion of wildlife resources may be in the context of the whole array of species in the system or it may focus on a single species or group of species. When thinking in terms of the whole array, or at least a substantially large portion of it, one thinks in terms of ecological function. Is a given species predator or prey? What assets and liabilities does a species contribute to the system? Is a species flexible or exacting in niche component requirements? How many niche components does it share with other species? Are there any species with which niche overlap is very large? What is its competitive ability for niche components? What is its reproductive potential relative to that of its competitors? These questions have a synecological perspective, i.e., how does the system perceive the animal or what is the animal's place in the system.

Normally when one focuses on a single species or group of functionally similar species, the approach is termed autecological. That is, how does the animal perceive the system? This type of thinking is largely concerned with the biology of populations. What population size can the system accommodate? What is the age and sex composition of the population? What is the nature of behavioral interactions among group members? What factors cause population growth or decline? What are the specific requirements for growth, maintenance, and reproduction in individuals?

This chapter will point out species attributes important to management considerations and elementary aspects of population biology. Hopefully, it will develop a perspective and level of knowledge that will enable the reader to inquire about inter-species and intra-species relationships.

Reproduction

Reproduction is the process of a species sustaining itself. Reproduction strategies vary widely among species. Strategy success is guided by the principle that the best method is that which has the highest probability of providing future breeders, considering the characteristics of the environment in which the species lives and its ability to find and compete for essential niche components.

There are five major sequential periods in animal reproduction: (1) pre-breeding period, (2) courtship and conception period, (3) gestation or laying and incubation period, (4) partuition or hatching period, and (5) offspring dependency period. This series of events is iniatiated and influenced by a number of environmental factors. The most common major factor initiating breeding is change in photoperiod (day-length). There are three possible ways in which change in photoperiod may stimulate reproduction: (1) increasing photoperiod length, (2) decreasing photoperiod length, (3) change in rate at which photoperiod length is changing. While photoperiod is usually thought to be the most common causal factor in stimulating breeding, factors such as light intensity, temperature, and rainfall can also be of substantial influence.

The pre-breeding period is initiated in a wild animal when environmental factors elicit a physiological response. A syndrome of processes is begun, at the core of which is the production of sex hormones. This syndrome may be manifested in the following ways: (1) increased appetite and weight gain, (2) increased interest in the opposite sex, (3) restlessness, (4) movements aimed at encountering the opposite sex, (5) agonistic behavior among males, (6) establishment of a breeding hierarchy and determination of dominant breeders, and (7) establishment of breeding territories. Every species will be characterized by two or more of these phenomena.

The courtship period is a transition from the processes that prepare for breeding to actual mating and conception. Courtship is the act of pursuing a mate. It is almost always a process dominated, in terms of energy expenditure, by the male, but the female determines how successful it will be. The courtship period is an energy-draining period, particularly for males of most species. Libido (the urge to breed) determines the mode of behavior and over-rides even appetite in many species, causing energy expenditure to exceed energy intake.

Courtship behavior takes many forms. Wild canids (dogs) and felids (cats) are noted for their playfulness and wooing in their courtship. Some species of birds attempt to entice a mate with gifts of food, while others use strategies involving vocalizations, dances and displays of colorful plumage. A male white-tailed deer will simply pursue a doe until she will stand and receive him.

The length of time over which courtship takes place, the intensity of courtship, and the nature of related social interactions are species dependent. However, in practically all species, the male will initiate courtship and when he does, he is already prepared and anticipating copulation; but it will be the female that will determine when copulation will take place. Since females, particularly among mammals, are only going to be receptive periodically to copulation with the male, it is important that the male be ready whenever she is receptive. If males were able only to breed at certain times within the breeding season, one can imagine the effect that the problem of synchronizing female receptivity with male readiness would have on productivity rates.

The desire for courtship is completely controlled by hormones in both the male and female animal. The endocrine system will also control sperm and egg production and determine the time at which the female will receive the male. Only the most elementary aspects of the endocrinology of reproduction can be mentioned in this book. Many large texts have been written on this part of animal ecology alone.

The physiological process associated with breeding among adult animals begins with environmental factors stimulating the hypothalamus gland to secrete substances which in turn stimulate the anterior pituitary gland to release the hormones FSH (follicle stimulating hormone) and LH (luteinizing hormone). FSH stimulates the secretion of estrogen from the ovaries. This hormone controls sexual behavior. It also stimulates the growth of egg follicles in the ovaries of the females and the production of sperm in the testes of males. In females, LH stimulates ovulation, i.e., rupture and movement of the egg follicle from the ovary, through the oviduct, then into the uterus of mammals where it can be fertilized. In males, LH stimulates the testes to secrete androgen which controls sexual behavior.

The physiological changes that begin in the pre-breeding period and are manifested in the sexual behavior of the courtship period synchronize the male and female into a state of readiness for successful mating (copulation that leads to conception). Conception occurs when a sperm cell unites with an egg cell to form a zygote (a single cell formed by the fusion of two cells). The formation of the zygote is the beginning of pregnancy in mammals and the establishment of a fertilized egg that has the potential to be successfully incubated in birds.

The zygote will reproduce itself in a process called mitosis. The multi-celled organism that develops from this single cell is called a blastocyst in mammals. In most mammals, the blastocyst attaches itself to the wall of the uterus fairly quickly and the process is called implantation. Before implantation the blastocyst is nourished by fluids in the uterus. Afterwards it is nourished through the circulatory system of the mother.

Some mammals undergo a process called delayed implantation where there is a substantial time lapse between conception and implantation. Mink (Mustela vison), least weasel (Mustela rixosa), river otter (Lutra canadensis), and black bear (Vrsus americanus) are some of the mammals that are capable of delayed implantation. The ecological function of this process is to allow breeding at an opportune time (possibly related to the effect of nutrition on ovulation) but delay the demands of a developing fetus and subsequent dependent offspring to a season when the probability is highest that the demands can be met.

In birds, following egg fertilization in the upper part of the oviduct, the yolk containing the blastoderm descends through the oviduct. As it does so, it is surrounded by albumin, which will be important to the nutrition of the embryo. It is then surrounded by a shell membrane, then a shell, after which it is soon deposited in a nest where incubation will begin. Obviously the length of time between when the first egg is laid and incubation begins depends upon clutch size which is species dependent.

The term gestation, as applied to mammals, is the period of time from the formation of the zygote until parturition (birth of the fetus). Incubation differs from gestation in that it is the length of time from when the female bird begins to brood her eggs until they hatch.

Another interesting comparison between birds and mammals is how they care for the developing embryo and prepare for its nurture outside the shell or the womb. In birds, the nutrition of the embryo is provided by the chemical composition of the egg yolk and albumin. These are highly proteinanous but with sufficient amounts of carbohydrates to provide energy. Development of the bird embryo is really a process of protein transformation within a closed "cell".

An essential to incubation is heat which is conducive to the biochemical reactions which must take place within the egg. This heat usually comes from the body of the bird brooding the clutch. During the pre-breeding period, females develop a "brood patch" which is an area on the breast and belly where blood vessels are concentrated and become engorged with blood. The feathers are shed from this area so that when the bird sits down on the eggs the amount of heat transferred from her body directly to the eggs is maximized. In species where the male also assists in brooding eggs, he too will develop a brood patch.

In mammals, the health of the embryo is more directly dependent on the health and nutritional status of the female. Once the blastocyst implants, a placenta begins to form around it inside the uterus. Nutrient transfer from the mother must be across the placenta and through the navel cord of the fetus. This is called placental transfer. The placenta serves in part as a filtering device that will screen out many types, but not all, potentially pathogenic organisms and toxins.

Growth of the fetus is relatively slow at first and gains momentum with time. The latter part of pregnancy is when growth and development is most rapid. Deer nutritionists and physiologists will frequently refer to the third trimester of pregnancy because it is in the last 60-70 days that the nutritional intake demands on the doe to support rapid growth of the fetus is greatest.

In addition to increased demands for fetal growth, the pregnant female must prepare for lactation in order to nourish the neonate (newly born). Lactation itself is a demanding physiological drain. Between the demands of the two processes it is easy to see how important habitat quality is in this stage of the annual cycle.

Hatching in birds and parturition in mammals are comparable processes in that organisms previously sheltered and nurtured in a closed or semi-closed environment now are exposed essentially to the same environment as their parents. Neonates are of two major types. Precocical young are those born or hatched with some type of insulation (hair or down) and are ready to leave the nest or bed quickly. Altricial young are almost completely helpless. They are born naked, and their eyes are closed for some days. They are incapable of only the most modest type of locomotion, and they are completely dependent on parental care for nourishment.

Precocial young are those normally living in a high risk environment such as hatchlings of ground nesting birds (e.g., bobwhite quail (Colinus virginianus), ruffed grouse (Bonasa umbellus), turkey (Meleagris gallopavo) and, among mammals, deer (Cervidae) fawns. Altricial young can be accommodated where their place of birth is reasonably well protected, as among denning mammals (red fox (Vulpes fulva), bobcat (Lynx rufus), gray squirrel (Sciurus caroliniensis)), and cavity nesting birds (common flickers (Colaptes auratus), eastern bluebird (Sialia sialis), tufted titmice (Parus bicolor)). Species of birds capable of placing nests on tree limbs that will be difficult for predators to negotiate will have altricial young as well as colony nesting birds. The latter ecologically can afford altricial young by placing nesting areas on land forms difficult for predators to reach. In addition, they can discourage predation by their sheer numbers.

Weaning in mammals and fledging in birds are functionally similar. Weaning is when the female mammal ceases to allow the young to be nourished by nursing. From that point on, nutrient intake by the young animal must be directly from its habitat. Weaning is a nutritional regime term and cannot be used to generalize about the ending or continuing of social interactions between parent and offspring. In species that breed more than once within one annual cycle, weaning may signal the end of social bonding between the parent and offspring as with rabbits and squirrels. In other cases, the offspring may remain with the mother for one or more annual cycles and may or may not be allowed social interactions with future offspring from that parent. In general, herding, flocking or family grouping species that are not migratory tend to continue social interactions with offspring longer than species that tend to be individualistic or migratory.

Fledging is when young birds are forced to decrease their dependency on parental care, although parental care even to the extent of some direct feeding may continue for awhile. Fledging is a term applying to altricial species because young of precocial species are rarely fed by their parents. They will be directed to sites of food availability, but obtaining it for ingestion is completely their task.

In his text, The Ecology of Reproduction in Wild and Domestic Mammals, R.M.F.S. Sadleir categorized breeding seasons into six categories. Four of these categories can be used when thinking about the ecology of reproduction in wild animals in North America. The fixed "optimal season" as used by Sadleir is a reference to the period of the year when the environmental constraints on the successful development of the young are minimal and the habitat qualities that support development are maximal. In the northern temperate zone this is usually thought of as spring and summer. The four applicable categories are as follows:

1 Length of time from conception to weaning longer than a single optimal season. Conception occurs when the environment is deteriorating in terms of accommodating the neonate but birth occurs when the environment begins to improve again. Example: white-tailed deer.

2. Length of time from conception to weaning is short enough to occur in one fixed optimal season. Conception occurs when the environment is improving or the time until improvement will begin is quite short. Example: beaver (Castor canadensis), red fox, striped skunk (Mephitis mephitis).

3. Length of time from conception to weaning is short enough for two or more conceptions to occur during a single fixed optimal season.

These are normally referred to as multiple-littered animals. Parental care of young after weaning is minimal if it exists at all. High birth rates while the environment is optimal is the mechanism for offsetting high predation rates. Example: cottontail rabbit, gray squirrel, most mice (Cricetidae), and moles (Talpidae).

4. Length of time from conception to weaning is relatively unimportant, as the optimal season continues throughout the year. The incidence of breeding may vary, but conceptions are found in every month. Examples: Florida panther (Felis concolor), bobcat, wild hog (Sus scofa).

Species that synchronize stages of the reproductive process with seasons of the year are called synchronous breeders. Those that do not are called asynchronous breeders. The degree of synchrony in synchronous breeders that are not migratory changes as seasons become less distinct. For instance, at the northern latitudes of the geographical range of the white-tailed deer, probably 90 percent of the fawning occurs in a two- to three-week period. In comparison, fawning in southern Florida has no comparable peak in time but is drawn out over many months. The obvious difference is in the length of the optimal period and how drastic the constraints can be in the period of greatest stress.

Species that are asynchronous breeders are among the most difficult to deal with in wildlife management. There are dependent young in the population at all seasons of the year which makes population monitoring and the implementation of humane control measures difficult to impossible. Most feral animals and some exotics are asynchronous breeders. A notable example of such a problem species is the wild hog.

While Sadleir's types of breeding seasons were formulated primarily for mammals, they also have some use when considering reproduction in birds. Essentially all wild bird species in North America fit into Categories 2 and 3. Some southern raptors, e.g., bald eagle (Haliaectus leucocephalus), red-shouldered hawk (Buteo lineatus), and great horned owl (Bubo virginianus) are winter nesters but would still remain in Category 2. The robin (Turdus migratorius) and the mourning dove (Zenaida macroura) are the most common examples of birds in Category 3.

Types of pair bonding are important to consider when thinking about reproduction in wild birds and mammals. It refers to fidelity between mates and it varies widely among species. There are three main categories of pair bonds, two of which have easily defined sub-categories. They are defined as follows:

I. Monogamy (paired to a single mate)

A. Paired for life or at least several successive breeding seasons. Examples include whistling swan (*Olor columbianus*), Canada goose (*Branta canadensis*), bald eagle, red-shouldered hawk, red-tailed hawk (*Buteo jamaicensis*) and raven (*Corvus corax*).

B. Paired for one season which may result in one or more broods or litters. Examples include ducks (*Anatidae*), most songbirds, beaver, otter, and red fox.

II. Polygamy (paired with two or more mates)

A. Polygyny (male with two or more mates) Examples include red-winged blackbird (*Agelaius phoeniceus*), eastern meadowlark (*Sturnella magna*), and elk (*Cervus canadensis*).

B. Polyandry (female paired with two or more mates). No known example in the eastern United States.

III. Promiscuity (no pair bounding; mating is completely opportunistic). Examples include grouse, turkey, woodcock (*Scolopax minor*), white-tailed deer, raccoon (*Procyon lotor*), and grey squirrel.

In this section we have only briefly touched on a few of the important aspects of the ecology of reproduction in wild birds and mammals. It is a fascinating subject and critical to an indepth appreciation of animal ecology. The reader is encouraged to thoroughly familiarize himself with the characteristics of reproduction of the species with which he is dealing on a management area.

Longevity

Life expectancy or longevity is an important consideration when thinking about the characteristics of a species and its population dynamics. There are two types of longevity. Physiological longevity is the span of time that an animal can live in an optimum environment where it is protected from death by causes other then natural physiological decline. Well-cared-for penned animals are frequently used as references for physiological longevity.

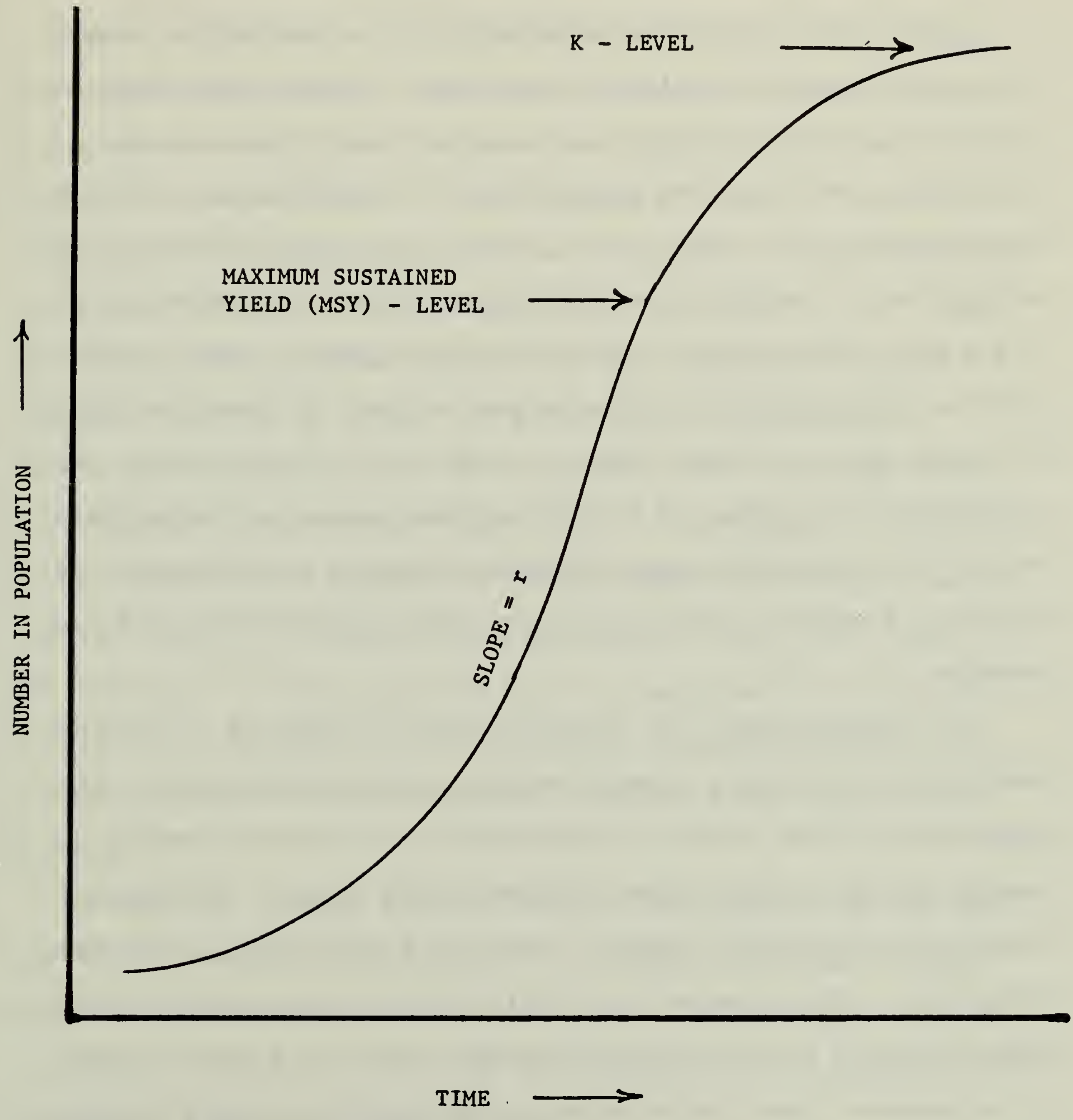
In comparison, ecological longevity is the life expectancy of an animal in its natural environment where it is exposed to all of the agents that may cause death and are innate to the system. Obviously ecological longevity is a shorter time span than physiological longevity for every species. Ecological longevity may also vary considerably among populations within species that occur over a wide range of environments, habitat conditions, predation pressures, levels of disease incidence, and levels of competition for food and cover.

Normally, the influence of man as an agent causing habitat changes and therefore affecting ecological longevity is accepted as indirect and man is excluded from consideration as an ecological factor. In most cases where man is a direct cause of death (such as in highway accidents and hunting), these factors are excluded as limitations on ecological longevity. This does not mean that these factors are totally ignored in considering management of a population. In fact, they may have a profound impact on mortality rate in some situations. It simply says that these factors are not a part of the animal's natural ecology and, theoretically at least, can be manipulated by changing man's activities.

Population Growth

Ecologists are often heard to say, "Populations tend to increase in a 'sigmoid fashion'." What they mean is graphically illustrated in Figure 2.1. The sigmoid, or S-shaped curve, as a model of population change with time indicates that population change begins increasing at a very slow rate but the rate changes with time. The steep part of the curve indicates that during that time interval the population increase rate is high. The population cannot continue to increase indefinitely, however, so the inflection point in the curve indicates the population level at which the rate of increase begins to decline. The top of the curve is called the asymptote and it indicates the maximum numbers of animals which the system can support on a long-term basis.

Figure 2.1. The logistic or S-shaped curve depicting natural population growth over time.



There are three characteristics to a population growth curve that are of primary importance. First, the slope of the curve at any point in time is the intrinsic rate of increase (r) for the population at that stage of its development and under the prevailing conditions of the ecosystem. Second, the inflection point is referred to as the point of maximum sustained yield (MSY). That is, the population is producing the largest number of young per unit of time that it ever has or ever will. And third, the asymptote (K-level) is the maximum number of individuals which the ecosystem can accommodate due to a combination of habitat resource availability and characteristics of the species.

To understand the growth curve, imagine a vacant habitat to which a few breeders are introduced. The population level which is accounted for by these breeders is represented in the lower portion of the curve. Relative to level of population demand, resource availability is almost infinite. The number of individuals being added to the population is small simply because there is a small number of breeders. But the stresses on the population are minimal in this situation. Productivity is maximal, survival of young is maximal, and ecological longevity is maximal (approaching physiological longevity).

As offspring become breeders while parents remain breeders themselves, the rate of increase becomes greater and greater until the slope of the sigmoid curve is at its maximum in steepness. This steepest area of the curve represents the maximum rate of increase. This rate is sustained until either resource availability or some behavioral mechanism innate to the species begins to suppress the rate at which the population is increasing. This inflection point, or MSY, indicates that the population has reached a point where the ratio of the number of animals being added to the population to the number of animals being removed from it is starting to decline for the first time in the history of the population as depicted by the curve. Limitations of behavior and habitat resource availability are beginning to lower ecological longevity and reproductive success.

When the number of additions to the population and the number of losses are equal, the K-level has been reached. Population reproductive capability or intrinsic rate of increase is matched by the environmental resistance to population growth for that species.

Species of animals are sometimes grouped according to the way their populations change. Species that find optimal opportunities for growth, maintenance and reproduction in just one seral stage that is relatively short lived must be able to reproduce rapidly. Their increase in a short period of time will be phenomenal. As the environment begins to disfavor them, their decline can be equally phenomenal. This type of strategy provides for the loading of good habitats with breeders so that a few will survive to invade newly developed habitats when the current site declines in support capability. Species in this category are referred to as r-selected. The "r" comes from the fact that the most notable aspect of the population growth curve is its steep slope representing high rate of increase. These species remain at high population size almost momentarily and then decline concommitantly with unfavorable changes in the habitat.

The second grouping of species by population growth characteristics is referred to as "K-selected." These species are adaptable to a number of environments and habitats. As a group they tend to be long lived relative to r-selected species, and they may experience several habitat changes in time and space but still be able to successfully carry on the life processes necessary for continuation of the species. The K-level is the most notable portion of their population growth curve. Their characteristic flexibility in habitat component requirements and innate abilities to obtain these requirements give them the ability to achieve population levels that can be sustained for relatively long periods of time.

Species of small herbivorous mammals are good examples of the r-selected group. Typically, they rapidly colonize the grass/herb seral stage of succession and practically disappear as forest vegetation develops on the site. Bobwhite quail are probably r-selected since they are fairly exacting in habitat characteristics under which they reach their highest population densities.

Most predators, both mammals and birds, tend to be K-selected. Behavioral feedback will limit these populations even when the environmental factors are optimal. The white-tailed deer is usually referred to as being K-selected, but like many other large herbivores, it is capable of a process called "herbivore overshoot". This phenomenon occurs when a species is somewhat insensitive with respect to reproductive processes to the population's approach to the maximum level which the habitat can sustain. It therefore exceeds or "overshoots" the K-level and begins to degrade the habitat. Dramatic crashes will occur in these populations with the new K-level being located substantially below the original one. This phenonmenon is common among species of feral herbivores.

Proximate and Ultimate Factors

Factors which influence population changes are of two types and are referred to as proximate and ultimate. Proximate factors are those that affect the vigor and health of individuals. Ultimate factors are those that directly cause death. Some factors, such as disease and nutrition, can be both. For instance, diseases which have an acute nature are ultimate. Examples are rabies and distemper. Other diseases are chronic and primarily debilitory in nature, they lessen the individual's ability to carry out its life processes. Examples are bucellosis and many types of parasites.

In the case of nutrition, obviously the animal must have food or it will die. If the plane of nutrition is sub-optimal, the life processes may be affected but not completely shutdown. If there is no food, death ultimately occurs.

In general, proximate factors include cover, competition for space, sub-optimal nutrition, chronic diseases, environmental disturbance, and non-lethal accidents. Ultimate factors would include predation, starvation, acute diseases, lethal accidents, and hunting.

Relationships Among Individuals

Within a population there are social mechanisms for maintaining order. These mechanisms vary among species. In addition, different species using the same mechanism may use it with various degrees of intensity. Perhaps the most commonly referenced behavioral mechanism is territoriality. Unfortunately, the term territory is often both overused and misused. A territory is the area defended by an individual, a bonded pair, or group for their exclusive use. Defensive behavior is usually expressed against other members of the same species, species that are very similar in appearance, or sometimes functionally similar species, i.e., those that would be in direct competition for some resource that is particularly coveted.

There are many types of territories. The most common among birds are those that are restricted to some aspect of the reproductive period and are referenced by the type of pair bonding. These might be broken down as follows:

I. Single pair-bonded species

A. Courtship, nesting and feeding occur all in one territory but territorial defense breaks down at or soon after fledging. Examples include robins, bluebirds, titmice, wrens, etc.

B. Territory contains nest only and is used only for incubation and brooding. Often only a few square feet in size. Examples include colonial nesting birds such as terns, gulls, etc.

II. Polygamous species

A. Territory is established by the male for courtship and breeding only. Location of the nest has nothing to do with territorial defense. Examples include woodchuck and ruffed grouse.

B. Territory is established for courtship, breeding, and nesting. Feeding is not restricted to the area. Best example among southern species is the red-winged blackbird.

A few species maintain some sort of territory throughout the year, although the sizes of these defended areas vary substantially from season to season. The red-cockaded woodpecker (Picoides borealis) is a typical example.

Ornithologists sometimes refer to categories of bird territories as types A, B, C, or hybrids of these types. A generalized description would be as follows: Type A--Feeding and nesting territories which include courtship, nesting and most foraging; Type B--nesting territories which include courtship and nesting space, with most foraging occurring elsewhere; and Type C--very small nesting territories, as in colonies in which courtship occurs and where the nest is located.

Territoriality is not nearly as common among mammals as it is among birds. The beaver represents an example of a socially grouping animal that establishes and maintains territory throughout the annual cycle. A male mink will defend a breeding territory but he may accommodate more than one female in it.

Two adult animals fighting or in some form of agonistic behavior does not mean that territorial defense is being acted out. Most frequently among mammals and sometimes among birds, this process is one of dominance determination. For instance, the most well-known feature of the rutting period in white-tailed deer is agonistic behavior. Confrontations with other males, however, is a process of determining who the dominant breeder is going to be. The chasing of a sub-dominant male by a dominant male simply prevents the contact of the former with a doe which the dominate is pursuing with the expectation of copulation. The sub-dominant buck is not being excluded from a defined area, instead, he is being socially restricted when in the presence of the dominant buck. The process is somewhat similar in the wild turkey.

The terms territory and home range are frequently confused. As previously indicated, territory is a defended portion of the landscape, but the nature of the behavioral phenomenon varies widely among species. The ecological function of territoriality is not clearly defined. Traditionally, ecologists have reasoned that it is the method by which habitat resources are divided among the strongest and most capable breeders. The logic seems sound, yet there are so many exceptions and contradictions to this explanation that its purpose probably should be judged on a species by species basis.

In contrast, home range is the area used by an animal in the process of meeting its needs for food, water, cover, space, and a chance to reproduce. The period of time during which this area is covered must be specified because few, if any, wild animals will cover the same area in one day that it would in one month, one season, or one year. Home range size varies among seasons and among individual seasons within individuals. Habitat component distribution, as determined by the nature of the system. The activities of man, can also affect the variation in home range size within a species.

Relatively few species of terrestrial animals in the world are nomadic in nature. That is, very few wander aimlessly on the landscape. For most species it is ecologically prudent to have an area with which they can be well acquainted as to where food, water, and cover are available, and to generally restrict their movements to that area. Assuming that habitat resources are generally well distributed over the landscape, the efficiency of this process in exploiting them versus one of random wandering and random discovery is obvious for most ecosystems.

Territory and home range, in terms of the defined area on the landscape, may be synonymous for some species such as the red-cockaded woodpecker. In others, only a portion of the home range is defended as territory during the breeding season (example: red-winged blackbird in nesting season). In still others, e.g. the white-tailed deer, home range movements can be well defined, but there is no territory.

Relationships Between and Within Species

Trophic Structure

The term trophic structure refers to how energy and nutrients flow through the ecosystem. Early ecologists described the pathway of flow as the food chain. More recently it has been called the food web because of an increased awareness of a great number of species that might function at more than one trophic level.

Ecologists differ in the details of how they describe trophic structure. For the purpose of this text, it will be described as having four levels--primary producers, primary consumers, secondary consumers, and decomposers. Primary producers are green plants which convert radiant energy (sunlight) into chemical energy which can be metabolized by an animal. They also function to take nutrients from the soil and concentrate them in tissue which a consumer or decomposer will utilize and then return them to the system. The primary producers are termed autotrophs because they are not dependent on the tissues of other organisms for their sustenance.

Primary consumers are herbivorous animals. They compose the first level of feeders to convert the nutrients and energy incorporated in plant tissue to animal tissue. Secondary consumers are carnivorous animals whose nutrition is primarily dependent on the energy and nutrients in the tissues of other animals. Decomposers are the micro-organisms responsible for the final breakdown of tissues into elemental forms or at least simpler compounds (usually gases). Nutrients are returned to the system and energy is released to the universe. Primary and secondary consumers and decomposers are heterotrophs because they are totally dependent on the tissues of other organisms for their nutrition.

Trophic structure is simple in concept; however, when one attempts to outline the functions of a given species in the system, it becomes somewhat more complicated. Omnivorous animals (those that feed on plants as well as other animals) are among the most difficult with which to work in this context.

Competition

Competition is a part of the struggle for survival in the wild environment. It occurs among individuals within a species and among species where niche overlap occurs. Competition for food and/or cover required for reproduction is the most common and the most severe.

Within a species, dominant animals have first claim on the food resources. Social structure will determine the nature of this hierarchy. Using deer as an example, the hierarchy for feeding at a site when the supply of forage is low relative to the number of animals to be fed is as follows: large bucks, smaller but mature bucks, old does (family group leaders), younger but mature does that are offspring of the old does, young of the year (both bucks and does). Very young and very old animals are the weakest competitors and will be the first to perish when the supply of forage is inadequate.

Another dimension to competition is in the realm of winning battles versus winning wars. Large-bodied animals will have the ability to usually dominate smaller animals in the competition process. On the other hand, it takes more energy and nutrients on a per animal basis to maintain a large-bodied animal than a small-bodied animal of the same species.

This phenomenon has been acted out in some feral hog populations. Populations of feral hogs that have had a history of high densities almost never have average weights within an age class that are comparable to those in populations recently established and in which competition for forage never has been severe. In very old populations of these animals there has been a selection for individuals that have a low nutrient intake requirement for maintenance and reproduction. In addition, they have been selected for the ability to store energy taken in that was in excess of maintenance and reproduction needs. This energy is stored in the form of fat and can be catabolized when metabolizable energy in the environment is inadequate. If the "naturally selected" animal was put in direct competition with a well-bred domestic hog of the same age, the domestic animal might outweigh the wild one by three to four times and would, by brute force, dominate the food supply. On the other hand, in the wild environment the domestic hog's intake requirements for maintenance would be so high and his fat storage mechanism so underdeveloped that in times of severe food shortage he would perish while the wild animal would survive.

The ecological strategy here has been to develop the optimal ratio of nutritional demand to habitat supply when periods of short supply could certainly be anticipated but not predicted as to timing. This strategy required an integration of behavioral and physiological characteristics that allowed the individual to put a higher priority on surviving periodic drastic changes in the environment than on winning every direct confrontation with a competitor, especially those competitors less well fitted to coping with drastic changes in food supply.

Theoretically, competition should provide a feedback mechanism to limit population growth when the ratio of demand for habit resources to the supply of those resources reach a critical level. (The inflection point, or MSY, on the growth curve.) Feedback may be in one or more of three forms. First, inadequate nutritional intake will lead to a decline in nutritional condition and possibly reproductive capability. Second, in species where certain site characteristics are critical for reproduction and these sites are used up, continued competition to take or hold on to a site may reduce reproductive success. And third, in territorial species, competition for space can become so severe that the feedback in emotional stress can cause a decline in physiological health, increase vulnerability to predation, and decrease reproduction.

Predator-Prey Relationships

It is a popular misconception that predators evolved with the purpose of controlling prey. This is about as logical as saying that green plants evolved for the purpose of using up sunlight, carbon dioxide, and water. More appropriately, we might say that predatory species evolved in response to the availability of energy and nutrients in prey species.

Populations of predators are more regulated by the availability of prey than are populations of prey regulated by predators. For example, large populations of mice and voles may exist in grass-herb fields from which all predators are excluded. If some predators were confined to these fields and all of the prey were removed, the predators would soon starve. This does not say that predators do not influence prey populations, it simply says that, in general, the influence is not nearly as profound as is usually believed.

Several aspects should be considered when thinking about predator-prey systems. First, how large is the array of prey species? If there is a large number of species which are potential prey in the ecosystem, then the removal of any one species may not be critical. For example, foxes may feed on mice, voles, birds, rabbits, squirrels and some insects as well as on some plant matter. One facet of this array of food resources could disappear but other alternatives would be acceptable as compensation, provided they were in adequate supply. In contrast, the Everglades kite (*Rostrhamus sociabilis*) feeds exclusively on apple snails (*Pomus depressus*), a prey whose availability has tremendously diminished. The result has been the near extinction of this bird in North America.

The other side of this coin is where the population level of prey species is such that losses of only a few individuals means a significant percentage loss. This situation may exist with raptor predation on fox squirrels in open forest habitat. The raptors which hunt these areas take a variety of prey, but because of low numbers of fox squirrels, even occasional predation on the species may be an important supressant to population growth.

The second aspect of predation is the availability of vulnerable prey. This is the integration of two factors: (1) numbers of potential prey, (2) ability of the potential prey to resist the predator. The first of these factors mainly has to do with probability of encounter. As the population density of a prey species increases, the probability that a predator will encounter a member of the species becomes larger. It follows then that the greater the number of encounters the more important that particular prey species will be in the diet of the predator.

Several factors could keep this change from being linear. First, the development of a "search-image" on the part of the predator is important. At this point, the predator is not taking the prey on random encounter but has developed a conditioned response as to where, when, and how to look for a food reward of a particular kind. High abundance of opportunities initiated the process, but success reinforced and refined it.

A second factor causing the change to be non-linear is called "threshold of security". The threshold of security in the population level at which space and/or escape cover have become limiting. The stress of intraspecies competition over space and cover that is inadequate for the population size can make prey more vulnerable than they would be when these resources were adequate. In most species, it is only as the population level climbs above the threshold of security that predation becomes an important control mechanism.

Resistance to predation may come through two categories of mechanisms. The first category is the prey's ability to resist detection and may involve strategies such as cryptic coloration, suppressed scent emission, and freezing behavior. The young of deer and of birds such as quail, turkey, and grouse use these mechanisms. Another category involves the emission of offensive odors. Examples of such species would be skunk, weasel, and mink. The third category involves escape by speed of flight or agility in seeking refuge. Most adult birds depend on winged flight while some species of mammals such as deer and rabbits attempt to outrun their potential predators. Some large rodents such as squirrels and woodchucks (Marmota monax) have tree and ground dens to which they may hastily retreat when pursued.

The direct confrontation of the predator occurs occasionally in deer, usually among carnivorous mammals, some species of birds particularly when defending young against raptors, and among raptors themselves. One type of direct confrontation is called "mobbing behavior". The most common example is that of crows attacking hawks or owls. Mobbing is usually an event initiated by potential prey species as a mechanism to drive the predator from the area in a predation preventive measure.

The well known "crippled wing" act of birds seeks to lure a predator away from a nest of young. While most birds exhibit this behavior it is probably most effective against carnivorous mammals. Most predators such as snakes, jays, crows, and squirrels are little affected by what might appear to be the easy-to-capture crippled adult. It may be effective in the protection of precocious, ground-dwelling birds where the young are distributed through the cover of at least a small area and have additional protection from cryptic coloration and freezing behavior.

The ecology of predator-prey systems has been widely studied and debated. The effectiveness of predators in controlling prey populations has been illustrated in some cases but not in others. Five categories of effects which predators may have on prey populations are as follows: (1) no effect, (2) enhancement of population growth, (3) enhancement of population stability, (4) cause of population decline, (5) population eradication.

First, predation will have no effect or at least a negligible effect on the prey population when a small percentage of non-breeders that have little to no potential for breeding are being removed. This would be the case where the prey species has a very high reproductive capacity and its population may erupt dramatically but somewhat unpredictably. The predator has other prey alternatives and is being opportunistic. Individual prey tend to have a low probability for survival even in the absence of predation. This sometimes happens when populations of ungulates are rapidly expanding. In this situation, environmental resistance to the growth of the prey population is low and the intrinsic rate of increase of the predator is far below that of the prey.

Predation may enhance population growth rate when it is concentrating on individuals that are liabilities to the prey population and removing substantial numbers of them. Individuals that are liabilities are those chronically weak and/or sick, who produce offspring with poor genetic quality but who would otherwise continue to compete for habitat resources with the healthy individuals.

The role of predators as population stabilization agents primarily occurs at prey population levels above the threshold of security or the MSY point on the prey population's growth curve. Environmental factors, including the decline of the habitat resource availability below optimum conditions, are making the prey more vulnerable. The predator population has expanded to a point to where it is probably being controlled by minimum space requirements (minimum territorial area acceptable). By this time a search-image has been well developed. Predation is an important cause of mortality in the prey population and the prey species is a very important part of the predator's diet.

Predation becomes an important cause of prey population decline usually when the prey are concentrated in an easily defined habitat that is not extensive in area. Predators find it convenient to focus their efforts on these areas and possibly several species of predators are simultaneously foraging on the prey.

The eradication of a prey population is likely only when one or both of two factors exist. First, the prey species is already in trouble because it is ecologically poorly fitted to the current environment. Second, the predator is an exotic species, foreign to the ecosystem containing the prey, but when introduced to the system it has the capability to adapt and rapidly take advantage of available resources. Prey species eradication rarely if ever occurs in stable environments occupied only by native species.

Some Other Interspecific Relationships

Several other types of relationships among species are important. One of these is "mutualism". This is a situation where two species coexist with neither being dependent on the other but both receiving benefits from the relationship. An example of such a situation is the relationship between the cattle egret and grazing livestock. The cattle egret (Bubuleus ibis) feeds on many of the larger flying insect pests on livestock as well the herbivorous insects made more vulnerable by the movements of the grazers.

Commensalism is a situation in which the benefits received by one species is not dependent on any negative or positive feedback to the other species. Rats are termed commensal rodents in their relationship with man. They may be harmful to man in an indirect way, but it is not to their advantage to be in this role.

Parasitism among wild vertebrates is probably best illustrated by the nesting habit of the cowbird (Molothrus ater). This species lays its egg in the nest of another bird which has already prepared its own clutch for incubation. The cowbird may even cover the eggs already in the nest with debris. The cowbird egg is incubated sometimes at the expense of the other eggs. Even if all eggs hatch, the cowbird hatchling is frequently the largest and strongest of the hatchlings and therefore dominates the nest when the adults bring food to it. Usually the other hatchlings die and the cowbird lives to be fledged. In this relationship, incidence of success in one species is dependent upon incidence of failure in another.

Parasites and Diseases

The level of susceptibility of an animal population to the effects of parasites and diseases is determined by animal species characteristics, population density, and predisposing environmental conditions. Many parasites and disease-causing organisms are, at least to some extent, host specific. This means that there is a particular species of animal or group of species which possess the characteristics needed to accommodate the pathological organisms in some form. For example, the virus which causes distemper in carnivores does not infect herbivorous mammals. The viral strain which causes feline distemper does not infect dogs and the one that causes canine distemper does not infect cats, but both may infect raccoons.

The effect of population density has two aspects. First, the stress of competition for space or habitat resources can lower the animal's resistance to disease. And second, the probability of animals coming in close contact with one another will be related to the population density.

In other words, at low population density levels, the probability that a sick animal will pass its disease organisms on to one or more healthy animals before it recovers or dies is much lower than it would be at high density levels because of a lower frequency of contact.

Environmental conditions affect the importance of diseases to animal populations in several ways. First, warm and humid environments are more hospitable to most disease-causing organisms than cool, dry environments. Second, widely fluctuating seasonal weather tends to cull animals already weakened by disease or whose resistance to stress is poor. And third, where the nutritional aspect of the environment is poor, the animal's capability of resisting diseases is lowered.

Another environmental factor is pollution. Some pollutants have a direct disease effect on the animal, as was the case with DDT in raptors. Theoretically at least, some other types of pollutants could have debilatory effects that could lower the animal's resistance to disease-causing organisms.

When considering parasites and diseases in an ecological context there are several questions which will be basic to discussing a situation with experts in the animal pathology field. First, what is the causal organism, i.e., is the disease caused by an internal parasite, external parasite, a virus, a bacteria, a protozoa, or a fungus? Wild animals differ substantially from domestic animals in their level of tolerance for parasites. For instance, most domestic animal specialists are amazed at the internal parasite loads in wild animals that appear to be healthy. Actually, very few adult wild animals would not show signs of having had one or more diseases if autopsied and their tissues examined.

What species might be affected by the disease? Diseases are rarely limited to a single species but they may be limited to a taxonomically related group. The same pathogenic organism may also affect different species of animals in different ways. For instance, pseudorabies (caused by a virus) primarily causes abortions in hogs, but has no other major effect on the adult animal; the same disease is fatal to adult raccoons. In cattle, pseudorabies is called mad-itch. It primarily is manifested by bitting, rubbing, and licking parts of the body until terrible sores develop, often followed by death.

Different types of the same virus can produce related but different diseases in different species of animals. For instance, a serologic type of the virus which causes bluetongue in cattle causes EHD (epizootic hemorraghic disease) in deer.

Individuals, as well as species, may react to the same infectious organism differently. Frequently, but not always, infected individuals that do not succumb to the disease become carriers of the disease to other animals. Sometimes these survivors develop an immunity, sometimes they just remain chronically ill, and sometimes they shed the organism after some length of time but can be infected again.

How is disease spread? Diseases may be spread by direct animal contact, by an insect which carries the organism (or some developmental stage of the organism) from one animal to another, or it may be picked up from the environment where it was shed from an infected animal. An example of spread by direct animal contact is brucellosis. This bacterium cannot survive long in an environment outside of the living animal and is spread primarily during the breeding process. EHD virus is spread from one deer to another by a biting midge. The spread of heartworms among foxes requires that the eggs of the worm in an infected animal be picked up by a mosquito taking blood from that animal and reinjecting it into an uninfected animal. Eggs of mange mites may be dormant for years in vacant dens previously used by an infected animal but can infect a new animal that may take over the den.

A highly important aspect of disease in wild animals is that of their importance to human health and the economic effects on domestic livestock. Rabies is probably the most common disease believed to be primarily harbored in wild animals and of which there is dreadful fear of infection in man or domestic animals. The discovery of a wild animal population playing the role of a reservoir for a disease like rabies in a management area could result in some drastic resource management procedures being taken.

Where there is substantial probability that a disease could spread from wildlife to domestic livestock, another type of problem can develop. For example, a number of diseases can occur in both cattle and deer. If a disease, such as hoof and mouth disease, was discovered in a park deer herd, it is highly probable that an immediate deer depopulation program would be ordered. This principle also has a very important impact on considerations for the use of biological controls for park wildlife even when the chances of negative effects on nearby agriculture are small.

Only a few of the most elementary aspects of the ecological considerations concerning wild animal diseases have been mentioned here. Books and journals are devoted to this subject. The field worker is encouraged to refer to this literature and to always discuss his observations with experts in this field.

CHAPTER 3. MIGRATION, ORIENTATION, AND NAVIGATION

Migration, orientation, and navigation are very important aspects of wildlife ecology. They are also the least understood aspects. Even the experts seem to have difficulty in agreeing on explanations for some of the most basic phenomena in this subject area. For this reason, and unlike other chapters in the ecology section, this chapter has at the end a list of selected references pertinent only to it.

Migration

Definition

Scientists have difficulty in defining migration because it is a behavior used by a wide array of life forms ranging from some of the simplest, such as plankton, to the most highly evolved, such as large vertebrates. Three of the more recent definitions that have been offered are:

1. Migration is the act of moving from one spatial unit to another.

2. Migration is the movement from one habitat to another for the purpose of obtaining better environmental conditions.
3. Migration is specialized behavior especially evolved for displacement of the individual in space.

With respect to wild vertebrate species, the third definition comes closest to fitting our needs. Dr. Hugh Dingle (in Gauthreaux 1980) authored this definition and uses it with strong reference to specialized physiology and ecological advantage.

Evolution of Migratory Behavior in Birds

The two earliest, widely-accepted theories on how bird migration began concerned the movements of the glaciers in the ice ages. One theory proposed that migratory bird species originated in the North and the other that they originated in the South. Glacial advance and recession over the land masses of the northern hemisphere were supposedly the cause of migration and determined the routes of travel used in the process. A third theory suggested that migration was associated with continental drift.

All of these old theories have been disproved. Modern science now attempts to explain why and when birds migrate based on the selective advantages of doing so. Today's theories recognize migratory behavior differences between species, subspecies, populations, and individuals. They recognize that there is no single explanation for this specialized behavior and that there is great variation in causal factors within and among these groups (i.e., from the species level to the level of the individual).

In general, migration can be seen as an adaptive strategy through which a species can gain various advantages. These advantages vary in importance among and within groups and might generally be placed in the following categories: (a) energy balance, (b) level of competition for available forage, (c) competition for site dominance and nest density, and (d) drastic deterioration in habitat condition.

While no single explanation will suffice to explain migratory behavior in all migrant species, some generalizations can still be made to help us think about this phenomenon. First, it may be helpful to consider migrant species as fugitive species, i.e., they have no constant home. They are very much opportunists. Evolution has favored those migrant species which "learned" that summer breeding in the temperate zone was highly advantageous because of the superabundance of resources. In addition, compared to the conditions in most tropical areas, food in temperate habitats is likely to be more predictable in both space and time.

Food is a very important aspect of migration. As expressed by Dingle (in Gauthreaux 1980), "Individual migration routes, distances and life histories are the result of the cost-benefit ratios for the particular species or population. Northern seed-eaters need move only to more southerly areas in winter where seeds are still exposed, whereas insectivorous species must migrate to the tropics and subtropics".

The study of migration has fascinated bird watchers and amateur ornithologists as well as scientists. Some of the best early data on the return of migrants to their original nesting areas were obtained by amateur ornithologists doing banding work in their backyards. Perhaps, though, our most extensive data bank is concerned with the movements of waterfowl.

Federal and state banding efforts and study of band returns (mostly from hunters) allowed the description of four major waterfowl flyways in the United States. These flyways are known as: (a) Atlantic, (b) Mississippi, (c) Central, and (d) Pacific. Most species of waterfowl can be found in each flyway. Primarily, the nesting area in the northern breeding grounds determines which flyway a given population will use. Even though some exchange of birds occurs between flyways, the amount is small enough to allow these biologically recognizable areas to be used as basic formats for setting waterfowl hunting regulations.

Some species other than waterfowl also use these flyways. The American woodcock, for example, is managed according to the flyway format, albeit loosely. The U. S. Fish and Wildlife Service recognizes two management regions for woodcock in the United States. The Eastern Region coincides with the Atlantic flyway and supposedly applies to all woodcock fledged east of the Appalachian Chain. The Central Region deals with all birds fledged west of the Appalachians and includes the Mississippi and part of the Central flyways. The establishment of the boundaries for these management regions was based on extensive banding data. This type of data is required to gain insight into the life histories of species and populations before a great deal can be said about their migratory movements

Terrestrial Mammal Migration

Large Mammals: Apparently, the migratory movements of most, if not all, large mammals are stimulated by changes in food availability. In northern areas, barren ground caribou (<u>Rangifer arcticus</u>) may move for hundreds of kilometers due to snow accumulation preventing access to forage. Elk, deer, and moose (Alces alces) carry out substantial altitudinal migrations; they often stay high in the mountains until the lack of forage forces them to the lower elevations where warmer temperatures and different plant communities exist.

Bats (Chiroptera): As a group, bats generally are not migratory, but some migrant species exist. Bats are typically slow flyers and are not well suited to long-distance movement. Most bat migration apparently occurs between hibernation and breeding areas although the hoary bat (Lasiurus cinereus) may migrate long distances to seek better foraging opportunities.

Small Mammals: (Cricetidae): While a great deal of folklore has evolved around the migration of Norwegian lemmings (Lemmus lemmus), many other small mammals also migrate. Migration and its causes are particularly complex in this group of animals, however, because they incorporate the phenomenon of dispersal behavior. Also in this group of animals, migration is usually either immigration, as when vacancies in a habitat are filled, or emigration, as when animals leave an area frequently because of social stress, although it may be a food supply stimulus. The Norwegian lemming exhibits two types of migration. The first is a migration from dry, winter habitats to wetter, summer habitats. The second is a dispersal due to social stress which occurs at high population densities.

In North America, we see migration or dispersal phenomena in many species of mammals. Behavioral scientists often refer to these two terms as consonants, although it may not be good practice in discussions of wildlife management (or applied wildlife ecology). Possibly a good compromise might be to use dispersal and migration synonymously when dealing with species that are r-selected and that attain high density population levels. Such species may be found among mice, voles, and some squirrels. Dispersal among K-selected species that may not typically reach high density levels, e.g., beaver, woodchucks, and some species of marmots (Marmota spp.), probably should be referred to as dispersal. In the former situations, many individuals may be experiencing a stimulus that will cause them, as individuals, to elect to emigrate. Because the density level is so high, the movement may appear to be a population movement when actually only a portion of the population is moving. The individuals in that portion may have special qualities that predispose them to a "fugitive's strategy". In comparison, the movement of young animals from a beaver colony is the result of a force that would be applied no matter what generation they might be born in on the beaver population growth curve for an ecosystem. Also, because there are so few animals involved, each individual is significant to the characterization of the behavior.

It has been proposed that the causes for migration in small mammals should be recognized in two categories: (a) "innate" or genetic causes, and (b) environmental causes. (These may also be referred to as intrinsic and extrinsic, respectively.) Theoretically, genetic factors could trigger migratory behavior among individuals in a population that was below carrying capacity (presumably K-level) as a population regulation mechanism. The migration in this case is referred to as "presaturation dispersal". Migration at or near carrying capacity is the movement of excess individuals and is referred to as "saturation dispersal".

Much of the literature on movements of small mammals in response to stress caused by increasing competition for resources references the theories advanced by Dr. D. Chitty. He theorized that, among cyclic species of small mammals, genetic selection was for aggressive (i.e., highly territorial) individuals during the population lows. However, stress among such individuals would increase greatly as the population density increased and dispersal would be great during the increase phase of the cycle. The general theory seems logical but all of its aspects have not yet been proven. It has been shown, however, that in several situations dispersers are genetically different from those that remain in the population. It has also generally been shown that dispersers are primarily juveniles and young adults.

Bird Migration and Physiology

"Perhaps in no other area of biology has the question 'when?' been posed with more persistence than in avian physiology. Because migration involves precise internal organization as well as external integration of the total animal in its social and physical environment, accurate timing is literally a life and death proposition. Migration must relate properly with reproduction and molt, metabolism must support behavior, behavior must provide for metabolism, and the total animal must find its way to the ancestral breeding and wintering areas at the appropriate times."

This quote form Doctors A. H. Meir and A. J. Fivizzani (in Gauthreaux 1980) should alert the reader to the complexity of a web of mechanisms synchronized to carry out the process of bird migration. It was the preamble to a discussion of endocrinology and the mechanisms that trigger hormonal responses which goes well beyond the scope of this book. I will summarize some of their more general points to develop some insight into this subject area.

Possibly the best documented physiological change associated with bird migration is premigratory fattening. Percentages of the bird's weight in fat tissue may go from 3 to 5 percent in intermigratory periods to 20 to 50 percent during migration. Storage of energy in the form of fat is important because it is a low density, high energy yield material. Several hormones affect this phenomenon. Prolactin may be important indirectly by stimulating increases in food consumption. Glucagen may importantly affect glucose and free fatty acid contents of blood and it in turn may be affected by insulin. Vasotocin and oxytoxin may also influence energy metabolism and have an effect on the free fatty acid contents of blood.

The timing of physiological changes that are concomittant and migration begins with environmental cues. The three cues that have the greatest influence are: photoperiod, temperature, and rainfall. Of these, photoperiod appears to be by far the most important. The increasing length of days in winter and spring trigger hormone production in pineal and thyroid glands; this results in heightened movement activity and metabolic changes. In addition, it "sets" one or more "biological clocks" in the bird. These clocks regulate physiological changes which assist the bird in orientation (which direction to travel) and navigation (how to get to a specific place).

Even more mysteriously, the internal clock, which is "set" in the spring, exerts a primary influence in initiating physiological changes that result in the autumnal migration. The influence of these biological clocks results in what is known as circadian rhythms. That is, changes occur in organisms without an environmental stimulus at the time of occurrence. More specifically, the biological clock phenomena in relation to migration are referred to as "circannual" rhythms because they need to be reset by an environmental cue, e.g., increasing day length, every seven to fifteen months. (This is based on results of laboratory experiments where birds were exposed to the initial environmental cue and then held under constant environmental conditions.)

Orientation and Navigation in Birds

The mechanisms for orientation and navigation have tantalized the minds of scientists for many years. Every year, the gross aspects of these phenomena are observed during both local, homing, and migratory movements. While a number of types of references have been identified, behavioral scientists are still unable to document exactly how they are used and how back-up systems take over when one reference is lost. (Example: Use of the position of the sun as a reference point is lost on cloudy days, yet migration or homing behavior continues.)

A highly simplified and generalized description of orientation and navigation phenomena is as follows: The internal biological clock is set by some environmental cue, such as changing day length. Once the clock is set, it begins to give cues (endogenous cues) to the bird that must be synchronized with cues from external reference points in order for the bird to correctly orient itself. It is important to recognize that the internal cues are being constantly given and that the message changes with time in synchrony with changes in the reference point. For instance, a migrating bird that uses the sun for a reference point must be able to adjust for changes in the position of the sun throughout the day and for changes in the bird's position relative to that of the sun as the bird moves form latitude to latitude during migration.

That these types of synchrony exist has been shown in at least two ways. First, the artificial resetting of the biological clock by changing photoperiods under laboratory conditions can cause birds to migrate in the wrong direction if the clock is adjusted by six months. Experiments with homing pigeons in which the clock is adjusted by a few weeks can cause incorrect orientation and navigation by these birds.

The second approach to studying these phenomena was to leave the biological clock alone (i.e., the endogenous cues were correct) but to alter the reference points. This was done by releasing nocturnal migrants in a planetarium in which the night sky was correctly projected for that time of year and monitoring the preferred direction of movement of the birds within the planetarium. If the positions of the stars were correct, then the birds oriented themselves appropriately for the time of year but as the positions of the stars were adjusted with the projector, the birds also shifted their direction of orientation from that which would be correct for the time of year to an incorrect direction. The degree of shift correlated with the amount of change in the artificial night sky.

As previously mentioned, the circannual rhythms of cueing are important because it is the timing of the onset of vernal (spring) migration that will set the time for the autumnal migration. Importantly, the syndrome governing orientation and navigation in spring must be adjusted to take the bird in the reverse direction in autumn. Actually, no one knows how the internal biological clock works. We know that something that gives the bird clues similar to those needed by a man when he navigates an airplane or a ship by taking sun and star measurements is at work. It is a matter of observation that it works very well.

A number of types of references that might be used by a bird for orientation and navigation have been studied. Of these, the sun and stars appear to be the best documented. Others include the moon, landscape features, prevailing winds, sounds from the earth's surface, currents and waves in water (as for sea birds), polarized light, and the earth's magnetic field. All of these have been researched to some extent, but documentation of the importance of each mechanism has never been achieved. Dr. K. P. Able (in Gauthreaux 1980) theorized that no species depends on only one type of reference. The process of evolution has selected species that are able to use several systems for migration, although one may be primary. This theory seems to be obviated by the fact that diurnal migrants continue to migrate even when they cannot see the sun on cloudy days. Also, nocturnal migrants migrate on cloudy nights when they cannot see the stars. It is also a matter of observation that these systems can be jammed by storms which cause disorientation and atypical stoppage of migrational progress.

Summary

Hopefully, this chapter has given the reader some idea of the multi-dimensional aspects of animal migration and the mysteries surrounding them. Scientists investigating these phenomena face some of the most complicated problems in the study of animal ecology. However, the information gained over the past two decades has been substantial and the promise for greater understanding in the future is considerable.

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Chapter 4. SOME PRINCIPLES OF WILDLIFE MANAGEMENT

Albert Einstein once said, "God did not create the universe with a throw of the dice." By this he meant that the world around us is not arranged in helter-skelter fashion, but instead its organization is definable and its processes predictable. Our constant challenge is to understand nature's arrangements and the processes of arranging and rearranging. As understanding develops, we can make descriptive statements called principles.

Consider the vast number of possible combinations of abiotic and biotic factors that might affect each phase of a wild animal's life. Also consider the broad array of species of wild animals on the planet. The total futility of trying to understand nature would soon become obvious if every animal-habitat relationship was unique and unpredictable. Fortunately, there is logic in most of the ways that animals relate to each other and their habitats. We refer to these situations as ecological relationships and we call our study of them ecology. The principles of wildlife management are ecological principles.

This chapter introduces some of the principles important in wildlife management. They are listed below:

1. There is a finite limit, called carrying capacity, which describes a species' population size and composition which the ecosystem will support.
2. When the rate of exploitation of a habitat exceeds its primary productivity, succession will be retrogressive.
3. Two species cannot occupy the same niche on a sustained basis.
4. The number of animal species in an ecosystem is directly related to the diversity within and among communities within that ecosystem.
5. The success of a species is directly related to its flexibility regarding niche component requirements.
6. The existence of a species in an ecosystem depends upon the availability of a niche to accommodate it.
7. Population size is directly related to niche space.
8. The process of community succession results in the gain of new niches, the modification of space in other niches, and the loss of others.
9. When plant community succession reaches climax, the number of animal species and their populations will approach a state of dynamic equilibrium.

10. Animal population productivity is ultimately related to soil fertility.

Carrying Capacity

The concept of carrying capacity is the most basic of all the principles upon which wildlife management is based. It is also one of the most difficult to explain because of its abstract nature. If one understands the individual components of the concept, however, the concept, albeit abstract, will take form.

First, the principle simply explains that if an ecosystem is to maintain its integrity, there is a finite limit to the resources that can be devoted to the needs of a single species. It then follows that if there is a limit to the resources that can be devoted to a species, then there is a finite limit to the population size which the ecosystem can accommodate.

Understanding that there is a "limit" is not difficult, but describing this limit is a matter of interpretation. First, how is the limit set? The limit is set by environmental resistance to population increase. Environmental resistance is that force which is built up as the species fills its niche space, i.e., its allotment of food and cover, and for a territorial species, its habitat area.

Next, what is the limit and when is it reached? The carrying capacity limit has been viewed from several perspectives. On the sigmoid curve describing population growth, carrying capacity is said by some authors to be at the MSY-level. The reasoning here is that the population has its highest net productivity at this point. Others argue that carrying capacity is at the K-level on the sigmoid curve because it is at this point that the population has truly filled its niche space and the rate of mortality equals the rate of recruitment.

The population growth curve extends over a number of annual cycles. Within each annual cycle the population fluctuates from a high point during the season of least stress (usually the time of most births) to a low for the year at the end of the season of greatest stress. Some authors have argued that carrying capacity for that point in time (i.e., a given year) is quantitatively the highest population for the year. Still others have said that it was the lowest population for the year.

Two important aspects of carrying capacity need to be mentioned at this point. First, when Aldo Leopold developed this concept, he was thinking in terms of range management. He begged the question, "How many animals can be supported per unit of range?" He knew that the wildlife manager had to be sensitive to the range itself. Populations can be insensitive to the beginnings of habitat deterioration and often show latent responses. When habitat deterioration begins due to exploitation by a population, carrying capacity has already been exceeded. In such situations corrective measures may be required to prevent catastrophic changes in the habitat, in the population responsible for over-exploitation, and in other species secondarily impacted by the environmental changes.

The second aspect in need of mention is how to quantitatively express population size when referring to carrying capacity. Population size should always be on a density basis, i.e., so many animals per unit area of land. Ideally, population levels on large management areas should be discussed on a density basis broken down by habitat type. Obviously every habitat type will not have the same carrying capacity and the total area's ability to support some overall density must be calculated according to the proportional contributions of each habitat type.

Finally, when Leopold developed the concept of carrying capacity, he placed almost total emphasis on food and cover and little on behavioral requirements such as territory. In territorial species, this aspect can be important especially in systems where food and cover are abundant. These resources may in fact be in excess and minimum space requirements may set carrying capacity for the system.

In summary, the carrying capacity of an ecosystem for a given species is the maximum population density which the system can support throughout one annual cycle without the redirection of community succession or adverse impact on co-inhabiting species.

Over-exploitation and Retrogressive Succession

When the rate of exploitation of a habitat exceeds its primary productivity, succession will be retrogressive (reverse of the normal direction). This principle applies to herbivorous species that have no behavioral or physiological feedback mechanisms that prevent their populations from greatly exceeding the carrying capacity of the habitat. In the eastern United States, the most common example is the excessive population densities of white-tailed deer which overbrowse forest vegetation.

Timing, in terms of stage of community structural development, is critical to causing retrogressive succession. In its mildest form, over-exploitation will eliminate a few plant species that are highly palatable and highly sensitive to browsing damage. A somewhat stronger impact would be to eliminate a few species and change the stocking density of those species which become permanent members of the community. Even stronger impact can result in a subclimax community where species composition and structure have no resemblance to that normally expected. In its worst form, forest and grasslands can be reduced to bare soil in which the fertility deteriorates under the stress of erosion and nutrient loss. This last retrogressive type of response is more usually caused by over-exploitation by man and his domestic animals than by wild populations of herbivores.

There are two factors which predispose the community to over-exploitation by wild herbivores. The first of these is site capability, i.e., the potential of the site to support vigorous plant growth. The demand by consumers must be substantially greater in order to change succession on good sites than on poor sites. And second, timing in terms of stage of community development is also critical. For example, a forest community that has reached at least the sapling stage of development will be little affected by excessive populations of deer, rabbits, or mice in terms of continuing in a normal direction. None of these animals has a substantial effect on forest tree growth except when the trees are in the seedling stage. As the forest community matures with more and more of its biomass and nutrients tied up in large trees, the more unlikely it is that vertebrate herbivores could change the direction or rate of this development. On the other hand, an insect epidemic resulting in high mortality rates among mature trees could reverse succession very rapidly.

Some of the most dramatic examples of over-exploitation and retrogressive succession can be seen in central Pennsylvania. In some areas, clearcutting in forests where forage supplies were not generally adequate has tended to concentrate deer on the cut areas to feed on new shoots, herbs and grasses. When the site was poor and/or droughty, the tree species response was slow. Concentrated browsing killed or suppressed the most palatable woody plants and the competitive advantage for growing space went to unpalatable or browsing-tolerant species. This latter group of species composed excellent small mammal habitat and a dramatic population increase ensued. Seed consumption and tree seedling girdling by the small mammals accompanied, by the developed habitual use of the area by deer, shunted succession into an herb-shrub subclimax. Even if the mammals were removed, this stage would probably continue to maintain itself by virtue of community structure which would prevent invasion by tree species.

Niche Exclusiveness

The principle stating that two species cannot occupy the same niche at the same time applies where the two species demand exactly the same niche components. When such a situation occurs, competition is severe. The individual must compete both at the interspecies and intraspecies level. By virtue of the fact that there are two species then there will be differences in physical body size, reproductive capability, longevity, and, in general, capabilities to effectively and efficiently use niche space. The species with the characteristics which give it superiority over the other will eventually exclude the inferior rival.

There are gradations of this principle that are less theoretical and which commonly can be seen. These are usually referred to as "niche overlap". This is a phenomenon where one or more niche components are shared by two or more species. Niche component sharing becomes a problem for a given species when the component is in minimal supply and is an ultimate factor in the life processes for that species. For example, the eastern bluebird is a cavity nester. When cavities in trees and fenceposts on farms became scarce and starlings dominated those that were available, bluebird numbers on farms drastically declined. A cavity for a nesting site was only one niche requirement of the bluebird, but it was an ultimate factor if the species was to remain in the community.

Sharing the food resource is perhaps the most common type of niche overlap. Deer and cattle, for instance, can occupy the same range provided that the range will support their combined demand for forage production. Deer can survive on range when cattle cannot because the deer has a wider foraging amplitude (i.e., it uses a wider range of forage types) than the cow and is better physiologically synchronized with seasonal changes in forage availability and quality. However, cattle take the most nutritious forages on the range. Also, when natural forage availability is low, supplemental feeding by man will allow them to survive and deplete potential deer forage to a level below that required for successful maintenance, growth, and reproduction in the deer herd.

Sharing a niche component is most successful when the component is available in excessive amounts. A good example of this is the fall acorn crop. Acorns are not essential to any wild vertebrate, but many species capitalize on them when they are available. A plentiful supply of acorns with their high concentrations of digestible energy provides large energy reserves stored in the form of fat in animals which feed on them. Species inhabiting ecosystems with large amounts of oak forest are more successful in good acorn years. In years when acorns are highly abundant, availability usually exceeds demand. In years of low availability, however, competition can be very keen resulting in the least competitive species entering the winter period in a poorer nutritional condition than it would otherwise.

The aspects of niche overlap are at the core of the problems with exotic animal species in parks. One of the most basic biological concerns is for the proportion of the ecosystem's resources naturally alloted for the native wild animals that are being consumed by exotics imposed on the system. In order to become a problem, an exotic species must be successful in an ecosystem. It is normally assumed that park systems are in equilibrium, or this is at least a long-term management goal. At equilibrium, all niches are filled. The successful exotic has therefore had to overlap a number of niches in order to survive. At best, its consumption of niche space is spread over so many niches that no particular species is dramatically affected. At worst, the overlap is so complete or its consumption of one or more resources is so large that one or more native species are displaced in the system.

Diversity and Species

The number of animal species in an ecosystem is directly related to the diversity within and among communities. A high level of diversity indicates a large array of niche components and consequently a large number of potential niches. Niches tend to be filled as they become available, so as diversity of the landscape increases, the number of vertebrate species using it increases.

One theory on the changes in numbers of niches and succession states that numbers of niches are maximal in the climax community. However, this theory tends to be very climate and site dependent. For instance, it appears to be true for maritime forest communities which exist in high stress environments. On the other hand, the upland climax coastal plain forest community in the South is live oak. Old growth live oak stands are far simpler in structural complexity or diversity than some of the mixed pine/oak communities that preceded them.

The effect of site in determining direction of change in niche quantity and therefore numbers of animal species is more easily considered a factor is secondary succession than in primary succession. In primary succession, the site itself may undergo some substantial changes, while in secondary succession these changes tend to be subtle. Of course, there are some exceptions.

On good sites, such as cove hardwood sites, structural complexity and animal abundance can be expected to be greater in the early stages of stand development than at its biological maturity (a secondary succession climax) or old growth state. On moisture-and-nutrient-stressed stony slopes, however, the old growth tree/ericaceous shrub ground cover is unquestionably more diverse and contributes to the support of more animal species at biological maturity than it did at any earlier stage of development.

While some areas are managed as examples of undisturbed ecosystems, to do so requires the sacrifice of beta diversity. The importance of having disturbance which ultimately creates greater diversity has led to the "let burn" policy for lightning-caused fires in portions of some parks and prescribed burning in some others. Such policy changes appear to have been advances in park management and will have the effect of maintaining the size of animal species arrays in these parks by maintaining diversity.

Niches and Species

The existence of a species in an ecosystem depends upon the availability of a niche to accommodate it. A species which is either introduced to a new ecosystem or attempts to invade a new ecosystem has three alternatives for success.

First, if it can find a vacant niche which accommodates all of its requirements for growth, maintenance, and reproduction, it will fit the system and be successful. Second, if it can find a suitable niche occupied by a species which it can outcompete and displace, then it can be successful. The system will have lost one species, but it will have gained another. Whether or not this represents a step in ecosystem deterioration will depend on how well the new species can confine its population demands to the limits of the available niche space and if it carries out this process at least as well as the species which it displaced. Whether or not the displacement resulted in a deterioration in the aesthetic quality of the ecosystem is a value judgement by men.

The third alternative for the species is to be highly flexible and competitive. With these capabilities it will take its niche requirements from a number of aspects of the ecosystem. Only the most sensitive species will suffer major damage. Other species will share in the sacrifice of resources required by their populations. They will not be displaced, but their status in the ecosystem may decline as population levels decline.

Most exotic species that have been successful in parks have the characteristics of flexibility and competitiveness. This is logical when one considers the low probability of a vacant niche in an ecosystem or an exact exchange of one species for another. Far greater probability of success is for those which are not exacting in niche requirements and which have the ability to take resources from other potential consumers, at least at a level that meets their minimum needs.

Flexibility and Species Success

The success of a species is directly related to its flexibility in niche component requirements. The species that requires exact niche components is unlikely to survive even moderate environmental change. Such species are the first to disappear from an ecosystem altered by natural or man-caused influences.

Change is a natural phenomenon. The climatological changes which ended the dinosaur age were quite natural as were those that began and ended the ice ages. Large numbers of species unable to cope with those changes disappeared forever. A few species which had great capabilities for adaptation survive in the world today. An example is the opossum (Didelphis virginiana).

Possibly the best example of acclimation to major environmental changes caused by man is the white-tailed deer. These animals, once painted as symbols of wilderness, today utilize habitats that vary from pristine forests to the lawns of housing developments. The best physical specimens are found where there are substantial mixtures of forest and farmland. In some areas today, deer are causing major problems in the form of agricultural crop and timber regeneration damage in areas where 60 to 70 years ago they had been practically extirpated by over-hunting.

There are three major characteristics of species which reach an endangered status. First, the species is exacting in one or more niche component requirements. Second, one or more of these niche components is undergoing substantial adverse change in quantity and or quality. And third, the species has a naturally low reproductive capacity. A fourth characteristic for many endangered species is that they are weak competitors for niche space.

Man has caused many of the adverse changes leading to practical extinction of some species, but the high sensitivity of these species is largely based on their characteristic inflexibility. This is not a comment on man's environmental ethics, but a statement of a species' requirements for survival. Many species on the endangered species list were having poor success in claiming and holding niche space before man's activities began to impinge on it.

In summary, a species can be looked upon as a business corporation. Corporations which diversify and produce many different products and services survive even drastic declines in demand for one of these. The corporation whose total survival is based on one product ceases to exist when there is no demand for that product. The species which can take advantage of a large array of niche components to meet its requirements for growth, maintenance, and reproduction is more likely to survive than one whose innate characteristics limit it to the utilization of a small array of resources.

Niche Space

Population size is directly related to niche space. Niche space is closely related to carrying capacity. The difference between the two is that niche space has a completely ecological definition, while carrying capacity is primarily related to management goals. Niche space for a given species is measured by the population size that the ecosystem will accommodate. All of the habitat factors necessary for growth, maintenance, reproduction and behavioral needs are factors which limit niche space and are called natural limiting factors. Theoretically, if all of these factors are examined in terms of the ratio of the need of a given population for a niche component to the availability of that component, then the component with the smallest ratio is the limiting factor. That is, it is the factor which is currently preventing the population from increasing in size. It is the factor limiting niche space to accommodate the population.

Whenever a niche component is present in excess of the population's needs, i.e., it is not the critical factor limiting the population at the moment, then it can be shared with other species with no adverse effect. Niche components which are utilized by only one species in an ecosystem are very rare. Interspecies competition for a resource can therefore limit its availability to one or more competitors and cause it to become limiting.

Niche component availability and distribution in the ecosystem can also interact to limit population size. For instance, it has been shown that when food is abundant for a number of territorial species, territories are smaller than when it is scarce. Examples in recent literature include wolves (Canis lupus) and peregrine falcons (Falco peregrinus).

Breeding populations of cavity nesting birds can be limited by the number of trees suitable for cavity excavation or by their minimal breeding territory size requirements. For example, Species A excavates cavities in dead trees for nesting and roosting and has a breeding territory area requirement of a minimum of 20 hectares. If on a 1,000 ha tract of land there were 50 dead trees suitable for cavity excavation and these trees were evenly spaced over the tract, then it would be reasonable to expect that the area could accommodate 50 nesting pairs of Species A. On the other hand, it would be possible to have all of the suitable trees on a tract in one 10 ha stand and have only one breeding pair if that pair's territory encompassed the whole stand.

Succession and Niche Change

The process of succession results in the gain of new niches, the modification of space in some, and the loss of others. In focusing on this principle, try to imagine the changes that take place on an abandoned southern farmstead with its pastures and croplands. At first, the grasses become rank and coarse and tall herbs become prominent in the absence of grazing animals. Deer will forage heavily on the green grasses and herbs whenever they are available. Meadow vole and cottontail rabbit populations peak under these conditions of high availability of food and cover. Meadowlarks will forage and nest here along with field sparrows and bobwhite quail. Raptors will hunt these areas particularly in winter.

In 10 to 15 years the picture will change dramatically. The vegetation will be almost entirely high shrubs and trees of sapling to pole size. Meadowlarks and field sparrows (*Spizella pusilla*) will be replaced by rufous-sided towhees (*Pipilo erythrophthalamus*), brown thrashers (*Toxostoma rufum*), and hermit thrushes (*Hylocichla guttata*). Meadow voles (*Microtus pennsylvanicus*) will be replaced by white-footed mice (*Peromyscus leucopus*). Screech owls (*Otus asio*) will replace the soaring raptors. Deer will forage here but the type, quantity, and quality of forage will be drastically different. They will use the area primarily for resting cover. The cottontail rabbit will continue to use the area to some extent, but its numbers will only be fractions of the previous population levels. Some usage of the area by gray squirrels may begin.

In another 25 to 30 years, the picture will change greatly again. A host of songbirds, particularly cavity nesters, and tree bole feeders that were either not previously represented or were in small numbers will be abundant. Numbers of towhees and brown thrashers will drop but not to zero. Cottontail rabbits will barely be represented although deer will be using the area for both foraging and resting. The fall crop of hard masts will become very important in the annual nutritional regimes of many species. Horned and barred owls will be the primary nocturnal raptors while red shouldered and red-tailed hawks will use the area during diurnal periods. (The red-tailed hawk will also use the first stage described, but it will skip the second.)

As the forest progresses to biological maturity or a climax condition, the species array will remain essentially the same for birds and mammals although some population sizes, e.g., for gray squirrels, may change substantially as den sites and foraging opportunities become more abundant. As one can see, the procession of change (succession) involved the gain of new niches and species, the loss of others, and the modification of other niches and species' population sizes.

Climax and Changes in Species and Populations

When plant community succession reaches climax, the numbers of animal species and their populations will approach a state of dynamic equilibrium. At climax, there will be no further additions or losses of niche components, and therefore the numbers of niches will be constant. Theoretically, since losses and gains of species are determined by losses and gains of niches, then the community has the potential to support indefinitely the same species array.

Similarly, since at equilibrium there are no net changes in energy and nutrient levels in the system, i.e., net primary production equals zero, then niche space is constant. Populations naturally fill their niche space allotment, so when the allotment ceases to change then theoretically, population size should become constant.

Constancy in a natural system, even at climax, is primarily an imagined state. At best, even with the exclusion of the influence of man, species and populations eventually achieve some type of dynamic equilibrium based on interspecies and intraspecies competition. For instance, rises and declines in populations and the relative abundance of species in the system may be greatly affected by weather patterns that are unpredictable and may occur over periods of several annual cycles. The state of equilibrium can be perceived only for time periods that cover many annual cycles.

At climax, sharing of niche space among species can be a hazardous arrangement for species which have self-limiting mechanisms for their own populations if they are sharing resources with species which can easily overshoot niche space allotment. For instance, deer populations out of balance with the rest of the system may so overbrowse understory plants that niche space for other species, such as some songbirds, may decline.

Man can modify species arrays and population sizes in climax communities without removing niche components. He does so by modifying the components with pollutants which may have been transported long distances by natural forces before entering the system. The influence of pesticides on systems secondarily contaminated by man's activities is an excellent example of such a situation.

Soils and Wildlife Production

Animal population productivity is ultimately related to soil fertility. The occurrence, distribution and abundance of plants are influenced heavily by soil characteristics. Rich soils support a wide array of plant species and dry matter production on good sites is high. Poor sites support small arrays of plant species which tend to have poor production. Species on good sites have lush growth which is more palatable and digestible than species on poor sites. High production of palatable, digestible forage will support large populations of herbivores and the predators which feed on them.

This phenomenon can be easily understood when the differences between the nutrient economies between good and poor sites are considered. We can compare the alluvial soils of a river bottom floodplain with residual soils weathered from sterile sandstones along a ridgetop. In the floodplain situation there is no nutrient or moisture stress. Nutrients are periodically added to these sites during flooding so that nutrient capital is probably in excess of plant growth needs. Waterlogging of the soils may occasionally be a problem, but most of the species present are able to survive periods of anaerobic soil conditions. Since nutrients and water are almost always adequate or in excess, rapid lush growth can be sustained. Plant species in these sites will have few needs for mechanisms for nutrient or water conservation.

In contrast, species growing on nutrient-poor, drought-prone soils have a great need for mechanisms of nutrient conservation. They are under moisture stress much of the time, so mechanisms that minimize water transpiration through the leaf tissue are important. In addition, nutrient input to these sites is largely influenced by atmospheric fallout, i.e., from rain and dust. The low nutrient capital in the soil and the inability of sandy soils to maintain a substantial nutrient capital because of rapid leaching make it necessary for most of the nutrient capital to be in plant tissue.

The leaves of most plants on moisture and nutrient stressed sites are very waxy. This waxiness helps prevent high rates of transpiration. They are also leathery, i.e., they have a high fiber content. They also tend to be high in tannins. These features make plant materials resist high rates of decay so that nutrients are released slowly to the system resulting in a minimal probability of loss before a living plant on the site can incorporate them. These same features make plant materials low in both palatability and digestibility.

In summary, plant communities on good sites tend to produce larger amounts of palatable and digestible tissue for vertebrate herbivores than communities on poor sites. High energy and nutrient availability are requisite for herbivore productivity both in animal numbers and health status.

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PART II. DEVELOPMENT OF DATA BASES ON PARK WILDLIFE

Introduction

Wildlife management, regardless of the level of intensity with which it is practiced, requires a basic understanding of the land and how species and their populations are distributed over it in both space and time. As the manager's level of knowledge and intimate understanding of a given ecosystem increases, his competency to do his duty increases. Concomitantly, his self-confidence increases.

Nothing builds self-confidence like the experience of personally seeing and doing. The building of a data bank on an ecosystem is a result of many experiences in which observations are made, studied, and interpreted. The soundness of a data bank depends first on the collection of good data. This section deals with the types of data on wildlife that might be useful in parks and discusses the considerations that should be made when collecting, examining, and interpreting them.

CHAPTER 5. QUALITATIVE DATA ON WILDLIFE

Qualitative data on wildlife resources is important for several reasons. First, management personnel should be cognizant of the occurrence of species and have some idea of their relative abundance. A person's competence to make decisions regarding an ecosystem depends in part on this type of knowledge. Secondly, for many wildlife species, qualitative data is all that is really needed for practical management decision making. It is unlikely that sound quantitative data exist on the populations of every vertebrate species occurring on any plot of land larger than a few hectares anywhere in the world. It is also unlikely that substantial amounts of quantitative data on more than a relatively few species will be available for any large management area in the foreseeable future. On the other hand, this situation does not justify total ignorance about any species.

Finally, in parks, most questions asked of managers concerning wildlife resources are of a qualitative nature. Questions such as "How many indigo buntings do you have in the Park?" probably can best be answered by saying, "We do not have a good quantitative estimate of the population, although they are commonly seen from May through August in the field and meadow types of habitat." In this sentence the visitor has been told when the bird can be expected to be seen in the park, where it can be found, and that it is fairly abundant in certain habitats since sightings are common. No particular research or quantitative monitoring has been required to satisfy an easily anticipated question, to show sensitivity to both visitor interest and status of the resource, and to demonstrate personnel competency.

In order to demonstrate competency and accountability, it is very important to anticipate data needs and the kinds of effort that will be required to meet them. Somehow American wildlife managers have slipped into a rut of "killing the snakes closest to them" while losing sight of the need to prepare for what comes next. "An ounce of prevention is worth a pound of cure." applies to the need for the development of some level of knowledge about all wildlife species on a management area. The manager is always on the defensive when he spends all of his time thinking only about current problem situations.

What Species to Expect

It is important for the managers to know what species of wild vertebrates characterize the physiographic region in which they work. It is reasonable that these species could be expected to occur on most management areas that have the habitats to accommodate them. It is desirable that the managers be cognizant of when and where the species could be expected on an area. He should also obtain documentation of their occurrence when possible.

A data bank of this nature can be developed with modest cost in time and effort. First, go to the most current field guides on vertebrate species and determine which species occur in the physiographic region where the management area is located. Field guides are normally arranged by vertebrate group--birds, mammals, and amphibians and reptiles. The better field guides present information on migration and habitat selection.

Next, check texts written on the occurrence of wildlife species in the state where the management area is located to see what species have been observed either in the park or nearby. An example of such a text is <u>Birds of South Carolina</u> by Sprunt and Chamberlain. In addition, check with local bird clubs about the occurrence and relative abundance of birds and other vertebrates which they might have observed during their birding trips.

Third, make notes on where and when you or other personnel have seen various species. This is particularly important in two ways: (a) if environmental changes are occurring within the area, one needs to be aware of the distribution of species and populations before these changes take place in order to detect even gross effects on wildlife; and (b) if a species needs to be located for observation for some reason, then the best place to begin the search is known.

Finally, prepare a booklet which lists all of the species which might occur on the management area at some time during the year. Indicate which species have definitely been identified in the area. Discuss the current distribution of each species or species group by habitat type, relating when and where (under current conditions) each species might be observed. The likelihood of seeing a species or its sign should also be discussed.

Another aspect of discussion for some notable species will be their past histories in the region and on the particular management area. This is particularly important for species whose populations have undergone dramatic changes.

Such information should be of a quality suitable for distribution to the public and as a document for agency archives. It should be updated every five to ten years. If properly researched and prepared, it can provide a qualitative sense of changes in the wildlife resources over time for both current study and future archival research. Be sure to date any such publication.

Detection of the Occurrence of Species

Sighting

Sightings of a species in an ecosystem may be difficult for one or more reasons. Species which are nocturnal and which characteristically avoid the presence of man naturally are difficult to see irrespective of their population size. On the other hand, species with very low population densities in all portions of an area may be difficult to see irrespective of behavioral characteristics. While sighting a species is usually sufficient evidence of its occurrence, frequency of sighting does not necessarily establish its relative abundance unless benavioral characteristics, particularly avoidance behavior, are taken into consideration.

Sometimes sightings (especially if they are rare) are not accepted as sufficient proof of occurrence of a species. A case in point is the situation with the eastern cougar. Reports of sightings of this species along the Blue Ridge Parkway, for instance, are numerous when considered collectively over time. However, even after substantial effort by the U. S. Fish and Wildlife Service to document sightings, the occurrence of the species remains officially accepted as restricted to the state of Florida and primarily south Florida.

There is substantial probability that at least some of the reports of cougar sightings outside of Florida are valid. However, most sightings have involved a very brief period of observation of an extremely alert, quick, and elusive animal. Attempts to find second lines of evidence such as discovery of tracks, hair, scats, kills, etc. have so far all failed.

In the case of the bobcat, a species less rare than the cougar but with similar behavioral characteristics, sightings are usually more quickly accepted as proof of occurrence. Second lines of evidence, particularly the location of scats and tracks, seem to be more easily established for this species than in the case of the cougar. It should be noted that a substantial frequency of daytime sighting reports of this or any other primarily nocturnal species, e.g. the raccoon, may indicate a substantial population. It may also indicate an imbalance between predator and prey populations since nocturnal movements appear to be insufficient for food gathering.

The presence of many bird species can be established by sightings, although bird identification is a skill that must be developed through well-disciplined study. With experience, an individual can become able to identify dozens of species from a moving vehicle because he is attuned to the characteristics of size, shape, and color patterns.

An excellent way to develop this skill is through mist netting. Federal and state permits are required for mist netting and it is usually done as a method of capturing birds for banding purposes. From the standpoint of the study of species occurrence, it allows the worker to have a wide array of species in hand so that the bird can be closely scrutinized for size, shape and color pattern. Mist netting is an excellent method of developing a sense of intimacy with the birdlife of an area.

Three groups of animals that frequently go unnoticed but may be on an area in large numbers, are the small mammals (bats, mice, voles, and shrews), amphibians, and reptiles. Many of these species are secretive and blend well with the habitat. Many live in tunnels, nests, and in dens in trees and logs as well as underground.

Some species in each of these groups can be trapped in order to visually document their occurrence. Mist nets have been used on bats. Line and snap traps have been used on other small mammals. Devices called "drift fences" (fences of small mesh wire or light sheet metal) can be set up so that as the animals move through the habitat they encounter the fence which guides then into buckets (traps) buried in the ground. Once they have fallen into the bucket they cannot escape and can then be visually observed by the field worker.

Hearing

The presence of many species can be detected by hearing and identifying their vocalizations. This is particularly true for birds and frogs. Developing the ability to identify these animals by their calls can become a lifelong pursuit. On the other hand, many can be learned by simply purchasing recordings from some place such as the Cornell University Ornithological Laboratory and listening to them until they are learned.

Taped calls played on a portable tape recorder with amplifier have also been used to elicit calls of the same species in order to detect their presence in the habitat. This procedure works best for most species during the breeding season. The procedure seeks to antagonize a territorial male and cause him to at least announce territory or possibly even attempt to locate and attack the bogus intruder. It is most commonly used on birds.

A second method involving taped calls to detect bird species is to play a recording of an owl to elicit a type of mobbing behavior that will involve many species. This procedure also usually involves the placement of a full mount of an owl, a replica of an owl, or a live, but tethered or caged, owl at the location of the caller. Species that join the attack against the predator may be identified by sight or sound.

Detecting the presence of tree frogs and other small frogs is primarily by vocal identification. Their size , cryptic coloration and nocturnal habits make them almost impossible to detect in any other way.

Animal Signs

Several types of animal signs can be used to detect the presence of various species. These include: (a) tracks, (b) scats, (c) lost hair or feathers, (d) evidence of foraging, (e) beds,dens, and nests, and (f) carcass remains.

Tracks: The identification of tracks in mud, dust, sand, or snow is one of the common methods of detecting the presence of a species in an area. Detection by track identification, however, is primarily limited to mammals and larger species of birds such as turkey, grouse, and pheasants (Phasianus colchicus). Field guides to animal tracks are available and are of great usefulness in this procedure.

Tracks in muddy, medium-textured soils are the easiest to study because of the identifiable detail. Tracks of medium-sized to large animals on wet sand can be fairly distinct, while tracks on dry sand and dust tend to be less detailed and easily disturbed by even light winds.

In situations where tracks are being sought on snow, fresh, wet snow yields the most detailed tracks. Fluffy, dry snow has a tendency to cave in around the edges and is easily windblown. Tracks made on a wet snow that freezes will continue to be good until thawing starts. As thawing progresses, a deer track can enlarge to a size appropriate for an elk.

Plaster casts can be very helpful in the study of tracks, particularly when one species is being avidly sought. The U. S. Fish and Wildlife Service widely distributed plaster casts of eastern cougar tracks to help field personnel to : (a) get a good idea of the track size and shape, and (b) quickly assist in detailed separation of a possible cougar track from that of a dog or large bobcat. Casts of tracks can also make an excellent educational display.

Plaster casts are easily made if the track is in a suitable medium. Medium to fine-textured soils that are wet but not soggy will be best. Simply surround the track with a hoop made of stiff paper. (File folder paper is perfect in thickness, strength, and smoothness.) The distance from the soil surface to the top of the hoop should be 1/2 to 3/4 of an inch. A cast that is too shallow will break easily. Mix common plaster with water until the mixture is about the consistency of a cake batter ready for baking. If the mixture is too stiff it will not pick up the details of the track. If it is too watery, it will take too long to dry. After mixing, quickly poor the mix into the hoop until it is filled. Normally it will take about two hours drying time before the cast will be hardened adequately for moving. This procedure will not work well on snow tracks that are not frozen. The "setting up" process is a chemical reaction that gives off heat and will melt new snow causing a loss of track detail.

Interest in populations of furbearers has grown greatly during the last 10 to 15 years. A number of states have begun routine furbearer surveys using scent posts to lure animals onto a bare soil site in hopes that they will leave identifiable tracks and thereby document their presence in the area. Some surveys have also used smooth metal sheets covered with lamp black in hopes of obtaining greater detail on tracks. (Lamp black pads of metal or glass can also be used for detecting species of small mammals when trapping is either not possible or not desired.) The scent posts are treated with one or more animal luring scents (usually urine)to attract individuals to the site. Some will be attracted to mark territory and others will be attracted out of curiosity.

Scats: Scats are animal droppings or dung. Their size, shape, and composition can give important clues to the presence of some species. In the case of turkeys, even the sexes can be differentiated by their droppings. Scat collections are often made for two purposes. First, they can be used to teach field personnel what a scat that is characteristic of some species looks like. Second, they can be used to analyze the food habits of species.

While scat appearance will vary somewhat with diet composition, with experience the field worker will usually be able to make an identification. For instance, deer feeding on fresh green herbage in spring will normally drop boluses of feces as opposed to the pellets which are characteristic throughout most of the year. Deer and rabbits have similar diets. Their pellets are similar in shape, but those of deer are normally larger. In addition, at the site of defecation deer pellets will be splattered over a small area while those of the rabbit will usually be in a small pile.

The scats of bears and raccoons may be similar in shape and composition but those of the bear will almost always be larger. Site of deposition can also be a clue for raccoons--they usually defecate near a feeding site and prefer to deposit the feces on a log, stump, rock, or something higher than the ground surface.

A few of the other native mammals in southern parks whose scats can be identified with a little experience are red fox, gray fox, bobcat, bats (by group), and squirrels (by group).

Five species of feral mammals that occur in some southern parks and whose scats have been studied for various reasons are horses, cattle, sheep, goats, and hogs. During periods when forage is relatively lush, the droppings of horses and cattle are fairly typical of those that would be found on a farm. However, during winter when forages are highest in fiber content and least digestible, the droppings of these two species can be difficult to separate. The pellets of sheep and goats are difficult to separate at all times of the year. They may also be difficult to separate from those of deer, but not rabbits. Scats of wild hogs also change considerably with the amount of fiber in the diet. They may change from a single large soft boluses resembling in shape those of horses when the diet is very fibrous.

The presence of at least four species of birds can be detected by identifying their droppings . Turkey droppings are unmistakable by size and shape. Droppings of ruffed grouse will be discovered at roost sites. They will resemble small piles of small macaroni and contain large amounts of woody fibers which will be obvious at first sight. Bobwhite quail roost in coveys with the birds arranged in a small circle with their heads pointed outward. The small droppings accumulate in the circle during the roosting period and offers easily identifiable evidence of the presence of the species.

Droppings of the American woodcock usually are called splashings for reasons that are obvious to the observer. All birds that forage primarily on animal matter, whether they eat fleshy insects, fish, mammals, or other birds, produce very watery excreta which looks like whitewash. (Birds have inefficient digestive systems and this white material is excreted urea nitrogen.) In woodcock the droppings look like a single splash of whitewash on a leaf on the ground, or on bare ground and is about the size of a fifty-cent coin.

Vultures (Cathartidae), owls, and hawks can be identified by groups by splashings. Vultures roost in flocks and frequently use the same roosting area or even the same trees repetitively. Splashings at roost sites may practically cover the ground. Hawks and owls are solitary roosters. Hawks are not particularly attached to a given roost site except when it is associated with nesting. Owls may use a roost site repetitively and therefore accumulate more sign. When a hawk defecates, the excreta on the ground looks like a small amount of whitewash thrown from a bucket, i.e., it is strung out. The splashings of an owl, on the other hand, are more like whitewash poured from a bucket.

Another type of sign indicating the presence of hawks and owls is called the pellet. Hawk and owl pellets are the regurgitants of animal material, such as hair, feathers, bones, claws, etc. which the bird ingested but was unable to digest. The digestive systems of raptors are such that these materials are made into boluses in the stomach and regurgitated as a part of the normal excretion process. Owl pellets will almost always be found beneath their roost trees and may occur in substantial numbers. Hawk pellets will be distributed throughout the home range with no particular pattern or place of deposition.

Hair and Feathers: The discovery of hair or feathers around dens, snagged on fences, lost in the molting process, around kill sites, or in predator pellets or droppings can give clues to the presence of a species. The differences in shape, color, and texture of the hair of many mammals are easily seen by the naked eye. Most species of mammals can be identified by microscopic examination of their hair, although this can require great technical skill.

Identification of many species of birds is possible by seeing just one feather. Again, however, this skill requires considerable experience in examining birds in hand. Mist netting and banding is a good procedure to gain this type of knowledge. The use of museum study skins can also be very helpful.

Evidence of Foraging: Evidence of foraging can sometimes be used for detection of a species. For instance, the rooting of wild hogs is good evidence that they are present in the area. However, close inspection may be required, to distinguish between hog rooting, turkey scratchings, raccoon foraging, and bear foraging.

Deer browsing is usually easily identified if there are no other ungulates in the area. Height above the ground at which browsed plant parts are noted can be a clue. When woody twigs have been browsed by deer, the ends of the twigs will appear ragged as if they were chewed off. Stems browsed off by rabbits, woodchucks, or beaver will have sharp ends as if they were cut with a knife.

Some species which girdle the stems of small trees and shrubs can be detected by the width of the incisor tooth marks on the girdled stem. Beaver foraging will be obvious even if a girdled stem is found a substantial distance from where it grew or from any other sign of beaver habitation. Rabbits frequently girdle stems of trees and shrubs during extended snow periods, although identification of the species of rabbit will be impossible without other types of information. Small seedlings are frequently girdled and sometimes severed by small mammals during the winter period. These rodents usually belong to the genus *Microtus,* but again, more evidence will be required to identify the species.

Examination of the remains of animals killed by a predator can sometimes indicate the type predator. For example, bobcats and cougars cover their kills with debris after consuming a portion of the carcass. Sizes of claw marks, tooth marks, and the area surrounding the carcass from which debris has been raked can all be evidence for separating the species. Kills by weasels frequently have only the head removed but care should be taken about quick interpretation of this information. When a raptor kills another bird, the first thing it does is pull the head off and eat it. This is also true of raptor kills of snakes.

Cuttings of acorns, hickory nuts, and pine cones give clues to the presence of squirrels. Cuttings of longleaf pine (*Pinus palustris*) cones in longleaf pine - turkey oak (*P. palustris-Quercus laevis*) stands are accepted usually as good clues to the presence of fox squirrels (*Sciurus niger*).

Beds, Nests, and Dens: The beds of large animals such as deer, bear, and wild hogs are easily identifiable. During non-hibernation periods bears may bed in any type of good cover, particularly cover of the thickest type. Deer beds on forest litter, in fields, or on snow are easily identified by size, form and associated tracks.

In mild to hot weather periods, wild hog bedding behavior is somewhat similar to that of bears. Particularly heavy cover is sought when biting insect problems are substantial. During cold weather and during farrowing, hogs can build elaborate beds or nests. These are composed of leaves, dried grasses and herbs, pine needles, and in summer, leafy shrubs cut off and carried to the site. They may be over one meter in height, 2.5 meters long, and 1.5 meters wide.

Bear dens in the ground will be obvious by their size, smell, nearby scats, and tracks in snow or mud. Evidence that a den may be present high in a tree can be suggested by scats and tracks near a very large tree with a broken top or places where a large limbs have broken away to leave large cavities. Claw marks on the tree may also be obvious.

Dams and lodges constructed by beavers make it obvious that the species has at least been present in the past. Examination of the area for fresh cuttings may be needed to determine whether or not a colony currently inhabits the site. A similar situation exists for the muskrat (Ondatra zibethica). Muskrat lodges in marshes document a past history of the species but newly constructed lodges or fresh cuttings will need to be found to validate it as a current member of the community. Both beaver and muskrats den in banks on deep lakes and large streams. Entrances to the dens will be below the waterline and will likely go undetected by the human observer.

Nests of squirrels will suggest their presence but their nests need to be scrutinized for condition to determine recent construction and repair to document current utilization. Nests of fox squirrels and gray squirrels are virtually identical in size and shape. The presence of fox squirrels in the South, however, may be suggested by the habitat type in which the nest is located. For instance, gray squirrels rarely use longleaf pine/turkey oak stands while fox squirrels use them extensively. Nests in these stands probably will be those built by fox squirrels.

Woodchuck dens are usually obvious by their size and location, and use is validated by maintenance activity during their active portion of the year. These dens may be shared with many other species during the winter period. Tracks and scats will be needed to identify them. If the den becomes vacant for some reason, other species may take it over for a reproduction site.

The nests of birds are identifiable by size, shape, the material used for construction, and location. The size, shape, color and color patterns of bird eggs can also be used to identify species. Texts which outline nest and egg shell characteristics are listed at the end of this chapter.

Animal Remains: The discovery of animal skeletons can give clues to the existence of species in a system. Size of the skeleton is the first and most obvious revealing characteristic. After that, the situation becomes a bit more technical. The best bones to look for are those of the skull, including the lower jaws. Textbook keys will illustrate skull anatomy and characteristic structure for most species. Many universities that teach mammalogy will have good museum collections for skulls and these can be consulted for aid in identifying a species.

Some important skull characteristics come from the teeth. One aspect of teeth characterization is called the dental formula. Knowing how to read a dental formula is basic to beginning an attempt to identify a skull or converse with an expert about it.

Four types of teeth that occur in mammals. Incisors are the front teeth and are indicated in a dental formula by the letter "I". Canines are on the side of the mouth, usually longer than any other tooth, particularly in carnivores, and are indicated by the letter "C". Premolars are indicated by the letter "P" and are between the canine and first molar. Molars are the largest jaw teeth and are indicated by the letter "M".

A comparison of the dental formulae for the genus Felis (includes cougar, ocelot (F. pardalis), margay cat (F. weidi), and jaguarundi (F. yagouaroundi) with that of Lynx (includes bobcat and lynx (L. canadensis) is as below:

$$\text{Felis: } I\,\frac{3}{3},\ C\,\frac{1}{1},\ P\,\frac{3}{2},\ M\,\frac{1}{1}$$

$$\text{Lynx : } I\,\frac{3}{3},\ C\,\frac{1}{1},\ P\,\frac{2}{2},\ M\,\frac{1}{1}$$

The numbers beside each letter indicating the type of tooth indicate the number of that type on each side of the jaw. Numbers on the upper line indicate the number of teeth in the upper jaw and those on the lower line indicate the number in the lower jaw. With respect to the dental formula, cats in the western world in the genus Felis have one more upper premolar than those in the genus Lynx. Otherwise, the teeth are the same in numerical distribution.

Bones other than those of the skull can also be used to identify wild animal remains. Characteristics of the long bones and the number of vertebrae in the backbone are examples. Once a species is identified, the characteristics of teeth and bone structure can give good clues to the animal's age and sex in some cases.

Bones are often discovered at random in the system where animals have died from diseases, starvation, accident, or old age. Bones of medium-sized to large mammals may remain after predation, but usually they are chewed up and digested in the gut of mammalian predators. In the case of raptors, however, bones, including skulls of small mammals, may be found intact in the regurgitated pellets. Owl roosts and nest sites are ideal for discovering small mammal skulls.

Other Types of Sign: Several species or species groups leave sign peculiar to them. For instance, no other animal will create a wallow in mud like a hog. Wallows will take the general shape of the hog creating it and be very smooth on its surfaces. Wallows can be found in every month of the year but they are far more likely to be found in the warmer months when the hog is seeking a wet area to cool its body.

Alligator (<u>Alligator mississippiensis</u>) wallows will not look anything like that of a hog, although they are created and used in part for the same purposes. Except in the driest of periods, alligator wallows will always contain a substantial amount of water. Typically they are fairly large (depending on the size of the animal constructing it), steep sided, and rough edged.

The wild cats and bears will mark trees with their claws for various reasons. Sizes of claw marks and distance above the ground to which the animal has reached can give clues to the species making the marks.

Types of pathways created for lanes of travel can sometimes be helpful in detecting the presence of certain animals. Pushed up ridges of soil will demonstrate the presence of various moles. Tunnels in grassy areas suggest the presence of voles. Slick, straight pathways from the tops of stream banks to the edges of pools may suggest the presence of mink, muskrat, or otter.

Some of the most common signs of wild animal activity in the autumn are tree rubs and scrapes made by buck deer in rut. In late August, bucks often use small trees and shrubs to rub the velvet off their antlers. Later, as buck testosterone levels increase, they create rubs by sparring and fighting with trees and shrubs that would offer resistance when pushed but still give a bit.

Scrapes are areas where the buck has pawed the ground until he reached bare soil. These areas will usually be about one square meter in area and contain the marks of the points of the front hooves and may contain other tracks. Frequently it will be obvious that the buck urinated on the spot. Scrapes are almost always under a low, over-hanging limb which would hang just above the level of the deer's head.

Dust beds of quail, grouse, and turkeys can be evidence of their presence. Dust beds can occur anywhere when the soil is dry and light, and the bird can scratch a small depression in the ground. In the dusting process the bird will erect its body feathers and fan the dust into its plumage by flapping its wings. The size of the depression, length of wings as evidenced by where the wing tips were striking the ground, and associated tracks will give clues for identification of the species.

Qualitative Indications of Abundance

Qualitative statements describing animal abundance involve few, if any, numerical values. Words such as frequently, seldom, common, uncommon, rare, and other similar adjectives and adverbs are the focal points of such statements. These statements are perceptions of one or more persons who agree on the message being conveyed. Perceptions are based on three basic inputs of information: (a) personal experiences in encountering a species or sign left by it, (b) similar experiences reported by technically qualified individuals, and (c) experiences reported by individuals whose technical qualifications and/or veracity are unknown.

The personal experiences and perceptions of even qualified individuals can vary considerably just because their routine movements and consequent encounters with a species differ. This possibility must be kept in mind when two field personnel are at odds in their perceptions of abundance of a species on a management area.

It is a matter of fact that people vary in their abilities to hear, see, and smell. They also vary in their knowledge of where, when, and how to hear, see and smell for information. In addition, they vary in their abilities to interpret what they have heard, seen, or smelled. The best woodsman is the one who can do all of these things well. The best park ranger will be the one who is not only a top woodsman, but one who can also accurately report his observations and perceptions.

When considering one's own perceptions of abundance of a species, it is very important to consider the reports by others. The context of their perceptions are important when comparing their viewpoints to yours. In the best of all worlds, several field personnel whose work routines vary widely will agree in their qualitative evaluations of the abundance of a species. Substantial credibility comes from a number of different perspectives. Such an agreement on a qualitative statement is rare, however.

When considering perceptions of animal abundance, it is important that the frequency of encounter with the species or its sign be set into perspective with characteristics of the species. For instance, how tolerant is the species of man's presence? While some species make great effort to avoid contact with man, others may seek him out, or at least ignore his presence. For instance, sighting a bobcat in a park will be purely accidental because of the bobcat's intolerance for close contact with man. In contrast, bears may become habitual users of sites frequented by man and very tolerant of his presence at those sites. Some songbirds appear to ignore man's presence so long as their habitat niche stays intact.

Intraspecific social behavior affects the detectability of a species. Species which travel in herds, flocks, or family groups are more easily detected than those which travel alone or in pairs. Species which are territorial and defend rather large areas are more difficult to detect than species with small territories or species which are non-territorial.

Seasonal changes in social behavior may affect detectability of a species. Most species of birds maintain only breeding season territories; therefore, detecting them by the calls of singing males announcing territory is generally restricted to that period. Movements of deer, particularly bucks, are far greater during the breeding season than at any other time of year. Probability of detection increases with amount of movement.

Species primarily active during daylight are normally more likely to be seen than those which are primarily nocturnal. Exceptions to this, however, are species which heavily use roadside areas at night and are encountered in the headlights of vehicles.

Finally, to the knowledgeable person, animal abundance is a species characteristic. For instance, a fall population of two gray squirrels per hectare in old-growth hardwoods would not be a high density. The astute observer might sight five or six squirrels in a one-hour period in this habitat. A population density of one deer per 4 hectares in this habitat also would be high, although an observer might not encounter more than three or four deer in a day's walk. Further, one bobcat per 80 ha probably would be a very high density here, but sightings would be rare. In summary, one must know something about what he is seeing if he is to interpret what he has seen.

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CHAPTER 6. BASIC CALCULATIONS FOR SUMMARIZING QUANTITATIVE DATA

Quantitative data on a species or its habitat are assumed to be hard evidence of the situation as it actually exists in nature. It is mandatory that this information be collected, analyzed, and interpreted without personal bias and error in methodology. Human error in measurement must be kept to a minimum.

Bias

One type of bias is a constant error made during measurement. It can easily be corrected if the source of bias can be detected and calculated. An estimate then can be corrected by applying a constant throughout the data set. Unfortunately, in wildlife work we are usually dealing with different types of bias. Sometimes the basis can be corrected and sometimes it cannot. It is always important to recognize the potential for bias, try to avoid it, and be honest about the possibilities of its existence in one's data.

An example of a data set in which there is a measurement error could be the estimation of the size of a deer herd. The following example of such an error and its correction is somewhat over-simplified for the purpose of illustration.

Suppose that we somehow know that 72 percent of a herd is composed of adult deer and that the sex ratio among adults is 50:50. We can assume (for our purposes here) that at the time of sampling all adult bucks have visible antlers. However, in our sample counts, antlered deer account for only 20 percent of the deer seen. But we know that in actuality they account for 36 percent of the herd (1/2 of the adult deer = 0.5 x 72% = 36%).

Now our knowledge of deer behavior tells us that adult bucks are more secretive than both does and young bucks during the time of the year when the sample was taken. We therefore are less likely to detect adult bucks. We can calculate the correction factor for this bias (error) simply by dividing the known percentage composition value for adult bucks (36%) by the observed value (20%) as follows:

$$\text{Correction Factor (CF)} = \frac{36\%}{20\%} = 1.80$$

Now to correct our estimate of herd size by our known bias against adult bucks we simply multiply the estimated number of adult bucks by the CF and add this to the estimated number of antlerless deer.

For example, let us say that a valid estimate of the antlerless deer was 200. Our uncorrected estimate for adult bucks was 63. We correct for bias in the buck population estimate as follows:

Corrected antlered estimate (CAE) = (Uncorrected estimate) x (CF)

CAE = (63) x (1.80) = 113

Our corrected population estimate is as follows:

Corrected total pop. est. (POP) = (valid antlerless est.) + corrected antlered est.)

POP = 200 + 113 = 313

The second type of bias is circumstantial in nature and is impossible to correct mathematically. It occurs in habitat sampling, for example, when the terrain is extremely steep and stony, or when the vegetation is so thick with briars that good samples cannot be obtained with reasonable effort and safety precautions. In working directly with animals, possibly there is a bias in detectability of those in poor health. But poor is a qualitative term. It is impossible to define it as a class in a data set because there is no way to mathematically establish when and to what extent state of health is affecting detectability.

In another example, the type of weather encountered during the sampling period could affect both animal movement and the observer's ability to see the animal or its sign. These factors are examples of those which may cause mathematically uncorrectable bias. The worker must always be aware of the potential for this type of problem and be totally honest with qualitative statements describing it.

Counts and Estimates

The word census indicates that a complete count of something has been made. All individuals in a population have been accounted for and examined for whatever characteristic is being monitored. However, in wildlife work the word census has come to include most procedures used to estimate a population or some characteristic of it. An estimate differs from a complete count in that it is based on sample counts or measurements. The estimate of the value for the population is then based on these samples.

The needs for sampling are obvious. First, let's say we want to know the number of deer on a 50,000 ha area that is under forest cover. There is no way we can count all the deer on the area. We therefore sample representative portions. If our sample areas are in fact representative, the the estimated deer density for the sample area should be a good estimate of the density for the entire area. If we need an estimate of the total area herd size, we simply multiply the density, possibly expressed as so many deer per square kilometer, by the number of square kilometers in the area.

In dealing with counts and estimates, we use two descriptive terms that should be clearly understood. The first of these terms is accuracy. When we refer to the accuracy of a count or estimate, we are referring to how closely our answer approximates the true situation in nature. For example, if in some academic exercise we knew that we had 100 animals in a population, but we counted only 95, then we would say that our method was only 95% accurate.

The term precision refers to how repeatable an estimate is. Again, using the 100 animal population, let us say that we had a sampling scheme that resulted in an estimate of 80 animals. Using simple statistical procedures (which will be explained later) we might can say with 95% confidence that if we sampled this population again and again using the same methods, our estimates would repeatedly lie between 82 and 78 animals. Our precision would be very high, but it would only be 80% accurate.

It should be noted here that accuracy can rarely be documented in field situations. On the other hand, precision can be documented. In most wildlife work, precision is more important than accuracy because we usually are most interested in detecting change if it is occurring. High precision is needed if small changes are to be detected.

Value Distribution and Value Estimate Precision

In dealing with statistics, the term variable is usually used when talking about some measurable characteristic. Examples of variables would be height, weight, and age. A parameter is descriptive of a population variable . A statistic is an estimate of the parameter value. For example, if we had 100 animals in a population and we wanted to know something about weight (a variable), we might determine the mean (a parameter) weight of all 100 animals. This population mean is usually denoted as x. Now suppose that we cannot afford to capture and weigh all 100 animals, but we can afford to deal with 20 chosen at random. The mean (x) of this sample of 20 is a statistic and estimates the parameter value (true population mean).

Here we will deal simply with values determined for different variables. We will use some habitat data to illustrate the statistical terms and their calculation. Let us say that we have been given a data set that was developed in an effort to estimate the amount of deer forage in a specified plant community. (See Table 1)

Table 1. Forage weight experessed in kilograms (kg) per hectare (ha) on 20 sample plots.

Plot #	Forage Weight (kg/ha)	Plot #	Forage Weight (kg/ha)
1	111	11	132
2	213	12	154
3	108	13	192
4	167	14	148
5	136	15	165
6	144	16	173
7	188	17	124
8	199	18	128
9	103	19	145
10	157	20	151

First we want to calculate the statistic which we call the sample mean. To do this we use the following general equation:

$$\bar{x} = \frac{\Sigma x}{n}$$

where x = forage weight on a plot

$\bar{x}$ = mean plot weight (forage weight)

Σ = take the sum of the x's

n = number of plots in the data set

Using the data from Table 1

$$\bar{x} = \frac{111 + 213 + 108 + \ldots + 151}{20} = \frac{3038}{20}$$

$\bar{x}$ = 151.9 kg/ha

We are estimating that the particular plant community is producing 151.9 kg of deer forage per hectare.

Now we might ask two questions. First, is this forage evenly distributed throughout the stand, or do the data show variability between sample plots? An expression of the variability among our sample plot values is called the standard deviation. The term is calculated as follows:

$$\text{Standard Deviation (SD)} = \sqrt{\frac{\Sigma x^2 - \frac{(\Sigma x)^2}{n}}{n-1}}$$

Where Σx^2 = the value for each plot squared and the squared values summed to a total

$(\Sigma x)^2$ = the plot values summed and this sum squared

n = number of plots

Using the Table 1 data:

$$SD = \sqrt{\frac{((111)^2 = (213)^2 + \ldots. +(151)^2) - \frac{(111 + 213 = \ldots.151)^2}{20}}{20-1}}$$

SD = $\pm$ 30.65

We interpret the SD as the description of how the plot values are distributed. If we add one SD to x to obtain a value and subtract one SD from x to obtain another, we can say that 66 percent of the plot values lie between these upper and lower limits. For example:

Upper limit: $\bar{x}$ + SD = 151.90 + 30.65 = 182.55

Lower limit: $\bar{x}$ - SD = 151.90 - 30.65 = 121.25

So 66 percent of the plot values lie between 182.55 kg/ha and 121.25 kg/ha. If we add and subtract two standard deviations, we can give the upper and lower limits for the distribution of 95 percent of the plot values. In this case those limits would be 90.6 kg/ha and 213.2 kg/ha.

A wide spread between the upper and lower limits means that there is a great deal of microsite variability in forage production within the stand (i.e., the forage is patchy). Narrow limits tell us that the forage is fairly evenly distributed throughout the stand.

A calculation in which the SD is used to express variability is called the coefficient of variation (CV). It is a descriptive term in that it relates the size of the variation among values to the mean of those values. It is calculated as follows:

$$\text{Percent CV} = \frac{SD}{\bar{x}} \times 100$$

Using our data:

$$CV = \frac{30.65}{151.90} \times 100$$

$$CV = 20.17\%$$

This can be further interpreted by saying that 66 percent of the sample values lie within 20.17 percent of the sample mean.

One note of caution should be taken in calculating the standard deviation. Sometimes situations occur where a few observations in a date set are so far out of line with the others (i.e., abnormally high or low) that the SD can be greater than the mean. Such data need to be closely examined for errors in measurement, recording, or the possibility of incorrect sampling procedures.

The second question that might be asked is how precise is the estimate? That is, if we resampled this population using the same same methodology but new plots of equal number, within what limits would our new mean likely fall? The expression of precision is called the standard error (SE). It is calculated as follows:

$$SE + \frac{\underline{SD}}{n}$$

The standard error of our estimated mean using the Table 1 data set then would be:

$$SE = \frac{30.65}{\overline{20}}$$

$$SE = 6.86$$

The next step to interpreting these data requires the calculation of a confidence interval. This requires that we go to a statistical textbook or book of statistical tables and obtain a t-value appropriate for the size of our data set. The t-table will have listed on its left side a column of numbers called degrees of freedom (df). The number of degrees of freedom appropriate for our confidence interval calculation is equal to the number of samples (n) minus one or:

$$df = n - 1$$

For our data set this would be:

$$df = 20 - 1 = 19$$

Next we look at the probability columns. These may be headed somewhat differently among different texts, but each column of figures gives the t-value to be used in calculating the confidence interval for a given number of degrees of freedom. Let us say that we want the t-value for a 95 percent confidence interval at 19 degrees of freedom. The tabular value is 2.093. For 99 percent confidence it is 2.861.

Now we can calculate the interval within which a new estimate of deer forage production likely would be if we repeated our sampling using the same methodology and taking the same number of samples. The general formula is:

Confidence Interval (CI) = (SE) x (t-value)

Now applied to our data:

CI at 95% = 151.90 $\pm$ (6.86 x 2.093)
= 151.90 $\pm$ 14.36
= 166.26 kg/ha to 137.54 kg/ha

CI at 99% = 151.90 $\pm$ (6.86 x 2.861))
= 151.90 $\pm$ 19.63
= 171.53 kg/ha to 132.27 kg/ha

We can now say that if we resampled the area we are 99 percent certain that the new sample mean would lie between 171.53 kg/ha and 132.27 kg/ha.

In summary, the most basic statistical terms used to characterize a data set are the mean, standard deviation, coefficient of variation, standard error, and the confidence interval for the estimated mean. It is unlikely that a sample mean will coincide exactly with a true mean for any variable, although we expect it to approximate the true mean value. How closely it comes to actually doing this we usually never known.

The standard deviation describes the variability in any population. It describes how these values are distributed around the mean. The coefficient of variation relates the magnitude of variability within a population to the mean value for the population by expressing the standard deviation as a percentage of the mean.

The standard error describes the repeatability of an estimate, that is, the level of precision that has been obtained when a particular sampling technique and sample size was applied to a particular situation. The calculation of the confidence interval allows a statement of probability of upper and lower limits within which a new estimate for the same population would likely lie.

In wildlife work, even though accuracy of an estimate is highly desired and sought, precision is usually of greater importance. This is because of two reasons. First, we rarely are able to document accuracy. And second, we usually are concerned mainly with detecting change. In order to statistically document change, we must have high precision.

Suggested Reference

Steel, R. G. D. and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill Book Co., Inc., New York. 481pp.

CHAPTER 7. QUANTITATIVE DATA ON WILDLIFE HABITAT AND ITS UTILIZATION

When developing a data base on wildlife habitat, one can easily become confused and begin to think that everything that is measurable should be measured. If indeed this is attempted, the effort will usually end in frustration and with a product that poorly justifies the time, energy, and money that have been spent. This mistake is not a new one, but it may be occurring with increasing frequency in the computer age. Computer technology provides the ability to handle massive amounts of data and do once laborious, repetitious calculations with comparative ease. To some people it has also given a false belief that they can stuff a bunch of numbers into a machine and that machine will put them in touch with the land and its dynamics.

The computer has catapulted us to levels of capability in reducing, analyzing, and summarizing data with accuracy, precision, and mathematical sophistication that far exceed our abilities to collect information in the field. The amount and quality of field data collection efforts are the factors that limit the size and quality of a wildlife resources data base. Efficient and effective data collection is dependent upon a person, who is personally in touch with the land, developing: (a) well thought out objectives, (b) a priority for the objectives, and (c) a sound approach to accomplishing the task. A fourth need is for the flexibility to make changes in the data collection scheme that unforeseen circumstances may require without scuttling the whole program.

One of the most common pitfalls in field data collection planning is the collection of information that "might be useful". These efforts are usually rationalized by saying, "As long as we are going to be out there, we might as well get..." This statement always sounds good back in the office, but it frequently adds considerable frustration to the field task. It usually detracts from the major objective of the work, and often goes no further than some data sheets stored in a file cabinet. When developing a procedure for field data collection, one must be very cautious of the impulse to include the collection of "might be useful" data.

A worker must be realistic about what can be accomplished in the field in a given amount of time and with a finite budget. Such realism normally requires experience. It is common even for the experienced person to overestimate what can be accomplished in most situations. It is predictable among ambitious but inexperienced workers.

Finally, in wildlife data collection, a lot of emphasis needs to be put on the word "wild". That is, natural systems of plants and animals tend to have diversity. Some are more diverse than others. As diversity or variability increases, the size of the standard error increases. In wild systems, accuracy rarely will be documentable. Precision will be unavoidably low, which will frustrate attempts to detect many subtle changes. In addition, the work situation in wild environments usually involves the obstacles of weather, insect pests, and fatigue, all of which may counteract efforts for accurate measurement and consequently decrease both accuracy and precision.

In summary, before launching a wildlife data collection effort, one must first define as clearly as possible what he needs to know. Second, one must have some knowledge of how much time, effort, and financial support will be required to collect the desired data. Third, one must envision how the data will be reduced, analyzed, and interpreted. And finally, one must make a judgement which will involve comparisons of informational need priorities, realistic expectations for improvements in management based on an expanded data bank, and costs of data bank expansions.

Measuring Forest Wildlife Habitat

There are four basic aspects of forest wildlife habitat: (a) overstory, (b) midstory, (c) understory, and (d) ground cover. This section presents a few of the simpler but frequently used methods for taking sample data in each aspect.

Overstory and Midstory Variables

These two aspects of forest wildlife habitat will be addressed jointly because the methods of sampling and measuring them each are the same. Furthermore, both can be sampled simultaneously on the same plots.

Overstory trees are those whose crowns comprise the forest canopy, i.e., collectively they are vertically above all other community members. The primary feature of the forest plant community is its overstory. Typically the overstory dominates the consumption of sunlight, water, and nutrients as well as the community's nutrient capital. Because of its physical prominence, most forest communities are identified by the species composition and size of the overstory trees.

The midstory is made of small trees and/or high shrubs which are obviously not associated with the crown canopy. Dogwood (Cornus florida), blackhaw (Virburnum rufidulum), and serviceberry (Amelanchier arborea) are samples of midstory species that have considerable wildlife value. High shrubs may include species like waxmyrtle (Myrica cerifera), rhododendron (Rhododenron maximum), and witch-hazel (Hamamelis virginiana).

We normally use three parameters to characterize overstory and midstory habitat. Density is expressed as the number of stems per unit of habitat area. Usually it is written as number of stems per acre, or, in the metric system, number of stems per hectare (1 ha = 2.47 ac).

The basal area (BA) of a single stem is its cross-sectional area at 1.5 meters above the ground. To determine BA, one measures the diameter at this height (referred to as diameter at breast height or DBH) and either go to a basal area table in a forest mensuration text for the conversion or calculate it as follows:

$$BA = (0.5 \times DBH)^2 \times (3.14)$$

This is the same as computing the area of a circle where one half of the diameter is equal to the radius which is then squared and multiplied by π (approximately 3.14).

BA may be expressed in square feet or square meters. The worker is cautioned that when using a table to go from DBH to BA to be careful of units. Also, when calculating BA, DBH must be expressed in the same units as the BA term.

When calculating the BA for a species on a given plot, the BA for each tree of that species is obtained and summed to obtain a plot value. When taking diameter data, normally the trees are tallied by some convenient diameter class. For example, a common diameter class for medium-to large-sized trees is 5 cm. The diameter class is usually labeled by the mean diameter for the class. That is, trees with DBH's from 2.5 cm to 7.4 cm would be in the 5 cm class. Trees 7.5 cm to 12.5 cm would be in the 10 cm class. Trees 12.5 cm to 17.4 cm would be in the 15 cm class, etc.

To find the BA for a given class, we multiply the BA class value by the number of stems in that class. For example, let's say we have a species on a plot that has five trees in the 5 cm class, six in the 10 cm class, and three in the 15 cm class. We will find the BA for this species by size class and for the total plot as follows:

For the 5 cm class:

$= (0.5 \times 5.0)^2 \times (3.14) \times (5)$

$= 98.13$ sq. cm or 0.00981 sq.m

For the 10 cm class:

$$BA10 = (0.5 \times 10)^2 \times (3.14) \times (6)$$

BA10 = 471 sq. cm or 0.0471 sq. m

For the 15 cm class:

$$BA15 = (0.5 \times 15)^2 \times (3.14) \times (3)$$

BA15 = 530 sq. cm or 0.0530 sq.m

Total plot BA for this species:

$$\text{Tot. BA} = BA5 + BA10 + BA15$$

$$= 0.0098 + 0.0471 + 0.0530$$

$$= 0.1099 \text{ sq. m}$$

The third parameter is frequency of the occurrence. This is the percentage of sample plots on which a species of tree or shrub occurs. This information is helpful in developing an idea of how a species is distributed through the community or stand.

In measuring wildlife habitat, each of parameters is meaningful in itself when calculated for each species in a stand. Sometimes, however, it is useful to combine these numbers and calculate a relative value for each species for the purpose of examining relative importance in the total stand composition. This process is called indexing. One type of index is called the Density-Frequency-Dominance (DFD) index.

Relative density is equal to the estimated mean density of a given species in the stand divided by the estimated mean density of stems of all species combined in the stand. This quotient is then multiplied by 100.

Relative dominance is equal to the estimated mean BA per unit area for a given species divided by the estimated mean BA per unit area for all species combined. This quotient is also multiplied by 100. Frequency of occurrence is already a relative term and is used without any transformation.

The DFD index for a species then is calculated as follows:

DFD for Species A = Rel. Density + % Freq. + Rel. Dominance

In the case of the midstory, the basal area of high shrubs is usually not measured although it can be. The reason for this is that the growth form of most of these species makes the diameter difficult to measure. Stems are frequently bent and gnarled. Whether or not to attempt diameter measurements in these situations is the option of the worker.

There are two features of the overstory of which the worker should be aware. The first of these is the crown position. Crowns of overstory trees are classified by four crown positions. <u>Dominant</u> trees are those whose crowns are receiving full sunlight. <u>Codominants</u> have crowns whose tops are getting full sunlight but their sides are sharing growing space with other trees. <u>Intermediates</u> are trees with only the highest portion of their crowns getting full sunlight. The sides of these crowns are overshadowed by dominants and codominants. <u>Suppressed</u> trees are those whose crowns are completely overshadowed by the rest of the crown canopy.

Recognizing the importance of crown position and being able to classify it is important in developing a picture of what is going on in the stand. Crown position is important in mast production. Intermediate and suppressed trees have little mast production potential. Note that this primarily applies to the overstory species. There may be a number of midstory species that are shade tolerant and have good mast production potential, particularly for soft masts.

The second attribute of the overstory is the height of the dominant trees. From the value of the mean height of the dominants we get a characteristic called site index. Site index (SI) has to be qualified by age. For instance, when we say that the SI at age 50 is 80, it means that the mean heights of dominants in the stand at age 50 years is 80 feet.

SI is a valuable piece of information. It gives us an expression of site quality, i.e., its ability to support primary production. It can tell us whether or not we should expect good forage production, and along with other data, something about predicting forage quality, and the plant species which will be available. It is one of the most basic pieces of information utilized by the forester and is also very important in wildlife work.

Overstory and Midstory Sampling

The first step in any sampling procedure is to locate the stand to be sampled on a map or aerial photo. Aerial photos with scales of 1:12,000 (1 cm on the map will equal 12,000 cm or 120 m on the ground) or larger (e.g., 1:6,000) are excellent for delineating stand boundaries for most wildlife work.

Once a boundary map of the stand or area to be sampled is produced, the proposed plots should be plotted on the map. In laying out the sampling pattern, two things must be remembered. First, you must sample along the gradient of change. Usually this means that your sample lines will run up and down a slope because slope pattern is usually the most easily identified factor causing changes in vegetative growth within a stand.

An example of gradient of change within a stand is going from a portion of the stand where the stem density is 50/ha to a portion where it is 100/ha. If some type of environmental factor is causing this change, then the change is usually gradual over some horizontal distance. Sampling should be done parallel to the direction of this change. Remember that the accuracy of the estimate will depend on sampling the actual variation in the distribution of the resource.

A note of caution should be added here. The location of a stand boundary may be a matter of judgement. Some changes in plant distribution may warrant breaking an area down into a number of stands because of the objectives of the habitat survey. In other situations, the objectives may allow the whole area to be treated as one unit.

The process of breaking an area into subunits for sampling is called stratification and the sampling is called stratified sampling. It is done when the feature of the area which we are measuring has a recognizable pattern of distribution. That is, the items which we are measuring are grouped and the differences between groups are large. By sampling within individual groups, subunits, or strata (these are synonymous terms) we develop an estimate for each strata and then proportionately sum these to get an estimate for the area. This procedure is likely to give a more accurate estimate of the tree value for the area because variation in sample values is confined to the natural variation within each strata as opposed to the variation for the area as a whole.

An example of proportionate summing of estimate means for several strata follows. Suppose we broke a 100-ha area into three strata for sampling an overstory and the BA estimate means were: Stratum A = 6.8 sq. m/ha, Stratum B = 13.6 sq. m/ha, and Stratum C = 27.2 sq. m/ha. Strata sizes were: A = 60 ha, B = 30 ha, and C = 10 ha. Total BA stocking on the 100 ha area would be:

Stratum	Size (ha)	BA Stocking Rate (sq. m/ha)	Total BA Stocking (sq. m)
A	60	6.8	408
B	30	13.6	408
C	10	27.2	272
Total	100		1088

Mean BA stocking = 10.88 sq. m/ha

Stratified sampling gives us the ability to describe how the resource is distributed over the area. For instance, it is revealing to show that 25 percent of the BA occurred in stratum C which accounted for 10 percent of the acreage. In addition, by confining variation among samples to the respective strata, precision of the estimate has been improved. The method of calculating standard error for a stratified sample is beyond the scope of this text. The reader is referred to an elementary text on statistical sampling for an explanation of this mathematical procedure.

Once the area to be sampled has been located, the boundaries established, and strata defined the worker is then confronted with the need to decide how many plots to sample, how large the plots should be, and how they should be distributed. Statistical procedures assume that all samples are taken on a random basis. The basis of this assumption is that there is no bias in selecting sample plots. A truly random sample has no organization in the distribution of sample plots. That is, the location of one plot has no relationship to the location of another. Such sampling is backed up by sound statistical theory; however, it lacks realism in wild systems. First, it assumes random distribution of the resources being measured throughout the sample area or stratum. We know that this is rarely the situation in nature. Usually, some conscious effort is needed to maximize the likelihood that the variation is being sampled. Second, true random sampling on areas larger than 5 ha is usually unreasonably demanding in efforts required to locate plots.

When working on large tracts of wild land, we normally use a systematic sampling scheme. In this approach we establish a grid of plots over the sample area. The grid size (distance between plots) depends on the number of plots required to adequately sample the variation in the area. On a tract that is roughly square and about 100 ha (247 ac) in size, we might select a grid size of 100 meters by 100 meters (5 chains or 330 ft. apart). Each sample point on this grid would represent a one ha (100m x 100m = 10,000 sq. m. = 1 ha) segment of the total area. In such a scheme we would have 100 sample points.

Such a scheme of sample point determination systematically locates plots, but by randomly selecting a starting point there is no bias involved in sample point selection. That is, the worker is not making any effort to avoid certain sample points. The starting point for locating the first grid plot is randomly selected, but once the first plot is located, the rest are fixed relative to it. That is, every other possible sample point in the stand does not have an equal chance of being chosen. So to this extent, the scheme is not random. For all practical purposes, however, it can be treated as randomly collected data.

After establishing how plots are to be located, the worker must decide the type of plot and plot size that will be used. Fixed plots are those which have fixed horizontal dimensions, e.g., circular plots with a 10 m radius. Every stem of interest would be tallied if its base fell within 10 m of the plot center.

A variable plot has no fixed horizontal dimension. Several approaches to variable plot establishment range from measuring certain specified trees nearest the plot center to sample tree selection by use of a device called a prism. The prism method is commonly used in overstory measurement. It works like a range finder on a camera, except it has a fixed range.

To use a prism, the worker holds the device at eye level and at a distance of 1 m from the eye and over the plot center. He views a stem at 1.5 m above the ground (same level as used to measure DBH). He will see two images of the tree bole through the prism. If these two images overlap, the tree is inside the plot. If density is to be determined, then the diameter of that tree should be measured.

Prisms vary by basal area factor which is determined by the manufacturer. (They also can be obtained for either metric or British unit measurements). The BA on a plot is obtained by multiplying the number of stems on the plot by the prism factor. For instance, if a prism is in metric units and has a factor of 10 (indicated by etching on the device by the manufacturer) and there were 12 trees on the plot, then the plot would have 10 x 12 = 120 sq. m of BA/ha.

The density of stems on the plot is determined by the following equation:

$$\text{Density (stems/ha)} = \frac{\text{Prism Factor}}{\text{BA for size class}} \times \text{Number of stems in size class}$$

For example, assume that we found four stems in the 15 cm size class using a prism with a factor of 2. Then:

$$\text{Density of 15 cm DBH stems/ha} = \frac{10}{0.018} \times 4$$

$$= 2224$$

Caution should be used in applying the prism method for midstory measurements. Growth forms of high shrubs may cause considerable problems because of bent and twisted stems and low hanging branches.

There are statistical methods for determining plot sizes and numbers of plots that should be used in various situations, and the reader is referred to texts on sampling for these statistical procedures. In practicality, however, plot size, number, and distribution normally will be a matter of judgement. Whether or not the decision has been a good one will become apparent after the work is underway. Usually, corrective measures can be taken if a mistake has been made and the area is being sampled with greater intensity than needed to meet the work objective or insufficiently to yield useful data.

There are a number of forms for recording field data on overstory and midstory variables. One suggested data form is given on page 180. Overstory and midstory data sheets should be kept separately.

Measuring Understory Variables

The separation of the understory level from the midstory is a matter of judgement. For wildlife habitat purposes, I normally consider vegetation under 2.5 m to 3.0 m in height but above 0.5 m in height to be understory. Criteria for the separation of these two aspects of habitat must be determined by the objectives of the particular habitat study.

Plot	DBH	Number of Stems by Species (Sp)				
#	Class	Sp.A	Sp.B	Sp.C	Sp.D	Sp.E
1	4					
	6					
	8					
	10					
2	4					
	6					
	8					
	10					

Understory vegetation may also be broken down into height classes. For instance, it is reasonable to believe that wild animals probably perceive a difference in an understory in which 75 percent of the stems are between 1.5 m and 2.5 m in height and one in which 75 percent of the stems are between 0.5 m and 1.5 m in height. Species of understory plants may also be categorized as tree seedling, shrub, or herbaceous.

Understory measurements normally involve counting numbers of stems in each established category. Plots are usually systematically distributed using the same sampling criteria used for the overstory and midstory. Plot size and configuration may differ somewhat, however.

One method of measuring understory is by line-transect. The line begins at a starting point selected by systematic or random method. The direction of the line is usually randomly chosen from all possible compass bearings. A cord stretched along this line facilitates determining which plants are intersected by it. The length of the line is determined using the same consideration as would be used in determining plot size in other fixed-plot sampling or for selection of prism factor in variable plot sampling.

Once the line is established, the most practical type of count is to tally each main stem which is in contact with the cord. It is possible to count every plant which has some part that overlaps the line. Where the understory is sparse, this approach can be used without great difficulty, but where it is dense this is almost impossible. The main types of data that come from line-transect sampling are documentation of species presence, frequency of occurrence, and relative abundance among species and categories.

Estimates of abundance of understory stems on a per unit of area basis must come from fixed-plot data. Plots may be circular, square, or rectangular in shape. Counts are made only of main stems which fall within the plot boundary. There is little difference in data that come from circular plots versus those from square plots of equal size. Circular plots have the advantage of less boundary per unit area of plot size, therefore fewer mistakes are made about whether a stem is in or out of the plot. An additional advantage is that circular plots can usually be worked more efficiently than square ones.

Rectangular plots in which the length dimension greatly exceeds the width dimension may be called a belt transect. Belt transects are excellent for understory vegetation because there is frequently a great deal of unevenness in the horizontal distribution of plants in this layer. Belt transects have fewer problems with zero values obtained when a species is not encountered on a plot but is fairly abundant in the community because the length dimension raises the probability of encounter.

As with overstory and midstory data, an understory data form is set up to meet the needs of the particular work being done. One possible form is shown on page 183. On this data sheet, growth form class is indicated as follows: tree seedlings=1; shrubs=2; herbs=3. Height classes are: stems equal to or less than 2.5 m but more than 1.5 m = 1; stems equal to or less than 1.5 m, but more than 0.5 m = 2.

Plots that are too small inadequately sample the habitat. Plots that are too large can be very inefficient

Plot #	Growth From Class	Height Class	Number of Stems by Species			
			Sp.A	Sp.B	Sp.C	Sp.D
1	1	1				
		2				
	2	1				
		2				
	3	1				
		2				
2	1	1				
		2				
	2	1				
		2				
	3	1				
		2				

and require the tallying of hundreds of stems on a single plot. Plot size must be adjusted to the situation. When deciding on appropriate plot size, the worker must balance considerations for time and effort with those that will be caused by sporadically occurring zero values in the data set. One can anticipate that estimates for understory variables will usually be accompanied by large standard errors.

Measuring Ground Cover Variables

Ground cover includes all living stems whose tops are close to the ground level. For many wildlife purposes, this would include all those less than 0.5 m high. As with the understory, ground cover can be broken down into height classes convenient for the purposes of the particular investigation. Growth-form classes for ground cover might include tree seedlings, shrubs, herbs, mixed grasses and sedges, mosses, and lichens.

Data on the tree seedling and shrub growth forms may be taken by the same methods described for the understory if estimates of stem abundance are desired. Frequently, ground cover is characterized only by the percentage of the plot area that is covered by the crowns of each species or growth-form class. Normally, percentage ground cover when taken using circular or square plots is obtained simply by visual estimates. Depending upon size, a plot might be broken down into a number of equal subplots, estimates made for each subplot, then these estimates averaged to obtain a plot value.

Visual estimates or percentage cover are always a disconcerting experience, and particularly so for the novice, because there is no documentation of the estimate from which confidence can be gained. It is important to note here also that the estimates of percentage ground cover for all growth forms on a plot combined may total more than 100 percent. This is because more than one layer of plants exist within the ground cover. For example, it is possible to have grasses and sedges growing beneath lightly stocked stands of low-bush blueberries. Both are included in ground cover and each may cover more than 50 percent of the plot area.

Several methods can be used to obtain percentage ground cover estimates that are more objective than the visual procedure. Most of these are time consuming and seek a level of accuracy that is not needed in most wildlife work. One such method often used, however, is the line transect. In this procedure, the amount of the line that is intercepted by plant parts belonging to various species or growth forms is measured and the percentage accounted for by each group calculated.

Decisions on plot distribution, plot size (area), or line-transect length are made using the same guidelines as previously described for the other stand aspects.

Measuring Dead Wood Variables

Dead wood is a habitat component frequently overlooked in habitat analysis. It provides habitat for insects in both adult and larval stages; therefore, a foraging site is provided for animals that feed on them. Hollow logs provide both escape cover and denning opportunities for many species. Standing dead trees are feeding sites for many species of birds and offer a site for cavity excavation for cavity nesters.

Standing dead trees are called snags. They can be surveyed using the same methods as described for the overstory and midstory. One problem that sometimes occurs, however, is that the sparcity of snags can make them difficult to detect using fixed plots or prism plots. A type of plot that might be useful is a belt transect with variable width. The transect is located and its length (L) is determined while traversing it. As dead trees are spotted to the left or right of the transect center, the perpendicular distance (w) from the line to the snag is measured. Mean transect width ($\bar{w}$) is calculated by summing all distance to snags measured and dividing the total by the number (n) of trees measured as follows:

Plot size (A) is calculated by:

$$A = (2\ w) \times (L)$$

Stocking density (D) of snags for a given transect is then:

$$D = N/A$$

Be careful to keep all measurements in the same units when making these calculations.

Snags should be categorized according to their height, DBH, and condition of deterioration. Normally, height and diameter class are much broader than those used for living trees, but this depends on the purpose for which the data are to be used. An arbitrary classification of condition of deterioration normally is used for reasons of practicality.

When formulating condition classes, two objectives should be kept in mind. First, it is important to know something about the dynamics of the population of snags. That is, how does the number being added due to various causes of mortality compare to the number falling down due to advanced decay or fire? And second, determining something about stage of decay gives us information on the snag's usefulness to wildlife.

An example of one classification scheme is given on page 189. This system is not recommended for universal usage, but it should give the worker an idea of how to formulate his own classes appropriate to his objectives.

Partially fallen (i.e., currently held up by another tree) or completely fallen dead material should be looked on differently than snags because it provides a somewhat different resource potential. Leaning snags, for instance, will not have as much potential for cavity nesters as erect ones. As the angle of lean (angle made by the stem and ground surface) decreases, the main stem's potential for cavity-nesting bird usage decreases greatly. On the other hand, large limbs that become vertical as the main stem moves toward the horizontal position may offer new potential for cavity excavation.

The same survey methods used for standing snags may be applied to leaning snags. Classification of leaning snags may also follow guidelines used for those still erect. It may be desirable to differentiate between angles of lean. A possibility would be to put those with an angle of lean greater than 45 degrees in one class and those with an angle equal to or less than 45 degrees in another.

Surveying dead wood on the ground for wildlife purposes should probably be confined to material with a main stem greater than 12.5 cm in diameter at its base. This limit is set arbitrarily for practical convenience. Again, the

SNAG CONDITION CLASSES

Condition Class	Criteria
1	Living tree but much of bole or major limbs dead and has obvious potential usefulness to wildlife
1A	Same as Class 1 but has one or more natural or excavated cavities
2	Recently dead or dying tree with little to no decaying wood obvious
2A	Same as Class 2 but has one or more natural or excavated cavities
3	Dead tree with large amount of bark already gone, or obviously sloughing off, or decay process well advanced
3A	Same as Class 3 but has one or more natural or excavated cavities
4	Dead tree with all or most all bark gone; advanced decay of bole obvious. All or most all small limbs gone and many large limbs gone
4A	Same as Class 4 but has one or more natural or excavated cavities
5	Highly advanced decay of bole; all limbs gone
5A	Same as Class 5 but has one or more natural or excavated cavities

worker must establish a limit commensurate with the purposes for which he is gathering data.

Fixed or variable plot methods may be used in the survey. On fixed plots, the base of the stem must lie within the plot for it to be tallied. For variable plots, the distance measured must be to the base of the main stem on the ground. The classification system used for erect snags could be used for downed trees which would include recently blown down material.

Measuring Den Tree Variables

Den trees are usually defined as living trees with cavities that are unlikely to become filled with water. It is reasonable to believe that living trees with cavities usually offer dens for escape, nesting, and reproduction for longer periods of time than snags with cavities. There is no assurance of this, however, because hollow trees are sometimes highly prone to main-stem breakage and being blown down. It can usually be expected that hollow conifers will be more prone to wind breakage than hollow hardwoods.

Surveying den trees may be done following the same methods as applied to the overstory. Classification should be by DBH, crown position, location of cavity, and cavity size. For practicality, these classes should be fairly broad. For instance, classification of cavity location might be as follows: 1 = base of tree; 2 = lower half of bole below the crown; 3 = upper half of bole below the crown; 4 = in-the-crown bole; 5 = large limb below main crown; 6 = limb in crown. Sizes might be classified as: 1 = small, could accommodate small birds or flying squirrels; 2 = medium, could accommodate pileated woodpecker (Dryocopus pileatus), wood duck (Aix sponsa), screech owl, gray squirrel, or fox squirrel; 3 = large, could accommodate large raccoon; and 4 = very large, could accommodate a black bear.

Measuring Forage Production

Vegetation production that is potential forage usually is categorized for survey purposes as (a) hard mast, (b) soft mast, (c) current growth stems of woody plants, (d) current growth leaves of woody plants, (e) herbs, (f) mixed grasses and sedges, and (g) fungi. The bark of some species can be forage for some animals but I have never heard of it being measured for wildlife purposes.

When a forage survey is being considered, the worker must first decide what and when to measure. What to measure is animal species dependent. That is, one must determine what categories of forage are utilized by the species of animal or animals of concern. It must also be determined where the potential forage must exist in the habitat in order for it to be available to a given species. For instance, deer and rabbits eat many of the same forages, but a rabbit cannot browse more than 25 cm above the ground surface, while a deer may browse to about 1.5 m.

In deciding when to make a survey, the worker must be aware that many forages are available in the habitat only for a portion of the year. This is particularly true of soft masts and is also true of some herbs and fungi which have living above-ground parts for only portions of the growing season. In addition, it is important to note that both the quantity and quality of plant tissue change with time. As the growing season progresses, forage availability increases, but, in general, its quality declines. It is very important in a forage survey that the last plot taken be similar to the first plot taken in terms of stage of plant growth.

There are three main perspectives of forage in the habitat. Total potential forage is the weight of all material that might be used as forage, but it is likely that some of it would be unacceptable because of low palatability. In this situation, the worker simply does not have information telling him which species to disregard.

Known palatable forage includes production among those species and plant parts known to be palatable to the animal or animals of concern. Digestible forage may be broken down into (a) total digestible, and (b) known palatable and digestible. Digestible forage production is calculated by multiplying the digestibility factor (percent digestible dry matter) times the forage production estimate. Total digestible forage estimates can be useful, but estimates of the amounts of digestible, palatable material are more easily interpreted.

Mast Surveys: Biologists have tried to develop methods for measuring mast production in trees and shrubs for more than three decades. To date, no method exists which yields an estimate with any reasonable precision. Mast traps of all kinds have been tried, as well as ground surface collections. There is just too much variation from location to location, from plant to plant, and between years for the same plant to obtain useful data.

Surveys which use qualitative evaluations of mast production are used by some wildlife agencies. Specified trails are walked each year in mid- to late summer and binoculars are used to make a reconnaissance of the fruit on mast-producing trees. Acorn production is usually the feature of greatest importance in these surveys. If very little mast is detected, then production is evaluated as poor. As better production is detected, categories of ratings might be termed fair, good, or excellent. While such information requires experience in perceiving what is poor versus what is excellent, having it in hand can be important as a guideline when making decisions regarding wildlife populations and the ability of the land to feed them through the fall and winter periods.

Forage Survey: The term forage, as used in this section, includes all living plant matter which an animal might eat except masts of trees and high shrubs which were treated in the previous section. Since deer forage surveys are among the most common types of habitat evaluation, we will use them as primary examples.

Quantitative estimates of deer forage production are of two types: (1) woody browse production, and (b) total forage production. Woody browse is sometimes quantified on a twig count basis. Current shoots (i.e., those that were produced during the last growing season) are counted and tallied by species. This is a relatively rapid method of assessing a portion of the total forage, but the data are usually taken in the winter habitat and have very limited possibilities for interpretation.

Better information can be obtained by applying the clip-and-weigh method. In this method, twigs are clipped at the point of the last terminal bud scar which would indicate the beginning of the current growth. Twigs are kept separate by species and weighed to determine a plot value.

Estimates of weight, of course, bring us closer to the ability to interpret production on a nutritional basis.

Woody twigs may compose an important portion of the winter diet of several herbivores including deer. This is particularly true when most other forages are covered with ice or snow. Biologists place far less emphasis on the importance of woody twigs in the annual diets of deer than they once did because research has shown that they are utilized when essentially nothing else is available.

Ideally, total forage production should be measured in each of the four seasons to get a good idea of the ecosystem's ability to nourish deer or whatever herbivore is important to the survey work. In addition, it should be noted that stratified sampling is very important because there may be very large differences in forage quantity and quality between different communities or stands.

The clip-and-weigh method is mandatory in a total forage survey. During the field sampling, the forages should be kept separate at least by category and major species. This can be done by labeling several different sample bags for each plot. In bags where several species have been composited, further separation can be done back at the lab.

All sample bags should be labeled as to plot number (individual plot identification), type of material, date, and bag number if there is more than one bag of that material-type on that plot. The bag number should indicate, for instance, that the bag is number two of three (2 of 3) bags of that material on that plot.

Some workers express forage production in green field weight. Air-dry weight (dried in a forced-air oven at 65C) is preferred and oven-dry weight (dried at 105C) is best. If the forage is to be dried, it must not be packed tightly in the drying bags. Normally, I dry forages in grocery store-type bags when determining air-dry weight. By definition, drying should continue until the forages cease to lose weight. In most situations, this will take about 72 hours.

Every bit of material that is collected on the sample plots does not need to be dried to obtain a dry weight estimate. In large sampling operations where the volume of sample material overwhelms the oven facilities, the materials can be subsampled. Subsampling involves the determination of the total green weight of a selected subsample. The subsample is then brought back to the lab, dried, and its dry weight determined. The percent dry matter is equal to the dry weight of the subsample divided by its green weight times 100. The plot sample green weight multiplied by the percent dry matter for the subsample should provide a good estimate of the weight of dry matter on the plot.

Subsampling should always be done on a species-by-species basis or at least by groups of similar species because of the very large differences in field moisture content of various forages.

The advantage of the oven-dry weight expression is that it allows one to apply nutrient concentration values directly to plot weight values to obtain weights of nutrients present in the habitat. A second level of subsampling is required to obtain the oven-dry weight value. Following forced-air drying, the subsample is ground through a fine mesh screen in a device called a Wiley mill. A subsample of about five grams of the ground material is weighed in the lab on a high accuracy analytical balance (preferably measured to the nearest 0.1 milligram). It is placed in a drying oven and dried for eight hours at 105C, cooled, and reweighed.

Percent dry matter at 65C is determined by dividing the weight after oven drying at 105C by the weight before drying at 105C. To find the oven-dry weight of the plot, we multiply the percent dry matter at 65C times the estimate of the plot's air-dry weight.

The guidelines previously outlined for developing sampling schemes in terms of plot size, shape, and distribution also apply to forage sampling. In the past, there has been a tradition of using square of circular plots either one milacre (0.0001 acre) or one square meter in size. (These are not equivalent). This size and shape of plot was easily worked in the field. Also, they had lower amounts of edge relative to plot area than belt transects of equal area; therefore, there was a lower amount of sampling error on a given plot.

On the other hand, since forages tend to be clumped in patches in most stands, belt transects will usually yield more precise data. (At least this has been my experience in both marsh and forest ecosystems). However, there are several problems with belt transects. They are more difficult and time consuming to establish and work. Also, the worker is more prone to oversample due to inability to maintain a perfectly straight line while clipping, and may also stray over plot boundaries. For example, a good belt transect size for forage sampling in a number of situations is 15 cm x 20 m. If we maintain a perfect length to the plot but overstep the boundary on each side by an average of 1 cm, then we will have an automatic error of plus 13.33 percent.

When setting up square plots of about 1 square meter in size, a good method is to build a light aluminum frame which is diagonally reinforced so that its shape and size are constant. Such a frame can be transported to the field and from plot to plot with relative ease.

Circular plots are best worked by placing a metal stake of small diameter at the plot center and dropping the metal ring of a fiber-type tape measure over it. The tape is then extended to the radius appropriate for the plot size and the plot is worked around its center.

In establishing a belt transect, a good method is to locate the beginning point of the transect and determine its orientation. Place stakes that extend about 1.5 m above the ground at the beginning point and ending point of the transect. Stretch a heavy cord between the two stakes. Cut a small stick equal in length to the transect width, then tie a cord at its midpoint. Loop the other end of the cord over the cord that extends the length of the transect and tie it so that it can be easily slipped along. This arrangement should have a plumb-bob effect so that a straight center line and correct width dimension can be maintained. Do not expect perfection, but strive for it.

Sampling for Nutrient Analysis

When collecting forage samples to be analysed for their nutritional value, it is important that they be placed loosely in sample bags and either frozen or placed in a forced-air oven at 65C at the end of the field day in warm weather. Samples collected in cold weather are less susceptible to undesirable changes in chemical composition, but still should be dried or frozen as soon as possible.

When compositing a field sample for nutrient analysis two things are very important. First, collect sample materials that are within reach of the animal whose forage is being studied. For instance, in the case of rabbits and woodchucks, collections should be made within 25 cm of the ground surface. Deer forages can be collected up to a height of 1.5 m. Second, composite the sample from plants widely scattered over the study area or its appropriate strata. Chemical makeup of plant tissue varies mainly between species, but even within a species it can vary from location to location on the individual plant and from site to site on the landscape. The composited sample should be truly representative of the particular species of the study area.

The type of composited sample described above is for a given plant part of a single species. Another type of compositing that is sometimes done is that of the same plant parts for different species or different plant parts from one species. This type of compositing is risky business.

If consideration is being given to compositing a sample, differences in density (specific gravity) of the different materials must be considered. If a composite is made of materials with greatly differing densities, such as leaves and twigs, heavier stem tissue will tend to work its way toward the bottom of the storage vessel after grinding. When the final subsample is taken for chemical analysis, it is likely that the leaf tissue will be over-represented and the stem tissue under-represented. The analytical results from such a sample could be very misleading.

The mixing of grasses and sedges of similar stem and leaf structure is usually acceptable, as is the case for most species in the herb category. However, the worker should consider individual analyses for any species that is viewed as important in the nutrition of the animal or animals whose habitat is being evaluated.

Obtaining Nutritional Data

Nutrient analyses of forages can be contracted to laboratories at most agricultural colleges. Soils and forage testing laboratories will furnish the field worker with information on their respective capabilities along with quotations of costs of analytical services and how to prepare and ship samples.

All laboratories will be able to analyse forages for crude protein and minerals. Information on crude protein is usually more important than that on minerals if a priority must be assigned. Calcium and phosphorus are usually the minerals of greatest importance.

Digestible dry matter determinations are offered by some labs and are very important if they can be obtained even though they tend to be expensive. In vitro dry matter digestibility involves a procedure that includes microbial breakdown of certain plant cell constituents and is applicable only to ruminant diet evaluation. Newer procedures called Van Soest methods yield more usable data. The Van Soest neutral detergent fiber procedure yields an estimate of the percent digestibility of a forage for monogastric animals (e.g., rabbits, squirrels, etc.). The acid detergent fiber test results in estimates of the digestibility of a forage for ruminant diets. It should be noted, however, that high starch forages such as acorns cannot be tested by the Van Soest procedures.

One final comment about nutritional evaluation of forages should be made. It is very important to have a general sense of the nutritional values of the more prominent forages in the habitat. It is equally important to know whether or not a given species is palatable. No matter how great the lab tests say a species should be as a forage, it is not a forage unless an animal will eat it.

Let us say, however, that we have two forages which we have reason to believe are of about equal acceptability in taste to the animal. Further, our habitat analysis has indicated that they are of equal availability on a weight basis. But, our lab results show one to be 60 percent digestible and the other only 40 percent digestible. This bit of information on nutrition has told us that one is probably 50 percent more important than the other in supplying energy for animal growth, maintenance, and reproduction.

Measuring Habitat Utilization

In order to understand the relationship between an animal and its habitat, it is important to have some awareness of aspects of the habitat which may be sought by the animal and those which appear to be avoided. Whenever possible, it is desirable to also know how different aspects of the habitat are used. Is a given area used primarily for foraging, or reproduction?

In attempting to understand how an animal perceives its habitat, we frequently think in terms of preference. A preferred aspect of the habitat is one which is used to a greater extent than it is available. (See Chapter 1) We calculate a preference factor (PF) as follows:

$$PF = \frac{\text{relative use of habitat resource A}}{\text{relative availability of habitat resource A}}$$

Sometimes when attempting to describe utilization compared to availability, it is best simply to say, for example, that some resources accounted for 30 percent of the resource availability but received 50 percent of the utilization. The reason for this is that ratios of percentage figures can be difficult to interpret when they stand alone. Problems are most likely to occur when a resource has a very high or very low availability.

Normally, we would say that as the PF decreases below 1.0 we have evidence of decreasing importance of the resource, if not avoidance of it. But let us take the example of a resource which is 70 percent available and receiving 50 percent utilization. The PF is 0.71 even though the resource is contributing 50 percent of the support for some aspect of the animal's life processes.

In summary, preference factors are commonly used to express the relative importance of some habitat resource. It can be a helpful term, but when using it, one needs to maintain an awareness of the values used in its calculation.

There are two types of habitat utilization analysis. The first involves the description of how a group of species (category), a single species, or a plant part is utilized.

The second involves the description of how a stand or plant community is utilized relative to other stands in the ecosystem.

An example of species utilization is an analysis of winter twig browsing by deer. Plots can be established using the same guidelines as were used for forage sampling. The numbers of browsed and unbrowsed twigs are tallied separately and by species. Percentage availability is calculated as follows:

$$\%\ \text{availability} = \frac{\text{total number of twigs in species A}}{\text{total number of twigs of all species}}\ x(100)$$

Percentage utilization is calculated by:

$$\%\ \text{utilization} = \frac{\text{number of browsed twigs in species A}}{\text{total number of twigs in species A}}\ x(100)$$

It is important to note that the above example simply says something about relative palatability. It seems reasonable to assume that the deer are not repeatedly biting off twigs of a species that does not appeal to them in taste. It does not, however, present a complete picture of the importance of the species as to its nutritional support of the animal.

Another example of utilization analysis would be to evaluate the importance of hardwood trees as compared to pine trees for squirrel nest sites. We would improve our insight into the situation by subdividing the two categories of species into size classes. We would probably take species category and size class information from an overstory survey. We might survey nest trees using a variable width transect. We could then determine the most important species category and size class within that category for squirrel nesting by comparing relative utilization to relative availability.

The second type of utilization is analysed from a perspective of available space. Using the above example of squirrel nesting, we might estimate the number of squirrel nests in hardwood stands and those in pine stands in a forest. We would know what percentage of the forest was accounted for by each type and the percentage of the nesting that occurred in each type. We would then be able to establish the preferred type for nesting habitat.

Probably the most important problem in utilization analysis is detecting and accurately estimating the relative amount of use. Two methods of studying forage utilization (often called food habits) are stomach analysis and fecal analysis. Both of these methods assume that forages will be detected in proportion to the amounts ingested by the animal. This is a broad assumption and is flawed by two facts. First, we know that all materials are not equally identifiable after being damaged during mastication. And second, we know that different materials have different levels of digestibility and therefore the least digestible materials will probably be overestimated as a dietary component. This same type of problem can occur in the field, for instance, where one cannot distinguish between rabbit and woodchuck feeding.

Utilization of communities from a relative amount of space perspective also has the detection problem. We have to assume that whatever method we are using is applied with the same accuracy and precision in all stands being compared. In actuality this is not true. For instance, if we are using deer pellet counts to indicate usage, we know that the pellet groups are going to be less detectable in stands with substantial low shrub ground cover than in a pure pine stand that has a bare forest floor only covered with needles.

We may run into some of the same problems using radio-telemetry techniques. In this case we compare percentage of times that the instrumented animal was located in a vegetation-type to the percentage of the animal's home range made up by that type. However, the accuracy of location determination is poorer in dense stands than in open stands. Many times we cannot be certain which side of the stand boundary the animal is really on.

Some mention should be made of the use of exclosures in studying utilization. Caution needs to be taken when attempting to interpret the differences in vegetation production between the outside and inside of animal exclosures. Workers who study pasture utilization using devices called pasture exclusion cages probably come relatively close to measuring actual forage consumption by assuming it to be the difference in production between the outside and inside of the cage. The first reason that they probably get a good approximation is that they are dealing almost entirely with one narrow category of species made up principally of grasses. And second, they sample the site every couple of weeks. These clippings therefore simulate the effect of the continuous grazing.

Wildlife exclosures are sampled typically at the end of each growing season. The difference measured in net production is not only what was consumed by the animals feeding outside, but also the adverse effects of grazing on growth of the plants. This is particularly true for the herbaceous and woody plant seedling components. For example, removal of the top half of some seedlings and herbs may cause mortality of the rest of the plant. The biomass of the total plant is lost but only maybe one half of it was actually consumed. A less drastic effect is seen when damaged plants on the outside of the exclosure demonstrate a slower rate of growth than those protected from damage.

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Chapter 8 MEASURING ANIMAL POPULATION CHARACTERISTICS AND THEIR CHANGES

The question most frequently asked of those who deal in wildlife is, "How many animals do you have?" It seems ironic that it is also the question for which we have the poorest quantitative answer in terms of precision and documentable accuracy. This lack of capability does not reflect the levels of intellect and energy among our scientists. It reflects the difficulty inherent in estimating the size of a population that: (1) is dynamic, i.e., it is constantly changing and rates of change vary both within the annual cycle as well as between annual cycles: (2) is mobile, i.e., unlike a tree, because you found an individual at one location today does not mean that you will be able to find it there tomorrow; and (3) the members usually seek to avoid detection and detectability may vary between individuals, age classes, sexes, time of year, and with changing weather patterns.

When considering the possibility of collecting quantitative data on an animal population, the worker should periodically review the following questions:

1. What do we want to know?
2. What do we need to know?
3. What factors other than cost will limit the quantity and quality of information that can be obtained?
4. How much information can we afford?

Sometimes workers believe that they need to have estimates on every characteristic of a population. These characteristics might include: (a) total population size on an area, (b) population densities by habitat type, (c) fecundity, (d) conception rate by age class, (e) age structure, (f) mortality rate by age class and cause, and possibly others. This would be a formidable task for any wild population although it occasionally has been accomplished. In most management situations, trying to get "data on everything" is merely optimistic thinking because of the time, effort, and costs involved. In addition, the level of intensity of effort that would be required to obtain this amount of information would, in most situations, almost certainly interfere with the natural processes of the population being studied as well as those of the ecosystem accommodating it.

Basic Assumptions

When one attempts to obtain information on one or more characteristic of a population, any conclusions about those characteristics are dependent upon two basic assumptions. The first of these deals with equal detectability. It is assumed that every individual in the population has an equal probability of being detected, observed, or measured if a measurement is needed. In reality, this assumption is usually not true.

An example of the problem could be the need for an estimate of the proportion of females in a population that were caring for young at some point in the annual cycle. Suppose that because of the need for brooding chicks or suckling young, females with young were less likely to be detected (say because of more limited movements) than females without young. If we did not know about this difference and its magnitude, then we would conclude that the proportion of females that had young was much smaller than it really was. Therefore, where such differences exist, they must be identified and estimated so that an appropriate correction factor can be applied to the data.

In my own deer studies, I have noticed the difference in detectability between bucks and does. Except during the rut, antlered bucks tend to be more secretive than does, even in unhunted populations. The problems are obvious. First, the population size estimate is biased downwards, and second, sex ratios calculated form these data are meaningless.

Changes in detectability with time can be very important, particularly if one wants to monitor population changes with time or before and after events. For example, unless some type of correction factor could be devised, the results of a spotlight count of deer in January would not be comparable to those of a count made in late October. This is because deer behavior and movements during these times are radically different and therefore their detectabilities are very different. Similarly, frequencies of visual observations of deer before and after a major hunt (say three to five days) in length are not comparable because the deer are more prone to attempt to avoid human observers immediately after a hunt than before.

Lastly, detectabilities of animals may vary with habitat conditions. Obviously, visual observations are more difficult in thick cover than in open cover. For this reason, extreme care must be used when comparing populations between different habitats. Also, in conducting a population survey, if the area is stratified by habitat type, care must be taken to avoid underestimating the contribution of habitats with low detectability factors.

The second basic assumption is that, for the purposes of the measurement, the characteristic being measured is constant during the measurement period. For instance, if the size of the population is being measured, then there must be no recruitment (immigration or reproduction) or losses (emigration or mortality) which are unaccounted for. If the age structure of the population is being described, then either the measurement period must be so short that individuals cannot move from one age class to another or such transitions are accounted for. If weight characteristics are to be described, then the measurement period must be so short relative to natural environmental and physiological changes that these factors do not substantially affect the measurements. That is to say an individual should have the same weight on the last day of the measurement period as it did on the first day of that period.

Population Characteristics of Interest

The most obvious characteristic of a population is its size. We usually want to know how many individuals compose it. We may express size as the total number of animals on a given area and refer to this value as total population size. A more often used and more easily understood value is population density. This is simply the total population value divided by the size of the area. For instance, it is usually easier to envision a population expression of, say, two animals per hectare, than to say, for example, 3046 animals on a 1523 ha area. On the other hand, the expression of total population size becomes important when you need to estimate: (a) the number of animals that might have to be removed from an area, and (b) how much effort may be required to carry out the program.

Population density values are of primary importance in evaluating habitats in terms of geographical zones or broad categories of vegetation or landscape. For instance, we are rarely interested in the total number of deer in various physiographic provinces but we commonly are interested in how the average densities compare between these regions. Also, we are rarely interested in the number of animals using a given habitat on an area with many habitats available, but a clue to the attractiveness of that habitat may be expressed by the ratio of the density of animals which it supports to the density of the entire area or some other selected habitat.

Age/Sex Structure

Understanding a population requires knowledge of how it is distributed proportionately over various age and sex classes. Sex classes are, of course, males and females. Age classes may be defined in many ways depending first on how accurately animals can be aged within the limitations of the methods used in the study, and second on what age classes are meaningful to the objectives of the study.

Small mammals are sometimes aged as nestling, immature or juveniles, and adults. Precocial species of birds may be classified as chicks (e.g., quail) or poults (e.g., turkeys), immatures, or adults. Altricial species are nestlings, immatures, and adults. Juveniles or immature animals are functionally similar to adults except that they are not potential breeders whereas adults are. Bird banding terminology uses the following designations: HY-hatching year, SY - second year, and AHY - other than hatching year.

Large animals frequently can be placed in more refined age classes. Deer and elk are often aged to the nearest half year by tooth replacement and wear patterns. Some large carnivores may be placed in one year age classes.

There are several important aspects to interpreting age/sex data. The first of these is the possible change in sex ratios with increase in age. Sex ratio at birth occurrence and magnitude of differential mortality and to seek an explanation for it.

Studies of age structure in a population can become very complex. The complexities are dealt with in computer models which are well beyond the scope of this text, but which represent our purest efforts in trying to mathematically understand the dynamics of populations. There are some simpler models, however, that give insight into the importance of age structure data. One type of model is the age pyramid. Let's say that we want to draw a pyramid using horizontal bars. The length of each bar represents either the number of animals or the percentage of the population in a given age class (Figure 8.1). We construct the pyramid by placing the bar representing the youngest age class on the bottom and the oldest at the top. A flattened pyramid says that the bulk of the population primarily is made up of young, and that a high mortality rate exists between the youngest and oldest age classes. A very steep pyramid says that the older age classes are well represented in the population and that there is not a great deal of difference in mortality rates among age classes. An inverted pyramid illustrates that the population is almost entirely made up of older animals and that either very few young are being produced or that there is a very high mortality rate among the very young.

frequently is very different from that in the adult population. It may be very important to document the occurrence and magnitude of differential mortality and to seek an explanation for it.

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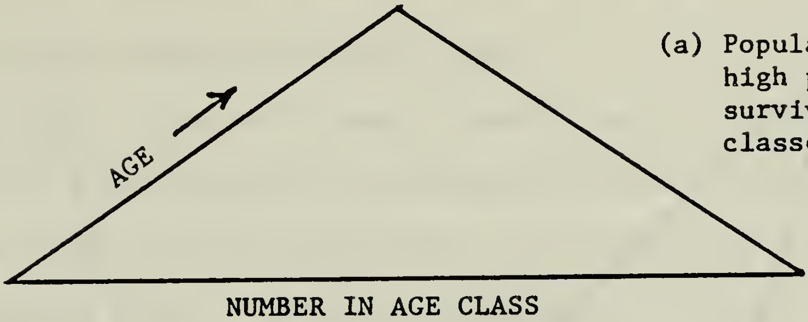
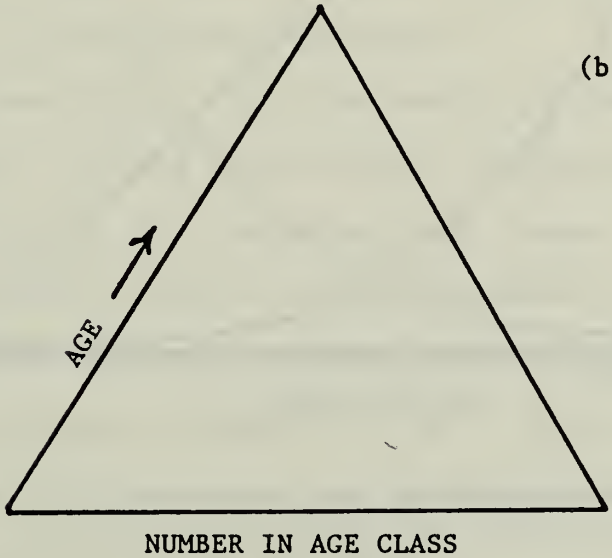
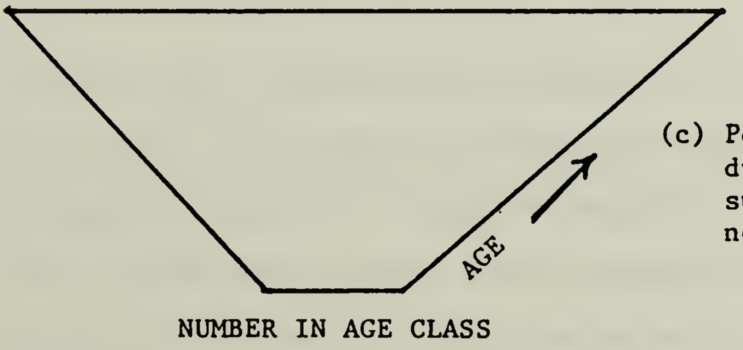
Figure 8.1. Generalized age structure pyramids for three population conditions.



(a) Population with relatively high productivity but low survival rates in all age classes.

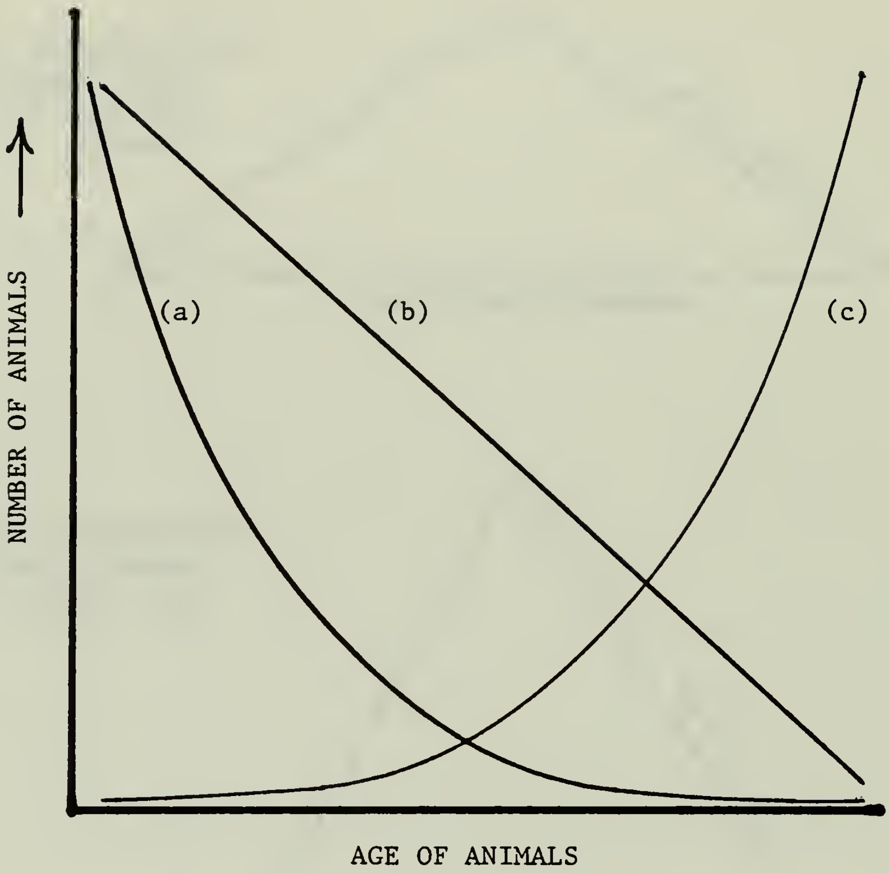


(b) Population with equal survival rates among all age classes.



(c) Population with low productivity or very low survival rates among neonates.

Figure 8.2. Generalized age structure line-graphs for three population conditions.



(a) Population with relatively high productivity but low survival rates (declining with age) among all age classes.

(b) Population with equal survival rates among all age classes.

(c) Population with low productivity or low survival rates among neonates (low recruitment).

young are being produced or that there is a very high mortality rate among the very young.

Another type of simple model is the line graph where number of individuals is indicated on the vertical (Y) axis and age class on the horizontal (X) axis (Figure 8.2). The magnitude of slope, direction of slope, and general geometry of the plotted line give us some clues about the dynamics of the population. (This type of representation is most appropriate for continuous breeders).

Age class data are the basis for the construction of life tables. There are several types of life tables and several methods of constructing them. R. L. Downing addresses this topic in his chapter entitled "Vital Statistics of Animal Populations" in Wildlife Management Techniques Manual (Schemmitz 1980). The reader is referred to that work if he wishes to develop greater understanding of the importance of age/sex data.

Aspects of Production

The three major categories of aspects of production in populations are: (a) those concerning males, (b) those concerning females, and (c) those concerning young animals. In the first category we may have a need to determine the percentage of the males in a population which are sexually mature or in breeding condition. These conditions are usually indicated by testicular measurements or determination of sperm production. A male may be sexually mature, but if it is a seasonal breeder it may not be in breeding condition simply because it is being observed at a time other than the breeding season.

There are many aspects to the information about production in the population which we can get from females. Pregnancy rates give a minimum estimate of the proportion of the female segment of the population which is sexually mature. Percentage of females lactating tells us about parturition success (live births) and the existence of dependent young in the population. In utero litter size (number of fetuses contained in the uterus of the female) is an estimate of maximum litter size at birth. It also gives us an estimate of the minimum conception rate. Clutch size of birds tells us the maximum number of hatchlings that are possible. In some species, examination of the uterus will indicate if the animal was ever pregnant before it died. Also, microscopic examination of ovarian structures can indicate the extent of recent egg production in mammals.

Information from young animals in the population combined with data on older age classes tells us about production and productivity. Production is the total number of young produced. Productivity is the rate at which young are produced. Productivity is usually expressed as number of young per adult or pair of breeding adults. We sometimes alternately refer to productivity and fecundity. High fecundity in a species or population means it has a high productivity rate. (Note: These terms are related to biotic potential which is the theoretical maximum productivity rate for a species or population. Normally this theoretical maximum is the maximum number of eggs which might be produced. Fecundity deals with actual conception rates and live births per female characteristic of a species or population.)

Information involving ratios of young to adult females is of two main types. Birth rate refers to the number of live young born per adult female. Reproductive rate is the number of female young born per adult female.

Recruitment rate (sometimes referred to as realized reproduction) is the number of young which survive to enter the breeding population. For most species, this is the most important aspect of reproduction because it determines whether or not the population will change or remain steady in size and, consequently, if there will be any changes in the functional relationship between the population and the rest of the ecosystem.

Mortality

The understanding of mortality in a population is equal in importance to the understanding of reproduction. The magnitude of mortality relative to the magnitude of reproduction determines whether a population will increase, decrease, or remain steady in size. Differential mortality among age and sex classes will influence importantly the age/sex structure of a population. Learning the causes of mortality and which segments are most vulnerable to various causal agents results in the ability to predict when, where, and how population losses will occur. Some types of life tables may detail the causes of mortality by age/sex class to demonstrate how a casual agent affects the age/sex structure.

In Utero Litter Measurements

Information from pregnant females has been mentioned already in relation to conceptions and live births. Normally, examination of the uterus of female wild animals is not possible unless the animal is dead. The uterus can be removed and fetuses examined. In some species, research has developed information that will allow the estimation of the age of fetuses. (Note: This has also been done for some species of birds to allow aging of the embryo in an unhatched egg). Several types of information can be obtained from these measurements. First, if one knows the age of the fetus, the date of conception can be estimated. It follows then that if we can obtain enough data on conception dates, we can determine the peak period of breeding. Similarly, assuming that the length of the gestation period is known, the peak period for birth can be predicted.

Observations of fetuses usually required for aging may include crown-rump length, weight, and development of hair (or down in precocial species of birds). Anyone expecting to make these kinds of measurements on a given species must search the literature on that species to determine the existence of guides, charts, or equations for estimating fetus age. Measurements must be made in the same units as used in the guide or as called for in the equation.

Another type of information that can be obtained from pregnant uterus observations concerns embryo resorption. This phenomenon occurs, but little is known about its importance. It is a type of mortality and is known to occur primarily in stressed female (e.g., severe nutritional stress.) Evidence of embryo death and resorption is most obvious when the fetal sac contains an amorphous material that has resulted from the breakdown of the embryo. In multiparate species (i.e., has two or more young at birth), vast differences in tissue characteristics will indicate that the abnormal embryo is dead and in the process of breaking down and being absorbed by the body of the female.

Body Size

Substantial changes in the mean weight of individuals in an age/sex class of a population usually indicate a change in the health of the population. (This normally means a change in nutritional regime, although other stresses could be casual factors.) Similarly, if there are substantial differences between two populations with respect to mean weight in comparable age/sex classes, then it normally can be deduced that one population is healthier than the other. The emphasis on weight by age/sex class designation should be obvious. The weight of an animal that cannot be designated as belonging to a particular age/sex class is meaningless.

Three other body measurements sometimes made on mammals are length, shoulder height, and heart girth. Body length is measured typically from the tip of the nose to the base of the tail. This measurement is not difficult to make on an animal which is either heavily sedated, anesthetized, or dead. If the animal is capable of struggle, this measurement can be difficult to obtain with meaningful accuracy.

Shoulder height is most often measured on large mammals, but it very difficult to obtain accurately. It should reflect the height of the animal at the shoulder when the animal is standing on the ground. Such a situation for measurement is rare with a wild animal. Measurement of shoulder height when the animal is lying on its side requires standardization of the procedure as to how the front leg will be held in position for the measurement.

Heart girth is the circumference of an animal's thoracic region measured directly behind the shoulders. A flexible tape is usually used for this measurement. Heart girth is related to body weight and, within limits, can be used to estimate an animal's weight. This technique is sometimes used where, because of the animal's size, location, or inconvenience of obtaining an appropriate scale, direct weight determination is not practical.

Physiological Attributes

Sometimes clues to the condition of a population can be obtained from physiological measurements that reflect the health of individuals in specific age/sex classes. The most common of these measurements fall into three main categories: (a) kidney fat, (b) fat content in bone marrow, and (c) blood chemistry.

Kidney fat is a condition variable that has been studied primarily in ungulates. This is the fat tissue deposited on and around the kidneys and can only be observed in the eviserated animal. Large amounts (measured by weight) of fat deposition are evidence of a high plane of nutrition, at least with respect to energy intake.

Two points should be noted about the kidney fat index. First, the age/sex class must be specified. Very young animals for instance will rarely have kidney fat because all of the chemical energy taken in is devoted to supporting growth and maintenance. This would be normal for animals in a young age class. Also, pregnant females have a very different energy balance than males or non-pregnant females in the same age class. Second, the techniques of removing fat must be standardized so that comparisons can be made. When there is very little kidney fat there is no problem. When there is a lot it may intergrade with other fat deposits on the body cavity wall. Therefore, beginning and ending points for removal must be specified and standardized.

Fat content of femur bone marrow has long been referred to as an index to nutritional condition of the animal, particularly deer, elk, and moose. Color charts have been published as guides so that the field worker simply needs to open the bone that has been excised from a dead animal, examine the marrow color, and evaluate its condition. Conditions range from a yellow, gelatinous type of marrow indicating very poor condition to a creamy white, firm marrow which indicates good condition. Age/sex class and pregnancy are again very important. Marrow fat in a healthy fawn, for instance, will almost always be red and firm in consistency.

An improvement over the color chart approach is to take the marrow from the center third (length measure) of the femur and have it analyzed for fat content at a laboratory. The marrow sample must be frozen while awaiting analysis.

Blood chemistry can be evaluated in either living animals or dead animals if the sample is taken at the time of death. Interpreting blood chemistry value in wild animals, however, is difficult for several reasons. First, there are very few standard values for wild species in free-ranging situations. By comparison, standard values and normal ranges in values for humans and livestock have been established for a long time. A veterinarian is needed to interpret blood chemistry values for a wild animal, but even he will have problems. He may compare values for a deer with those for goats, sheep, or cattle. He may evaluate values for a fox, coyote, or wolf with those for the domestic dog. This approach is one of necessity, but must be cautiously used.

Another problem in interpreting blood chemistry values occurs when the process of restraint and handling or the mechanism of death cause chemical changes in the blood. Researchers have demonstrated this problem for several blood parameters studied in penned deer. My own work in this area with free-ranging deer has involved collection of the animal with a high-powered rifle and the shot placed either in the head or upper neck region. We draw blood from the heart immediately using a large gauge needle and 15-20 cc syringe. The blood is placed in a test tube, kept on ice, and taken to the lab as soon as possible for centrifuging to separate the serum which is then frozen to await chemical analyses. A sample of whole blood may be placed in a test tube containing an anti-coagulant and kept cool (not frozen) for cell counts which must be done soon after collection.

Information from blood anaylses may be helpful in understanding the condition of a population. However, just because it sounds sophisticated and is common practice in human and veterinary medicine this does not mean that the procedure will have the same level of importance when studying wild populations. Also, I would not recommend that even a trained wildlife biologist attempt to interpret blood values without assistance from an animal physiology specialist or a veterinarian. It probably will take the biologist plus these other people to make a truly good interpretation. (Note: Blood chemistry values for various species are sometimes reported in the Journal of Wildlife Diseases).

Serological Surveys

Serological surveys involve the analyses of blood serum samples (sera) from a cross-section of an animal population to determine whether or not the population has been exposed to some given disease-causing agent. Properly carried out, it should indicate also the percentage incidence of exposure by age/sex class.

Disease-causing organisms produce antigens once they are inside the body of the animal. The presence of the antigen stimulates the animal's body to produce antibodies. Animal pathologists and physiologists have developed techniques for determining exposure to some specific diseases by testing blood serum for the presence of antibodies to the disease. The animal does not have to be showing any gross pathological changes in order for the antibodies to be present, but knowledge of their presence and how the incidence is proportionately spread through a population helps us understand the potential importance of a disease in affecting population dynamics. It also helps us understand the potential importance of a wild population to act as a reservoir for diseases potentially important to the health of humans or domestic livestock.

Determining Population Size and Size Change

Three basic approaches are used to quantify population size and size change: (a) census, (b) estimate, and (c) index. A census is a complete count of the number of individuals in a population. It is an absolute measurement, and therefore it has no associated variance term. An example of a census would be an island covered by short grass vegetation and inhabited by a population of large mammals that are distinct in this low profile habitat structure. Suppose these animals are spaced so that herding does not affect our ability to accurately count them. We fly over the island with a helicopter, sight every individual and count it. We have every reason to believe that our count is total and accurate; therefore, we have censused the population.

Situations like the one just described are very rare. More often we must sample a population and make an estimate of its size. Variance is, of course, associated with that estimate, therefore we must indicate the confidence interval around the estimate. In doing so, we indicate, with a stated level of confidence, the upper and lower limits of a range of values within which our estimate would fall if we repeated our sampling procedures and the population had not changed in the meantime.

If our standard error term is small, then a high level of confidence is placed in the repeatability of the estimate, i.e., its precision. In such situations we are often prone also to place confidence in accuracy of the estimate. However, accuracy is not documented by repeatability. Absolute documentation of accuracy of an estimate usually requires a complete census. Computer models which simulate the dynamics of populations may demonstrate errors in estimates in some situations, but even with the models there is no way to know what types of compensatory mechanisms are in play unless every factor in every equation can be empirically documented. This would be an unrealistic, if not impossible, task.

There are four basic approaches to estimating the size of a population: (a) sample counts, (b) capture-recapture, (c) territory recognition, and (d) models based on estimates of proportional distribution by age/sex class, birth rates, recruitment rates, and mortality rates. (Each of these factors typically is modeled as changing through the annual cycle). A simple example of a sample count would be to take the island situation used to describe a type of true census and imagine that the island is far too large for 100 percent coverage necessary for a complete count. We might therefore fly transects across the island and count the numbers of animals in each transect or sample plot. If we know the area of each transect and we have a complete count of animals in each of them, then we have a number of transects (or plots) for which we know the animal density. We can then calculate a mean and standard error for the estimated population density on the island. If we know the area of the island then we multiply the density times area size to obtain an estimate of the total population size.

As with the census example, the reader is warned that an opportunity to work in a situation as simple as that described above would be rare. It is described here only as an illustration of principle. More realistically, the field worker is in a constant struggle with basic tenets about his sampling procedures. First, he must assume that every animal within a sample unit has an equal probability of being seen. Second, if the population is not randomly distributed over the study area, say due to landscape patterns, then the sampling must be appropriately stratified. Third, if clumping of observations is occurring (i.e., animals are not randomly distributed), say, due to social behavior, then he must use appropriate statistical procedures in making his calculations. Finally, all aspects of detectability and constancy discussed earlier in this chapter must be addressed.

Mark-Recapture

Possibly some of the most damaging myths affecting wildlife science has concerned the simplicity of estimating wild population numbers with mark-recapture data. Dr. Graeme Caughley, one of the world's leading population ecologists, has warned "Mark-recapture analyses are not particularly robust and small deviations from their implicit assumptions can produce large errors in the results."

Dr. Caughley addressed mark-recapture data analysis in his text on vertebrate population analyses. Dr. G. A . F. Seber presented a review of mark-recapture designs and analyses in his text on population estimation. (See Selected References.) The reader who wants to explore these procedures in depth is referred to those texts.

In his text on population estimation, Dr. M. Begon listed the primary assumptions implicit in the use of mark-recapture data. I will paraphrase this material here with a slight reordering for emphasis.

1. There is equal catchability among all individuals in the population. That is, irrespective of age, sex, or physiological condition, one animal is as likely to be caught as another.
2. Being trapped, handled, and marked one or more times has no effect on an individual's subsequent chances for recapture. A common problem is for experience to cause an animal to be atypically "trap shy" (abnormally difficult to trap or observe) or "trap happy" (abnormally easy to trap or observe.)
3. Trapping, handling, and marking has no effect on the probability of death or emigration. For example, handling and marking must not change the individual's susceptibility to disease or predation or its movement pattern characteristics.
4. Traps are equally available to all individuals. That is, no home range is without a trap and the trapping of one animal does not prelude the trapping of another at any time at the same trap site.
5. Immigration, emigration, reproduction, and mortality during the study are accounted for.
6. All markings are permanent and equally observable on all individuals.

A method of using mark-recapture data which is alternately referred to as the Petersen estimate, Lincoln index, and Lincoln-Petersen method will be described here for three reasons. First, it was the first equation devised for estimating population size. Second, it is probably the simplest of the mathematical models. And third, it is based on simple logic. The reader is forewarned, however, that this model is deceivingly simple and absolutely all of the above-listed assumptions must be met in order for the results to be valid.

The logic is as follows: In a given period, a population of size N is exposed to trapping and the number of individuals trapped and marked is equal to Tm1. In a subsequent period of trapping, Tn animals are trapped and of these, Tm2 were marked in the first period. If all animals are equally catchable, and there were no changes in the population between the first and second trapping periods, then the following ratios will be equal:

$$\frac{N}{Tm1} = \frac{Tn}{Tm2}$$

Since we want to calculate the total population size (N), then

$$N = \frac{Tm1\ (Tn)}{Tm2}$$

For example, if we were studying a field mouse population, we might trap for five days and capture and mark 20 (Tml) animals. We might wait five days, and then conduct another five-day trapping and capture 30 (tn) animals of which 10 (Tm2) were marked in the first trapping period. Theoretically, we can calculate the population size (N) by

$$N = \frac{20\ (30)}{10}$$

$$N = 60$$

Transect Counts

Transect counts of observable animals include King's strip census. Frye's strip census, and flush radius methods. All of these are roughly based on the same field methods and assumptions with slight variations. Burnham et al. (1980) have discussed the use of transect data in detail. (See Selected References.) Anyone considering the use of these techniques should carefully review their treatise.

The logic of the transect count is as follows: If animals are randomly distributed over an area or within stratified subunits of an area and we know the length, width of a transect and number of animals counted on it, then we should be able to calculate the number of animals on the area. In principle, the equation would be

$$N = \frac{A}{WL} \times n$$

where N = number of animals on the area or its subunit

n = number of animals counted on the transect

W = width of the transect

L = length of the transect

A = size of area or its subunit

The simplest example using this approach might be with respect to spotting grouse all of which we assume flush on our approach and that we detect all flushes. Let's say that we walk a two-kilometer (L) transect of a specified width (W) of 100 m (0.1 km). We count 10 grouse along this transect and the study area is 5 sq. km. (A) in size. Now, we calculate the population (N) of grouse as

$$N = \frac{A}{WL} \times n$$

$$N = \frac{5}{(0.1)(2)} \times 10$$

$$N = 250$$

Here again, we have an example of a logical but deceivingly simple estimation model. The basic assumptions are almost always violated. These assumptions are as follows:

1. The study area is sampled (traversed) so that all habitats are sampled in proportion to their percentage composition of the entire area, or sampling is appropriately stratified.
2. If detectability in some habitat is different from that in others, then that habitat is surveyed to obtain a separate subunit estimate, the variance of which should be compatible with that for the rest of the area.
3. Distribution of animals along the transect reflects their distribution throughout the area.
4. No animals along the transect go undetected.

5. Animals pratice no avoidance behavior which results in redistribution along the transect or undetected escape.

Appropriate sample stratification is as important in sampling animal populations as it is for plant populations (Chapter 7). It is unlikely that every habitat is equally attractive to a species of animal, therefore we can expect unequal distribution. An extreme situation might be that where one habitat might only account for 15 percent of the area, but the average individual spends 75 percent of its time in it. Let's also say that animals in this particular habitat are less detectable than when they are in the other habitats. We now have two important reasons to identify this habitat as a special subunit in need of more intensive sampling than the rest of the area.

The assumption that the distribution of animals along the transect approximates the distribution throughout the area is important, but it has two pitfalls. Demonstration of actual spacial distribution at any point in time is, for all practical purposes, impossible. Observers are often confined to roads and trails which themselves may modify animal movements. Alternately, random movements of observers through an understory without broken trails may stimulate avoidance behavior in the animals that should be observed and can result in false conclusions about distribution.

There are three basic approaches to determining the width of a transect and which also address detection and behavior problems to some extent. The first method uses a fixed width deemed appropriate for the distribution of animals and is practical for habitat conditions. The second addresses the problem of uneven detectability among habitats and calculates a mean and standard error of sighting distances perpendicular to the center of the transect. This approach is acceptable in situations where it is known that the animals are not practicing avoidance behavior irrespective of their location relative to that of the observer or the transect center.

The third approach is the flushing radius method. It assumes that at a given location the animal will take flight at the same distance from the observer irrespective of its location relative to the transect center. For instance, a deer might be located 20 m from the center of a transect and detect an observer coming along the transect. It might take flight while the observer is still 100 m away. Theoretically, given the same location and the deer standing at 100 m from the transect, it will not begin flight until the observer on the transect is even with it. In other words, 100 m is the radius of the flushing circle for this animal in this habitat condition. That radius value will vary between habitat conditions and between animals in a given habitat. It should be noted that, particularly when trails or roads are being used as transects, the flushing distances theoretically may describe more of an elipse than a circle because detectability or sense of security may change with distance from the transect center.

As with mark-recapture techniques, transect count procedures are riddled with possibilities for violating basic assumptions. There may be some situations in which they can be used for population estimation; however, the results should be interpreted cautiously. My own experience is that they should be used primarily as indexes to population size. I have used them for this purpose on deer in coastal South Carolina (see Wood, et al. 1985. pp. 25-36 in Beasom and Roberson 1985).

Population Indices

A number of types of indices might be used in detecting changes in actual population parameters. The results of transect count procedures were mentioned above. Other types of indices include captures per trap night in trapping studies, call counts among various species of birds during the breeding period, the occurrence of various animal signs, and others (See Chapter 6).

Theoretically, the population index should provide a perspective of the relative differences between two populations at a given point in time, or the direction, magnitude and rate of change in a given population over time. Even though an index may be reported in units comparable to a population estimate, we are interested in its attribute of accuracy in a very different way.

For example, if we use transect count data to make an estimate of a population density, then we are very interested in how close that estimate is to the real density. If we accept the transect count data as an index, it may also be expressed in density units (e.g., deer per square kilometer). However, in order to be useful, the index must be developed for more than one population or for more than one point in time. Accuracy of the index is a statement of the constancy of the ratio of the index value to the actual population size value. Rarely,if ever, would we know the ratio for each population involved in the comparison, but we assume that they are equal.

Somewhat similarly, we assume that changes in the index over time are linearly correlated with actual changes in the population. In other words, if we could depict with a line on a graph the changes that were really going on in the population and with another line the corresponding changes in the population index values, the two lines would be parallel at all times. The extent to which this condition is not met is a statement of the inaccuracy of the index.

We strive for index accuracy using two forces. First, our best logic is applied to choosing procedures which logically should reflect actual population differences among or between populations. Second, the procedures are rigorously standardized in every respect in order to minimize possible bias and human error.

The second of these applied forces addresses precision of the index as well as accuracy. Herein lies the most valuable attribute of the index. Just as we rarely know the accuracy of a population estimate, we rarely know the accuracy of the index. But index information characteristically is more easily obtained and justified than that needed for a population estimate. Because of this feature of being more readily available, more of it can be collected and precision usually can be gained. High precision is required before meaningful comparisons can be made among and between populations. This level of precision is reached through the compilation of many observations using rigorously standardized procedures.

Territory Mapping

The idea behind this approach for estimating animal numbers is that certain species defend territories and maintain them for their own exclusive use for all or some portion of the year. The technique primarily applies to birds and is most usable during the breeding season when territorial behavior is most prevalent. The method applied to a species of songbird, for instance, would identify each male of a species in a given area, and identify each point on a map of the area where each male perches to announce territory. Theoretically, connecting these perching points with a line on a map should describe the territory of a given bird. When the outlined territory maps fill up the map of the area, then one knows that all breeding males have been accounted for. If the species is monogamous, then the number of territories times two equals the number of breeding birds in that area.

Spot counts are a variation of the territory mapping procedure. They involve the observer identifying the number of different males he may hear calling at a given "spot" on a map. The spots are frequently located along transects on large areas but also may involve only one point on a small area. The techniques may be applied to both monogamous and polygamous species, although in the latter it can only be used to estimate numbers of breeding males. The quality of even these estimates will vary among species. They may be good for species such as woodcock, dove, and possibly grouse, which rarely have subdominant males associated with them. In species such as turkeys and ringed-necked pheasants, however, social grouping of males may cause problems.

Population Models

The age of computers has brought great capabilities for studying populations through the process of modeling. Every model, however, has its limitations. These limitations come from the assumptions upon which the model is based. A good model is synthesized from three types of information sources. First, some person involved in constructing the model must have a basic understanding of the biology of the species and the factors which influence its survival, growth, maintenance, and reproduction. Second, someone involved in the process must be capable of understanding the qualitative description of the basic ecology of the species and translating this into a series of mathematical equations which will be sufficiently dynamic to approximate the dynamic changes in nature. And third, sound quantitative data on various aspects of the species ecology must be used in the formulation of constants and coefficients of variables if the empirical results are to have any meaning.

Dynamic modeling is far beyond the scope of this text. However, there are some simple models which only require a knowledge of basic algebra to use and understand. One such model devised for estimating deer population numbers was described by L. M. Lang and G. W. Wood (1976) in the Wildlife Society Bulletin (Vol. 4, No. 4, pp. 159-166). The reader is referred to that model for the primary purpose of gaining a perspective of the types of input information required in this type of procedure. Also, while the model was developed in Pennsylvania, it has also been found to work well in parts of the southern United States, particularly in Kentucky and Georgia.

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