Woodland Caribou Restoration at Isle Royale National Park

A Feasibility Study

Jean Fitts Cochrane

Technical Report NPS/NRISRO/NRTR/96-03

United States Department of the Interior • National Park Service
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Copies of this report are available from the author:

Jean Cochrane
Conservation Biology Program
University of Minnesota
100 Ecology Building
1987 Upper Buford Drive
St. Paul, MN 55108

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Jean Fitts Cochrane
Isle Royale National Park
800 East Lakeshore Drive
Houghton, MI 49931

Present address:
Conservation Biology Program
University of Minnesota
100 Ecology Building
1987 Upper Buford Drive
St. Paul, MN 55108

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Epigraph

"Here [at the Island Mine spring in August of 1918 or 1919] is where I first met the Isle Royale caribou. I had found their tracks at two or three points along the trail that morning and only a few minutes before had noticed that the juice was still flowing from a bitten milkweed. Then, right at the top of this rise, I rounded this little curve, and down there, where that rock lies by the road, some eight or ten rods away, stood three splendid young bulls, looking back to learn what followed them. Probably they had never seen a man before; at least they had no slightest fear. I stood for five minutes watching them and then walking forword [*sic*] until I had cut the distance in half before they turned and trotted over the little rise ahead. When I had climbed that, they were again looking back and waiting for me. To see what they would do, I yelled, but even then they ran away slowly, though I saw nothing more of them."

"[And then watching from the beach at Lake Desor, after a sunrise swim]. . . . A half mile away, headed from the largest island, where they have been spending the night, perhaps to keep the calves secure from attack by the wolves[1], a line of caribou is swimming toward the main shore. Noses up, antlers lying back almost upon their shoulders (the cows have antlers as well as the bulls) with the calves swimming bravely alongside their mothers, they make a swift passage; and we see them climb the bank, their dripping forms sharply outlined against the green background. We count a full baker's dozen of the adults and are a little in doubt whether there are seven or nine calves. It may be somebody has seen a better section of the Isle Royale caribou herd, but I have never heard them tell of it."

Woodland caribou swimming, Slate Islands, Ontario, Canada. Caribou are excellent swimmers and regularly swim between islands to seek refuge from predators. Photograph: H.R. Timmermann, Ontario Ministry of Natural Resources.

—W.P.F. Ferguson, "Wildlife and Adventures Along the Great Desor Trail on Isle Royale," *Detroit News*, 28 May 1922

[1] A popular term for the coyote *(Canis latrans)* in those days was "brush wolf."

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Acknowledgments

Numerous people aided this study immeasurably by discussing and sharing literature on caribou biology, caribou translocation, and Isle Royale's resources with me. Chris Martin's draft paper on the history of caribou on Isle Royale stimulated my interest in the project. Tim Cochrane contributed a wealth of historical leads and insights, especially concerning Native American use of Isle Royale and the island's relations to the mainland. Terry Kreeger's preliminary VORTEX modeling runs were invaluable.

Although brief, a June 1990 visit to Isle Royale by caribou expert A.T. (Tom) Bergerud of British Columbia and H.R. (Tim) Timmermann of Ontario was a great asset. Peter Gogan, Rolf Peterson, and Joanne Thurber assisted with study planning and discussions throughout the project. Finally, Bob Krumenaker, former park resource management specialist, was very supportive from the beginning of the study. Others who took time to share their knowledge were Dick Anderson, Tom Cooley, Bruce Connery, Gordon Eason, Jay Gore, Peter Jordan, Murray Lankester, Mark McCollough, Jim Nelson, Rick Page, Bill Samuels, Greg Servheen, Steve Schmidt, and additional members of the North Central Caribou Corporation. Thanks also to Mary Fitts, Nan Cochrane, Greta Pelto, Julie Cochrane, and Sue Salaniuk, and to Corrine, Andrew, and Madaline.

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Summary

Interest in restoring woodland caribou *(Rangifer tarandus caribou)* to Isle Royale National Park was sparked by recent caribou relocations on other Lake Superior islands in Ontario and by the marked decline of wolf *(Canis lupus)* numbers on Isle Royale[1]. Further stimulus came from caribou biologists (Bergerud and Mercer 1989) suggesting that the absence of white-tailed deer *(Odocoileus virginianus)* and predators other than wolves should favor caribou restoration on Isle Royale compared to most mainland sites.

National Park Service (NPS) policies provide direction for the restoration of native species in National Parks. Criteria that must be evaluated include the species' historical presence and the role of humans in its extirpation, and project feasibility including the prognosis for establishing a self-sustaining, viable population without harming other resources or people.

Woodland caribou roamed over Isle Royale for more than 3,500 years until they disappeared around 1928. Overhunting throughout the Lake Superior region in the 19th century, including on Isle Royale, initiated the species' decline. The caribou's regional extirpation has also been linked to the northward range expansion of white-tailed deer and the increase in moose *(Alces alces)* and wolf numbers that followed forest clearing by Euro-American settlers. While wolves and deer did not immigrate to Isle Royale before the caribou disappeared, moose and coyotes *(Canis latrans)* arrived on the island shortly after the turn of the century. Coyote and native lynx *(Lynx canadensis)* predation likely eliminated the remnant caribou herd on Isle Royale, which by this time was isolated from the caribou population in northern Ontario. Thus, humans contributed both directly and indirectly to the caribou's decline on the island.

The feasibility of restoring caribou to Isle Royale depends upon the suitability of habitats currently available in the park, the estimated vulnerability of a translocated population to extirpation, the logistics and costs of translocation and monitoring, and the likely impacts and management requirements of a restored caribou herd. Each of these topics is addressed in this study.

In brief, forage resources on Isle Royale appear to be suitable for caribou. The key predictor of habitat quality, however, is the adequacy of escape habitat[2] to buffer caribou from wolf predation. The numerous offshore islets surrounding the main island of Isle Royale would provide escape habitat, except in winters when ice forms between the islets and the main island. In some winters the weather may be severe enough to eliminate all water-related escape havens. We cannot predict whether wolves would learn to seek out caribou or whether introduced caribou would learn to use available escape habitat.

Population modeling indicates that a small caribou herd would have a high probability (90%) of extirpation within 40-60 years of release. This prediction assumes that wolves would be present at high densities (0.01/km^2), restricting the caribou to secure habitats and limiting the population to 54 or, more likely, fewer caribou. Hence, a self-sustaining, viable population would not be achieved in isolation from other populations.

[1] In this text, "Isle Royale," "the island," and "the park" refer to the main island and surrounding archipelago now comprising Isle Royale National Park.

[2] "Escape habitat" means physical features in the landscape that allow caribou to avoid detection by predators, or elude predators if they are detected and pursued. Examples include islands, large bogs, and rugged terrain.

Woodland caribou from the Slate Islands, Ontario, are available for translocation, duplicating procedures used successfully by the Ontario Ministry of Natural Resources. Disease and parasite screening and treatment for import into the United States could complicate the translocation process. The released animals would have to be monitored carefully for a number of years to assess the success of the restoration. Translocation and monitoring costs for a full-scale restoration project could reach $100,000 per year for three or more years.

Potential impacts of a small caribou herd include threats to rare plants and introduction of diseases or parasites to Isle Royale's isolated moose herd. Although woodland caribou are a historic element of the park, the island ecosystem has continued to evolve in the decades since caribou disappeared. These concerns would have to be investigated as part of the environmental assessment of any caribou restoration plan.

Isle Royale is a National Park and an island wilderness supporting unique floral and faunal communities. In this setting, managers face special challenges if they attempt to sustain or restore viable populations of large, rare animals, such as caribou and wolves, while maintaining other resource values.

Introduction

Restoration of extirpated species has been promoted since the first investigations of wildlife populations in the National Parks (Wright et al. 1933). In 1932, Wright et al. (1933) called for "biological engineering" to restore parks to their "primitive dynamic balance." Their proposed policy for the National Parks stated "that any native species which has been exterminated from the park area shall be brought back if this can be done. . . . Restoration of an animal which has been exterminated is desirable not only because it will bring back that species itself, but because it will fill once more the niche that was deserted. . . ." (ibid, p. 23).

In 1963, the Leopold Committee Report (Leopold et al. 1963) called for restoring naturally functioning ecosystems, with the goal that national parks "represent a vignette of primitive America" before Euro-American settlement. In a subsequent report titled, "National Parks: From Vignettes to a Global View" (often called the Gordon Report after the principal author), the Commission on Research and Resource Management Policy in the National Park System (1989) called for the National Park Service to maintain and restore native biota, but to resist establishing alien species. The Gordon Report urged NPS managers to become "ecological engineers" when necessary to keep ecosystems functioning (ibid).

Under current management policies (U.S. Department of the Interior, National Park Servce 1988, 1991) the NPS will strive to restore native species to parks wherever all of the following criteria can be met:

1. Adequate proof exists that the species occurred in the area and that it disappeared, or was substantially diminished, as a direct or indirect result of human-induced change to the species population or to the ecosystem.

2. Adequate habitat (land, water and other essential elements) to support the species either exists or can be reasonably restored in the park and if necessary on adjacent public lands and waters, and once a natural population level is achieved, it can be self-perpetuating (a "viable population").

3. The species does not pose a serious threat to the safety of park visitors, park resources, or persons or property outside park boundaries.

4. There are no significant problems with predators at the release site, or the problems can be resolved.

5. The subspecies used in restoration most nearly approximates the extirpated subspecies or race.

6. A review indicates that the prospects for natural reestablishment are minimal, but that restoration has a good chance of success.

7. A restoration action plan has been developed.

The purpose of this study is to assess the feasibility of restoring woodland caribou within Isle Royale National Park and address the NPS restoration criteria. A previous study (Martin 1988) reviewed the history of caribou on Isle Royale and provided a preliminary assessment of restoration potential. Interest in reintroducing caribou to Isle Royale has heightened recently due to transplantation successes on other Lake Superior islands and the decline of wolf numbers on Isle Royale (Bergerud and Mercer 1989, Cutler 1989). Bergerud and Mercer (1989) contended that, with no white-tailed deer, attempts at Isle Royale should be favorable compared to mainland sites infected with the meningeal brainworm *(Parastrongylus tenuis),* a parasite fatal to woodland caribou.

Study Objectives

This feasibility study addresses five objectives:

1. Determine historical caribou population levels and the causes of their decline on Isle Royale.

2. Assess the suitability of habitat on Isle Royale for sustaining a caribou population.

3. Analyze the vulnerability of an introduced population to extirpation.

4. Assess the feasibility of translocating caribou to Isle Royale.

5. Identify the potential impacts and management implications of reintroducing caribou on Isle Royale.

Background

Isle Royale National Park

Isle Royale National Park is a 544-km^2 island archipelago lying 24 km south of the Canadian mainland in Lake Superior (Figure 1). The main island of Isle Royale stretches 72 km long and 14 km wide and is surrounded by more than 200 smaller islets. A series of parallel ridges and valleys running the length of the main island characterizes Isle Royale's topography, with steep, north-facing cliffs and gradual south slopes (Figure 2). Inland lakes and linear bogs are numerous.

Isle Royale's climate is cool and moist, with a notable moderating influence from Lake Superior (Hansen et al. 1973). Mean growing season temperature is 11.6°C (Strommen 1969) and mean rainfall exceeds 5 cm every summer month (Slavik and Janke 1987). Snow falls from October to April

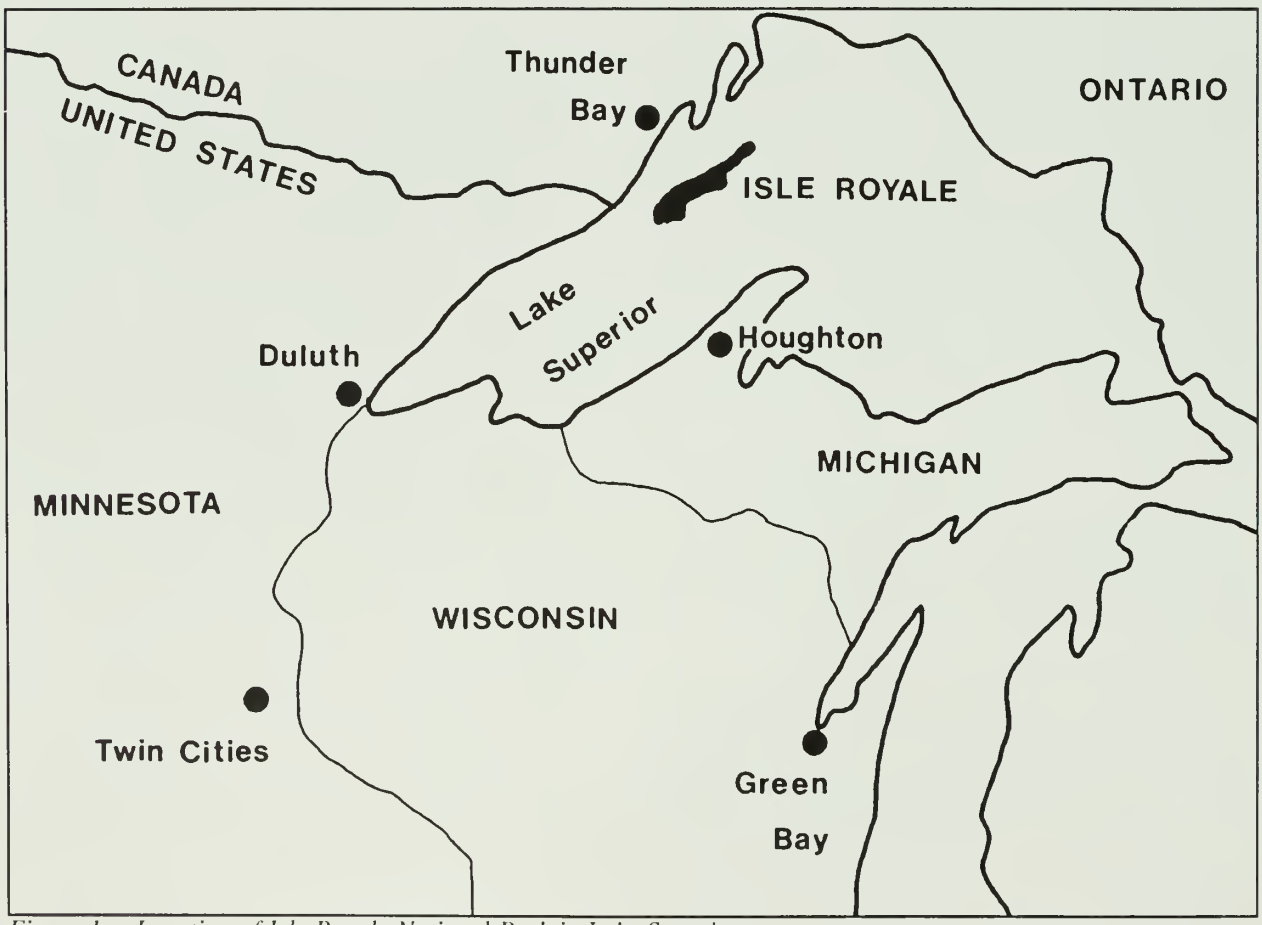

Figure 1. Location of Isle Royale National Park in Lake Superior.

or May, with midwinter snow depth usually 60-77 cm (Peterson and Allen 1974; R.J. Krumenaker, pers. comm.). Ice frequently forms between the closest surrounding islets and the main island, and ice occasionally forms around all islets and to the Canadian mainland (R.O. Peterson, pers. comm.).

Figure 2. *Topography of Isle Royale. This aerial photograph of the northeast end of Isle Royale illustrates the island's ridge and valley topography, with a fingerlike shoreline of long bays ringed by chains of islets. Photograph: Isle Royale National Park.*

Isle Royale falls at the southernmost limit of the northern coniferous forest region (Slavik and Janke 1987). The balsam fir, white spruce, paper birch, and quaking aspen *(Abies balsamea, Picea glauca, Betula papyrifera,* and *Populus tremuloides)* forest types cover nearly two-thirds of Isle Royale (Linn 1957, Hansen et al. 1973). At higher elevations away from the lakeshore, sugar maple and yellow birch *(Acer saccharum* and *Betula alleghaniensis)* forests dominate (Linn 1957), but cover only about 5% of the island (Hansen et al. 1973). This forest community represents a northern limit of the temperate deciduous or Great Lakes-St. Lawrence forest region. Other less prevalent plant communities on Isle Royale include black spruce *(Picea mariana)* bogs, northern white cedar *(Thuja occidentalis)* swamps, rock outcrops, and jack pine *(Pinus banksiana)* and black spruce stands. In 1936, a fire fueled by logging slash and drought burned nearly 20% of Isle Royale, resulting in an almost pure stand of paper birch (Slavik and Janke 1987). Natural fire frequency is probably only 0.5-1.0 fires per year (Hansen et al. 1973; R.J. Krumenaker, pers. comm.), and recent fires have demonstrated the typically slow-burning condition of forest fuels on Isle Royale.

Characteristic of an isolated island, the fauna on Isle Royale is less diverse than an area of similar size on the adjoining mainland. At present, muskrat *(Ondatra zibethicus),* beaver *(Castor canadensis),* snowshoe hare *(Lepus americanus),* short-tailed weasel *(Mustela erminea),* mink *(Mustela vison),* river otter *(Lutra canadensis),* red fox *(Vulpes vulpes),* timber wolf, and moose are the only larger mammals living on Isle Royale (Jordan 1981). Species composition has shifted markedly in this century, including the arrival of moose, red foxes, coyotes, and wolves, and the disappearance of marten *(Martes americana),* lynx *(Lynx canadensis),* coyotes, and caribou (ibid). White-tailed deer were introduced in 1910 but never prospered; none were seen after 1936.

In addition to reduced diversity, islands often support atypically high animal densities, and Isle Royale's moose and wolf populations fit this pattern. Moose arrived in 1905 and increased rapidly to 1,000-3,000 in the early 1930s, then the population crashed to about 200 animals by 1935 (Krefting 1974). Forest regeneration after the 1936 fire stimulated another less dramatic population surge followed by a die-off in 1948-50. Since wolves immigrated to Isle Royale in 1948, moose numbers have remained between 500 and 1,600 (Krefting 1974, Peterson 1992) (Figure 3). Wolf numbers remained in the low twenties through the 1960s, then increased in the 1970s (to 50 in 1980) and declined in the 1980s (to 12 in 1989) (Peterson 1990). As of March 1992, moose numbered about 1,600 and wolves still numbered 12 (Peterson 1992).

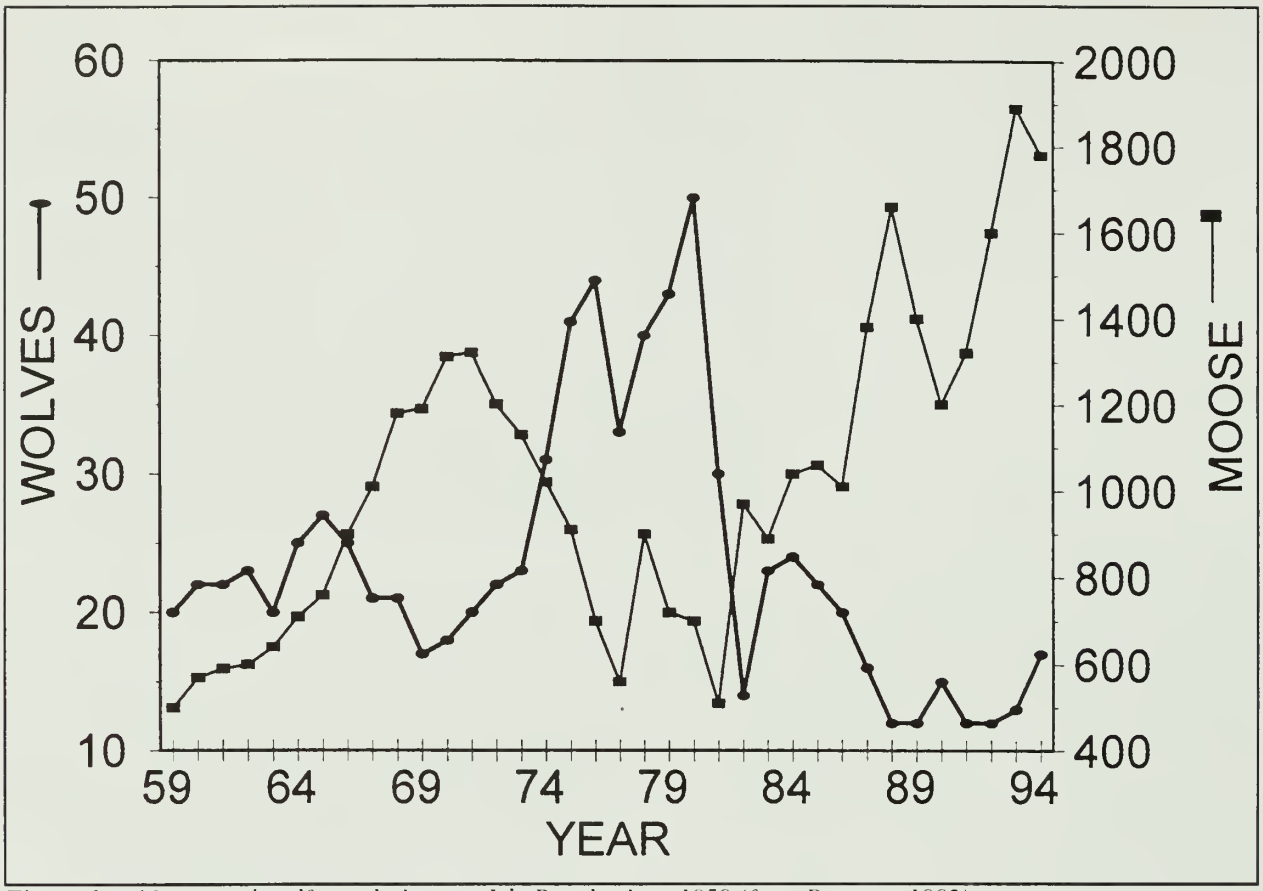

Figure 3. *Moose and wolf populations on Isle Royale since 1959 (from Peterson 1992).*

Isle Royale National Park was established in 1931; since 1977, 99% of the land area has been formally designated as wilderness (Karamanski et al. 1988). Humans have used Isle Royale, however, for over 4,500 years (Crane and Griffin 1965). Archeological evidence of seasonal hunting, fishing, maple sugaring, and copper mining during the Archaic and Woodland periods has been found at numerous Isle Royale sites (C. Clark, pers. comm.).

In historic times, hunting and trapping for subsistence and for the fur trade, as well as a commercial fishing operation for the American Fur Company, preceded the Ojibwa Indians' cession of Isle Royale to the United States in 1842 (Karamanski et al. 1988). Subsistence use by north shore Lake Superior Ojibwas continued at least into the 1870s. After cession, Euro-American settlement came haltingly with three copper exploration booms (in the 1850s, early 1870s, and early 1890s), Scandinavian fishermen, and finally tourism and summer homes in this century (ibid).

Presently, Isle Royale has no roads or year-round residences. Dwellings are limited to park headquarters on Mott Island, two main visitor entry areas at Rock Harbor and Windigo, five outlying ranger stations, and about 16 active life leases to summer residents, principally in Tobin Harbor (Figure 4). Approximately 15,000 persons visit Isle Royale each year from May to October, either staying at Rock Harbor Lodge, in private boats, or hiking and camping on the 267-km trail system. Camping is restricted principally to designated campgrounds, including 12 inland sites, 18 shoreline sites, and 6 sites on offshore islets. Winter occupancy is limited to the wolf-moose research team from mid-January to early March.

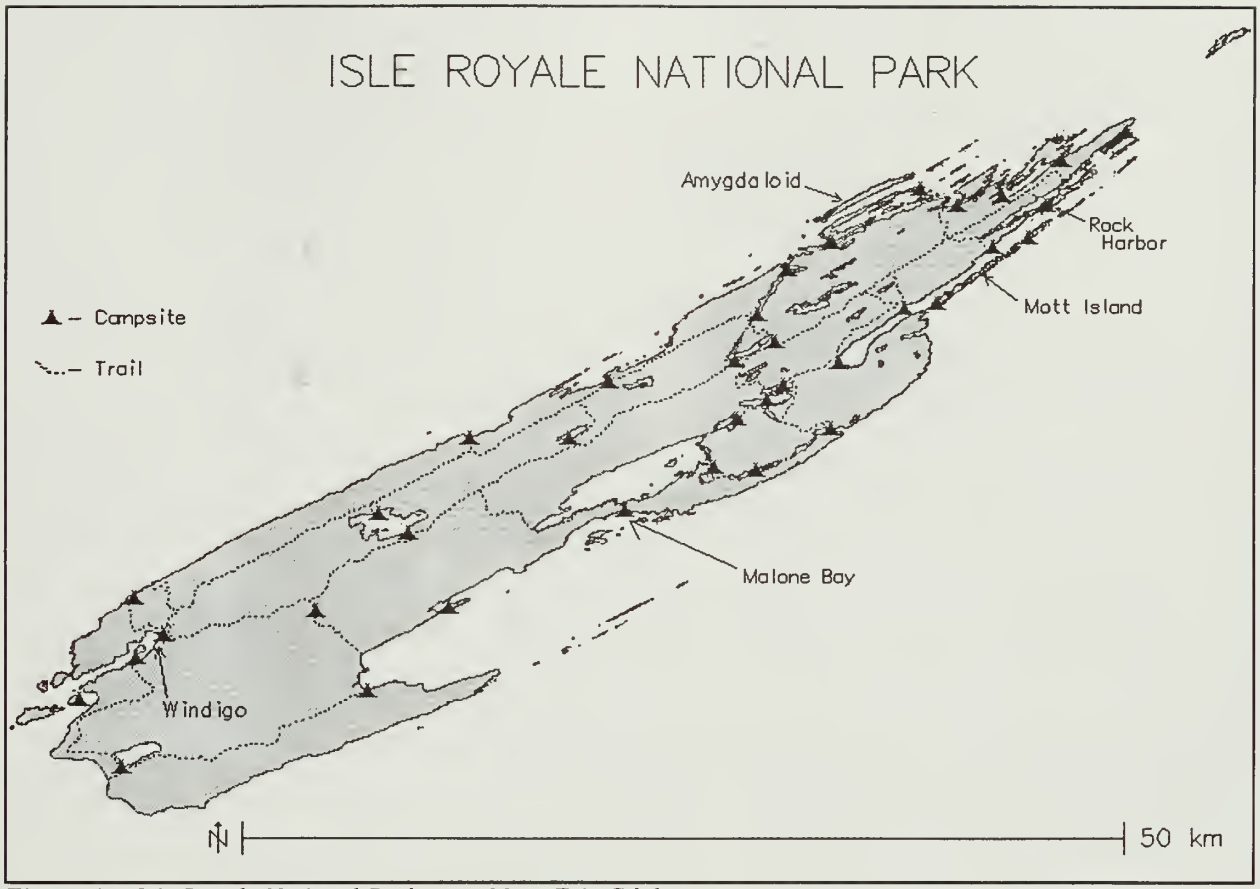

Figure 4. *Isle Royale National Park map. Map: Eric Gdula.*

Caribou Distribution and Decline in the Lake Superior Region

Before the fur trade and settlement caused major shifts in large mammal distributions in the 19th century, woodland caribou ranged southward from Lake Superior to central Minnesota and Wisconsin, lower Michigan, and southern Ontario (Figure 5) (Bergerud 1978, Baker 1983, Darby et al. 1989). During the late 1800s and early 1900s, the caribou range retreated steadily northward until these large ungulates disappeared from northeastern Minnesota and Isle Royale in the 1920s, and from northwestern Minnesota and Ontario north of Lake Superior to Lake Nipigon in the 1940s and 1950s. Relict herds have persisted in Ontario south of 50° latitude only on the Slate Islands, Pic Island, Pukaskwa National Park on the north shore of Lake Superior, and a few inland sites (Darby et al. 1989) (Figure 6). Together, these herds numbered approximately 500 animals in 1990 (Abraham et al. 1990). Recently caribou have been successfully translocated from the Slate Islands to Michipicoten Island and to Leach and Montreal islands and the Gargantua Peninsula in Lake Superior Provincial Park farther east on the Lake Superior north shore (Figure 6; Appendix C) (G. Eason, pers. comm.).

The woodland caribou's decline in eastern North America has not been explained conclusively. Bergerud (1974*a*, 1978; Bergerud and Mercer 1989) presents the following hypothesis for the northward range retraction of caribou. Woodland caribou have a comparatively low reproductive rate for an ungulate, which balances closely with natural mortality in undisturbed populations. When Euro-

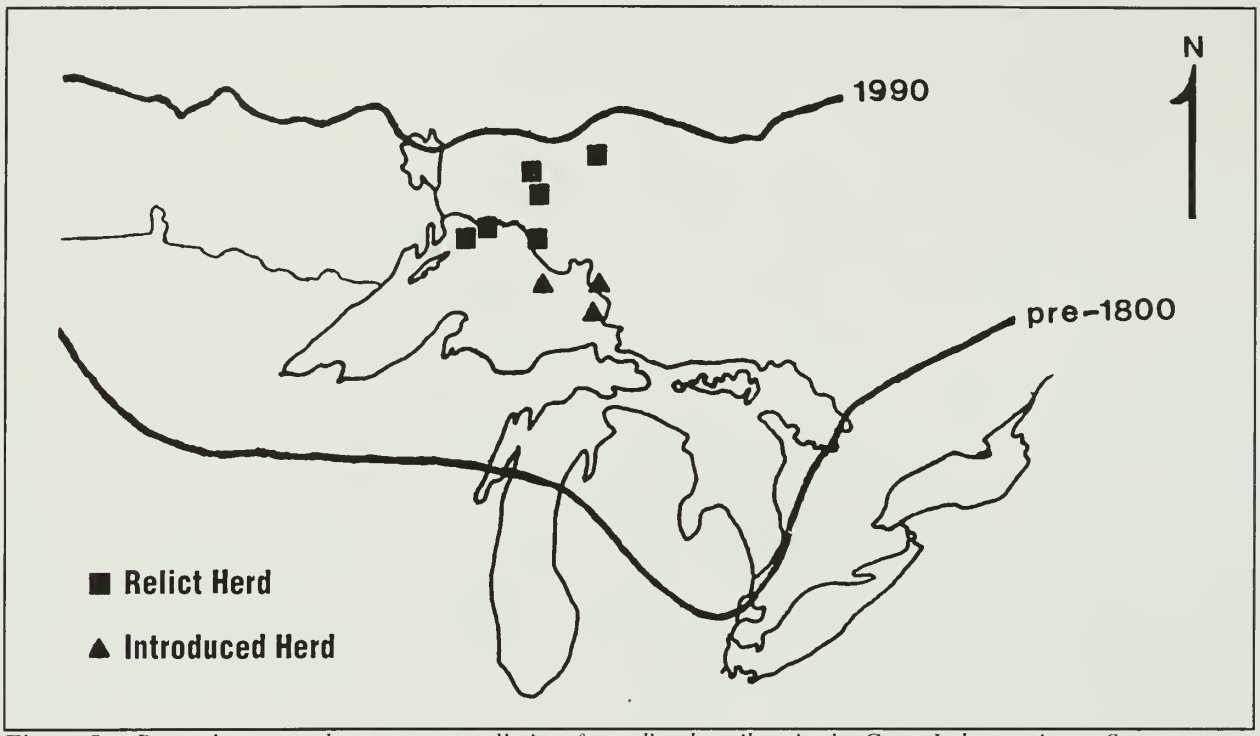

Figure 5. *Presettlement and current range limits of woodland caribou in the Great Lakes region. Sources: Bergerud 1978, Baker 1983, Darby et al. 1989.*

Americans brought firearms to native hunters and increased overall hunting pressure, caribou began to decline. At the same time, extensive forest clearing and burning were greatly expanding early successional habitats. This trend, possibly combined with a period of climate warming after 1860, facilitated the northward range expansion of white-tailed deer and the increase of moose and deer populations.

As the expanding numbers of ungulates increased total available prey biomass, predators, especially wolves, responded by increasing. Thus, both human-caused and natural mortality increased, perhaps sequentially, beyond the capacity for caribou to replace their losses. Bergerud (1978) explains that hunting mortality is typically additive to natural mortality in caribou. Thus, often "there is no surplus for hunters and any hunting will reduce future populations. In addition, population declines are difficult to halt. . . . Hunters can still find caribou [when they are rare]" (Bergerud 1978:93-94). White-tailed deer also carried a parasitic disease highly lethal to caribou, the meningeal brainworm. This parasite has eliminated caribou from any significant range overlap with white-tailed deer (Bergerud 1978).

Applying this hypothesis to the region south of Lake Superior, caribou would have been first severely overhunted and then exposed to the meningeal brainworm before the late 1800s. On the north shore of Lake Superior, overhunting was severe as early as the late 1700s (Lytwyn 1986). White-tailed deer invaded the fringes of this region after 1900, but high moose numbers, and hence, predator densities, are likely the chief control on caribou populations in northwestern Ontario at present (Abraham et al. 1990). Relict herds have persisted south of 50° latitude only where deer are few and refuge habitat insulates caribou from wolf predation (Bergerud 1974*a*).

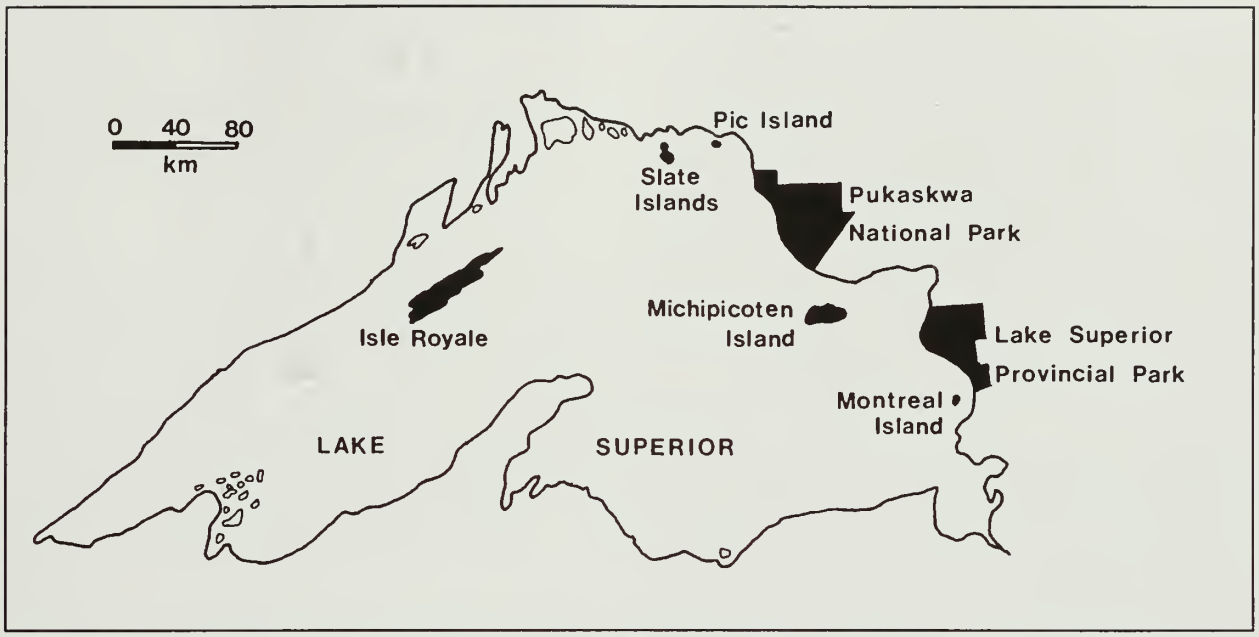

Figure 6. *Relict and introduced woodland caribou around Lake Superior. Source: Darby et al. 1989.*

Caribou on Isle Royale

Woodland caribou were present on Isle Royale for more than 3,500 years until they disappeared in the late 1920s. Their decline paralleled the species' retreat from northeastern Minnesota and Ontario north of Lake Superior. The caribou's decline on the island coincided with their disappearance from the nearest mainland, Ontario's Sibley Peninsula (de Vos and Peterson 1951, Cringan 1956), and these events are certainly related. However, unlike conditions on the mainland, the immediate cause of the Isle Royale caribou extirpation could not have been meningeal disease or wolf predation. Wolves were absent and white-tailed deer—although introduced in 1910—were few or absent on Isle Royale in the 1920s.

Caribou were probably overhunted on Isle Royale during the 1800s. Native Americans had a tradition of hunting on Isle Royale, which became an even more valuable resource when mainland game resources were nearly exhausted in the early 1800s due to the fur trade. Subsistence hunting by European miners and fishermen likely contributed to low caribou numbers on Isle Royale in the mid- to late 1800s.

After 1900, regional faunal changes spilled over onto Isle Royale, bringing a new competitor, moose, and a new predator, coyote, and isolating the Isle Royale caribou herd from mainland populations. Forest burning from 1850 to 1890 by mineral prospectors facilitated a population irruption of immigrant moose. By the late 1920s, moose overbrowsing could have limited caribou food supplies. But caribou were already near extirpation by that time, suffering from coyote predation in addition to lynx predation, and lacking traditional immigrants from the mainland to replenish their reduced numbers. Although a few white-tailed deer were introduced to Isle Royale in 1910, they never prospered and were unlikely to have transmitted the meningeal brainworm to caribou. However, caribou traveling off Isle Royale to the mainland could have been exposed to the parasite.

The density of wolves on Isle Royale is still high compared to most of their mainland range—12 wolves on 544 km^2, or more than twice the maximum density that Bergerud and Mercer (1989) predicted introduced caribou could tolerate. However, caribou escape habitat is available in an archipelago of offshore islands. Thus, Bergerud (pers. comm.) predicted that wolves might continue to depend on comparatively abundant moose, ameliorating predation pressure on caribou if they were restored to the island. Further, wolf researchers predict that wolf numbers are likely to continue a long-term downward trend (R.O. Peterson, pers. comm.). This decline in wolf numbers led Bergerud and Mercer (1989:118) to conclude that "now would be an excellent opportunity to reintroduce caribou to this National Park."

METHODS

Following is a summary of the methods used for this study and an overview of the Results and Discussion section.

Why Did Caribou Disappear from Isle Royale? I drew many historical references from Martin's (1988) draft report on the history and restoration potential of three Isle Royale extirpated species, marten, lynx, and caribou. Further research led to numerous sources in the Isle Royale National Park archives, unpublished fur trade records, the Michigan Historical Collections at the University of Michigan's Bentley Historical Library, and a variety of published literature.

Habitat Suitability. The initial proposal for this feasibility study called for adapting a northern Minnesota woodland caribou habitat suitability index model (HSI) to Isle Royale and assessing Isle Royale caribou habitat through the model. However, the model was not completed as expected in 1990. Thus, I completed a preliminary assessment of habitat characteristics for this report, drawing on published sources, park maps, some field reconnaissance, and consultation with caribou biologists. In the future, quantitative habitat evaluation will be feasible using the park's new geographic information system (GIS).

Population Vulnerability Analysis. I developed a synopsis of typical and projected demographic characteristics for a hypothetical caribou herd, based on published literature and advice from caribou biologists. Then, with assistance from Dr. Terry Kreeger of the University of Minnesota, I employed a computerized population model ("VORTEX," developed by Robert Lacy of the Chicago Zoological Park, Brookfield, Illinois; see Appendix B) to project the long-term viability of this hypothetical population. Repeated simulations resulted in a mean persistence time, probability of persistence to 100 years, and retention of genetic heterozygosity for different initial release alternatives and mortality rate projections.

Reestablishment Methods. I reviewed alternative reestablishment approaches from preceding caribou translocation projects in Canada and the United States. These methods are outlined only briefly in this report, based on the advice of experienced biologists and an understanding of the logistical constraints of work on a wilderness island. Detailed procedures would have to be developed for a restoration plan.

Impacts and Management Implications of Caribou Reestablishment. I tentatively identified the likely impacts of caribou releases on park vegetation and other animals through a review of pertinent literature, communication with other biologists, and familiarity with park resources. I discussed the relationship of this project to other resource management activities with park staff. I also considered examples from other parks, such as Pukaskwa National Park in Ontario. This report provides only a preliminary overview of potential impacts and management concerns that would have to be addressed in much greater detail if caribou restoration is subsequently pursued by the National Park Service.

Results and Discussion

Why Did Caribou Disappear From Isle Royale?

In this section, I outline and critique six hypotheses for why caribou disappeared from the park: migration, disease, competition with moose, predation, overhunting, and fires. This analysis is based on the detailed history of Isle Royale caribou presented in Appendix C.

Migration

The coincident timing of the caribou's disappearance from Isle Royale with the decline of caribou herds on the adjacent mainland has fostered a theory that these mobile animals may have been seasonal migrants to the island archipelago (Stoll 1924*b*, Mech 1966, Martin 1988). Yet caribou were clearly year-round residents on Isle Royale because they were documented there during summer as well as winter and spring. Lake Superior freezes infrequently between Isle Royale and the mainland and regular migration by swimming such a wide channel would be unlikely. Further, the environment on Isle Royale was probably suitable for caribou, providing no apparent impetus for a risky migration to potentially less favorable calving grounds on the mainland.

Yet the Isle Royale herd was not isolated. Caribou are well adapted for travel on ice and they were observed on the lake ice between Isle Royale and both Minnesota and Ontario (Figure 7; Appendix C). Periodic immigration may even have been essential to the long-term persistence of Isle Royale's relatively small herd of at most a few hundred animals. Immigrants would have prevented inbreeding depression and replenished the herd after "bottlenecks" or catastrophic declines, which are common in small populations (Gilpin and Soulé 1986). Thus, Isle Royale supported a resident caribou herd, but over time this herd may have been dependent on a flow of animals from the mainland. Severing this flow could have contributed to the demise of the island's remnant herd.

Disease

Martin (1988) suggested that migrants may have carried meningeal brainworm or other diseases to Isle Royale caribou, but we have no evidence for this hypothesis. The gradual decline of the island's caribou does not describe a population suddenly

Figure 7. *Woodland caribou crossing a frozen lake. Woodland caribou will cross large lakes over the ice, and a number of historical accounts indicate that caribou crossed the area between Isle Royale and the adjacent Ontario mainland. Photograph: H.R. Timmermann, Ontario Ministry of Natural Resources.*

exposed to a fatal parasite. White-tailed deer have not immigrated to Isle Royale, but they were introduced in 1910 by a Michigan state game warden (Wood and Dice 1924 in Martin 1988). Summer resident Frank Warren (1926, 1929) reported that seven or nine animals were released and individuals or tracks were sighted as late as 1925. The Michigan State Game Commission's reports that the herd "increased wonderfully" (*Detroit News* editorial, 3 December 1921) were refuted by others. For example, island visitor and journalist W.P.F. Ferguson (1922*a*) wrote in a letter to Albert Stoll, Jr.: "The [game commission's] estimate concerning the deer on the island is erroneous. Lively, the game warden, tells me that he has seen only two or three. They cannot live with the [brush] wolves [meaning coyotes]."

In 1916-17, W.H. Foster (1917), a warden, estimated that only 20 deer persisted on Isle Royale. Warren (1929) wrote to Albert Stoll, Jr., that coyotes had killed all the deer by 1929, a claim Dr. Frank Oastler (1929) supported after his survey of Isle Royale for the National Park Service. However, residents such as fisherman Ed Holte (Holte and Holte 1965) recalled seeing deer at a salt lick at Pickerel Cove in the early 1930s and that three deer were on Amygdaloid Island during the 1936 fire.

Deer were not reported after 1936 and never approached the density of 0.4/km^2 reportedly required for meningeal brainworm transmission to caribou populations (Karns and Lindquist 1986). Also, brainworm disease symptoms have never been reported in Isle Royale moose, including during the 1930s moose die-off. A report on meningeal brainworm larvae collected from Isle Royale moose feces (Karns and Jordan 1969) was subsequently refuted as an error (Lankester and Hauta 1989).

Competition with Moose

Another possible explanation for the caribou's disappearance from Isle Royale, based on the coincident timing of caribou extirpation with the initial irruption of the moose herd on Isle Royale, is that moose overbrowsing eliminated winter food for caribou (Peterson 1977, Martin 1988). Krefting (1974) summarized the history of moose on Isle Royale. Moose arrived by swimming or crossing the ice around 1905, possibly earlier, having become common on the north shore by the 1890s. A solid ice bridge in the winter of 1912-13 was a likely source of more immigrants. By 1915, the population was well established at 250-300 animals and numbers increased steadily thereafter. Krefting (1974) believed the best estimates for the moose population were 1,000 in 1921-22, 2,000 in 1925-26, and from 2,000 to 5,000 by 1930. The inevitable die-off began in 1933; moose numbers bottomed out at a reported 200 by 1935 (Krefting 1974).

The impact of moose browsing on the food supplies of Isle Royale caribou is difficult to surmise. In 1917, warden Foster (1917) reported that "lichens, which festoon the swamp trees profusely, are...[the moose's] principal diet." He said the caribou were also "lichen and moss eaters," and "edible lichens and tree mosses are abundant." When refuting the high game animal estimates published in the *Detroit News*, Frank Warren (1924) wrote:

> It is my best judgement and belief that the numbers of moose and caribou have been grossly overstated [e.g., by Albert Stoll, Jr.]. It will be many years before they crowd each other for feed (largely browse) except in their favorite places. There are many thousands of acres which I have seen where there are hardly any moose sign, where young poplars and birch abound.

At the time the last caribou were sighted on Isle Royale in 1928, moose density may have reached 4/km^2. By 1930, Murie (1934) recorded overbrowsing on all of the important moose winter foods, such as balsam fir, quaking aspen, paper birch, and American mountain ash *(Sorbus americana).* However, moose and their impacts were concentrated toward the west end of Isle Royale (Krefting 1974). While living on the east end of Isle Royale, Warren (1929)

did not see signs of moose browse on balsam fir until 1927 and in 1929, claimed overbrowsing was still localized.

By this time, Canada yew *(Taxus canadensis),* a primary winter food for caribou as well as moose, had been reduced from understory dominance to virtual absence on the main island (Murie 1934, Janke et al. 1978). Yet yew was still abundant on offshore islands, including Mott Island and Wright Island, as late as 1931 (Krefting 1974). A 1930 photograph of the "Desor Trail" in Albert Stoll, Jr.'s, collection shows a forest festooned with arboreal lichens (*Alectoria* and *Usnea* spp.). The condition of other caribou winter browse, such as ericaceous shrubs and ground lichens (*Cladonia* spp.), was not documented.

In summary, while the absolute abundance of caribou foods was diminished by the late 1920s, starvation is still an improbable explanation for the caribou's demise on Isle Royale. Competition with moose cannot have been the sole nemesis of Isle Royale's caribou because

1. caribou began to decline before moose were abundant (numbering as few as 30 when moose numbered only 250-300);

2. moose do not eat all of the plants that caribou can consume (e.g., ground lichens);

3. prime winter caribou browse was still available on offshore islands and, to a lesser extent, inland when caribou disappeared;

4. browse was still sufficient for moose numbers to increase or be sustained for about five years after caribou disappeared;

5. caribou are highly resilient to winter food shortages (A.T. Bergerud, pers. comm.).

Corroboration for this conclusion comes from the Slate Islands where caribou have survived for decades on minimal winter browse supplies—principally windthrown arboreal lichens (A.T. Bergerud, pers. comm.). Also, caribou can maintain normal fertility rates despite range depletion (Bergerud 1980, 1983). Reindeer introduced to islands have increased to densities over 12/km^2 before starving, without an appreciable reduction in annual productivity (Klein 1968).

Predation

Moose and disease were not the only potential threats arriving from the mainland in the period of great regional faunal change after 1900. Coyotes also arrived on Isle Royale, at least by 1912 and possibly by 1906 (Krefting 1969). By 1916-17, trappers were able to capture 60 "brush wolves," leaving 12 or more (Foster 1917). Krefting (1969) cited reports of increasing coyotes from 1918 to 1925, despite trapping by fishermen and state game wardens.

Coyotes can be effective predators on caribou calves. For instance, newly immigrated coyotes, in conjunction with black bears *(Ursus americanus),* have been implicated for the recent population decline of the isolated Gaspe Peninsula caribou herd in Quebec (E. Mercer, pers. comm.).

Isle Royale residents blamed coyotes for white-tailed deer failing to survive and even the dearth of moose calves in the park in the late 1920s (Ferguson 1922*c*, Warren 1929). Michigan Conservation Department official Hugh E. Green visited Isle Royale in 1928 "in the interest of improving game conditions in Isle Royale, as it had been reported that coyotes are becoming so numerous they threaten other wildlife" (Anonymous 1928). Predator control programs were common in this era and were apparent by the series of game wardens (trappers) that were placed on Isle Royale after 1916.

At the same time coyotes were colonizing Isle Royale, lynx were still commonly seen (Martin 1988). For example, Foster (1917) reported 67 lynx captured in 1916-17, and fisherman such as Milford

Johnson (1965) recalled that lynx were common and trapped occasionally in the decades before 1930. During periodic snowshoe hare population crashes, Isle Royale lynx may have been heavily reliant on caribou calves for alternate prey. Bergerud (1971) has demonstrated that lynx can control caribou herd recruitment during these phases.

Fisherman Pete Edisen (Edisen and Edisen 1965) raised the possibility of a third caribou predator. Pete recalled that most of the island residents owned dogs, an observation borne out in numerous photographs. These dogs bred with the "brush wolves" and ran in packs (ibid). Feral dogs can be efficient hunters. If they were roaming Isle Royale as Pete suggested, they could have contributed to the caribou herd's predation problems.

Figure 8. *Caribou hunters on the north shore of Lake Superior in 1925 or 1926. Photograph: O. Anderson, courtesy of H.R. Timmermann, Ontario Ministry of Natural Resources.*

Overhunting

None of the 20th-century invaders mentioned earlier—the hypothetical competitor, disease, or predators—explains why caribou numbers were apparently so low on Isle Royale in the 19th century. In North American boreal forests, caribou densities average 0.3-0.4/km^2 in association with natural predator numbers and scarce alternate prey (Bergerud 1980, 1983, pers. comm.). Covering 544 km^2, providing ample food supplies, and having only lynx for a predator, Isle Royale should have supported at least an average density of caribou in the 19th century—or 200 animals. Stoll's (1926) population estimates for pre-1920, 200-400 animals, exceeded this average boreal density. Other observers may have underestimated the number of these reclusive animals on Isle Royale, a common bias for estimates of dispersed animals in forested habitats (Hickie n.d.). In contrast, the evidence points to low caribou numbers on Isle Royale before 1900, specifically 1840-90.

These 19th-century dates coincide with a period of overhunting in the Lake Superior region, from the end of the fur trade through the peak of Euro-American settlement. Native American hunters would certainly have been drawn to Isle Royale when game was depleted elsewhere by the 1830s, especially given their tradition of visiting the island and Isle Royale's reputation for abundant game. Later in the 19th century, miners and fishermen would have been both well armed and typically short of red meat, with plenty of time in the winter to shoot caribou (Figure 8). Thus, despite finding few documented records, I conclude that caribou were probably hunted regularly on Isle Royale before 1900. Elsewhere, annual hunting mortality as low as 5% of a population has initiated caribou population declines (Bergerud 1980).

Fires

The extensive forest fires ignited by mineral explorers periodically between 1850 and the 1890s altered forest composition and successional stages on Isle Royale (Hansen et al. 1973, Janke et al. 1978). By reducing lichen biomass, fires can reduce habitat suitability for caribou for many years (Bergerud 1978, Abraham et al. 1990, Schaeffer and Pruitt

1991). In the long run, fires in mature conifer forests should benefit caribou by restoring ground lichen biomass (ibid). In habitats where caribou are not dependent on lichens for winter browse, the negative effects of fire may be minimal. Thus, fire may be a partial but secondary explanation, along with overhunting, for the caribou's decline on Isle Royale after 1840.

Summary

In terms of conservation biology, overhunting and perhaps fires in the 19th century most likely began an "extinction vortex" (Gilpin and Soulé 1986) for Isle Royale's caribou by reducing their numbers below a critical minimum level. The subsequent disappearance of caribou on the adjoining mainland shores broke a link to continental populations, assuring this remnant herd's isolation. An isolated herd of less than 50 animals could have vanished over time merely by chance demographic events, such as a series of years with poor recruitment, or from a random catastrophe, such as most of the animals wandering off toward Canada on thin ice.

I speculate that if numbers were actually as low as 30, as game warden Foster (1917) estimated in 1917, then the most likely cause of the caribou's final disappearance from Isle Royale was coyote and lynx predation. However, if numbers were still as high as 200-300 just before 1920, as Stoll (1926) suggested, then caribou were more likely to have suffered from direct competition with moose in addition to increasing predation. In any case, reduced food supplies could have exacerbated the downward population vortex by reducing individual fitness.

In conclusion, humans contributed to extirpating Isle Royale's caribou both directly and indirectly. Native American and Euro-American hunting reduced caribou numbers, perhaps greatly, in the 19th century. Extensive, human-caused forest fires may also have reduced Isle Royale's carrying capacity for caribou for some time. Overhunting and forest clearing on the mainland removed caribou from the adjacent shore and isolated the Isle Royale herd. By creating early successional habitats on the mainland, settlers also facilitated moose and coyote immigration to Isle Royale. Once on Isle Royale, moose and coyotes benefited from the expanse of early successional habitat created by miner's fires, at the expense of caribou. Thus, numerous, seemingly "natural" events—range expansions, disease, and predator responses—were played out on a landscape that human activity had greatly altered.

Habitat Suitability

The habitat suitability index model for woodland caribou in northern Minnesota, being prepared under contract to Voyageurs National Park (Gogan et al. 1991), was not completed in time for this study as anticipated. Hence, the following discussion is an overview of habitat resources on Isle Royale based on (1) prior vegetation surveys and maps (Hansen et al. 1973, Slavik and Janke 1987); (2) measurements of offshore islets using the nascent Isle Royale GIS at Michigan Technological University; (3) site visits on the northeast end of Isle Royale; and (4) assessments by biologists familiar with caribou, Isle Royale, or both.

Forage Resources

Slavik and Janke (1987:94-95) provided an overview of Isle Royale plant communities, as follows:

> Isle Royale is densely forested. Two distinct forest types reach their climax there. The island is situated at the southernmost limit of the northeastern coniferous forest. The spruce/fir/paper birch boreal forest type . . . achieves its climax here at the lower elevations around the periphery of the island where climatic conditions are moister and cooler (Linn 1957). . . . Other tree species commonly encountered in the boreal forest are northern white cedar and quaking aspen. Common ground cover plants found

in the mature northern boreal forest are large-leaved aster *(Aster macrophyllus),* wild sarsaparilla *(Aralia nudicaulis),* Canada dogwood *(Cornus canadensis),* clintonia *(Clintonia borealis),* twinflower *(Linnaea borealis)* and bristly club moss *(Lycopodium annotinum).* Tall shrubs are represented by thimbleberry *(Rubus parviflorus)* and mountain alder *(Alnus crispa).*

The second climax association is found on the westernmost end of the island. At higher elevations away from Lake Superior, where the soil is drier and the air warmer, the sugar maple and yellow birch association is the climax forest type (Linn 1957). Sugar maple is at its northernmost limit here as part of the temperate deciduous forest biome. This smaller climax association covers only about 7% of the island. . . . These two upland forest types which dominate Isle Royale are in sharp contrast to the lowlands between the parallel system of ridges. These contain a vast amount of wooded swamp composed of black spruce and northern white cedar.

Also in these lowland areas many bogs are found. The bog communities of Isle Royale are rich in plant life, with sedges often dominating the sphagnum mat. . . .

In 1936 20% of the island was burned and the humus layer was destroyed. This region, stretching from Siskiwit Bay in the west to Moskey Basin in the east, is now almost a pure stand of paper birch with scattered quaking aspen. The abundant ground cover species here are large-leaved aster, thimbleberry, bracken fern *(Pteridium aquilinum),* and wild sarsaparilla.

In the late 1960s, Krefting et al. (1970) produced a forest cover-type map of Isle Royale, which is described in greater detail by Hansen et al. (1973) (Figure 9). They recognized 27 vegetation types in 7 cover groups on Isle Royale (Table 1).

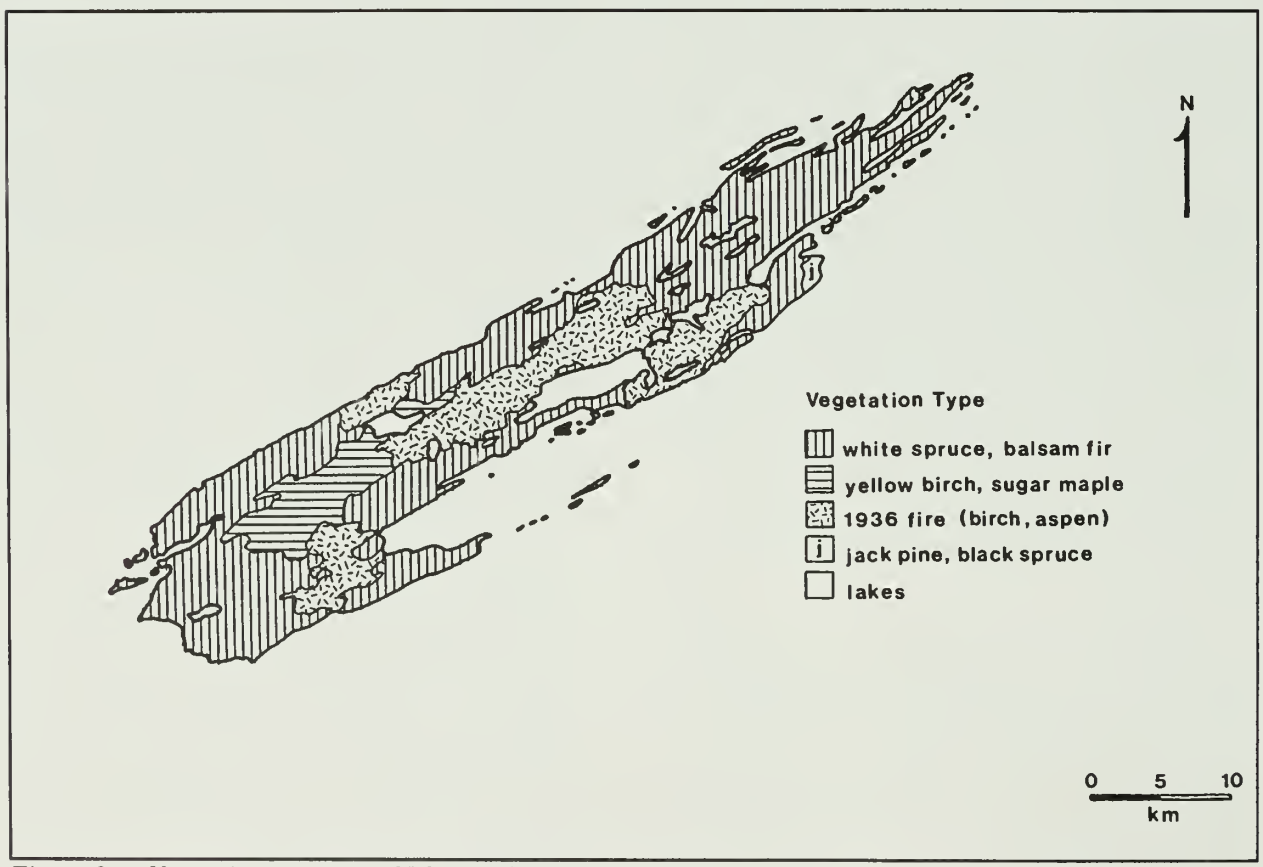

Figure 9. *Vegetation type map of Isle Royale National Park.*

Table 1. Isle Royale vegetation and nonvegetation cover types and areas covered.

Cover Type Description	Hectares Covered	Percent Covered
Quaking aspen, paper birch, balsam fir, white spruce	27,731	51
1936 burn	10,505	19
Black spruce, northern white cedar (and balsam fir, tamarack *[Larix laricina],* or both)	5,570	10
Yellow birch, sugar maple (and paper birch, balsam fir, or both)	4,161	7
Lakes (30 named)	3,415	6
Rock outcrop	2,011	4
Jack pine (and black spruce)	177	1
Shrubs	503	1
Beaver ponds	477	1
Total	54,550	100

Adapted from Hansen et al. 1973.

Moose browsing has profoundly affected forest composition on Isle Royale (Snyder and Janke 1976, Krefting 1974). For example, moose had virtually eliminated Canada yew from the main island by 1930, where it had been the dominant shrub (Murie 1934, Snyder and Janke 1974). After more than 60 years of heavy browsing, balsam fir, mountain ash *(Sorbus americana),* and shrubs such as red osier dogwood *(Cornus stolonifera),* squashberry *(Viburnum edule),* and highbush cranberry *(Viburnum trilobum)* have been reduced in dominance in the boreal forest type (Snyder and Janke 1974, Jordan 1978). Only white spruce is increasing among the main tree species, because it is not eaten by moose.

The net effect of moose browsing is a more open forest, with more abundant ground cover due to increased light penetration (Snyder and Janke 1974). Forage available to moose also declines unless replenished by fire or another disturbance (Figure 10). However, bryophyte and lichen cover are apparently unaffected by moose browsing (ibid). Despite the substantial effects moose have had on the Isle Royale forest, browse supplies have been sufficient to support a large moose herd for decades. Moose density has averaged 2.9/km^2 (Peterson 1992). Under current vegetation trends, carrying capacity for moose should decline gradually—but unpredictable events could alter this trend.

Snyder and Janke (1974) demonstrated that the effects of moose browsing have been considerably less on offshore islets than on the main island, especially on islets that are less frequently connected to the main island by ice. Thus, more remote islets remain barely touched by moose (Figure 11).

Woodland caribou and moose diets overlap somewhat. Yet, caribou usually bypass deciduous twigs and balsam fir, which are the staples of moose winter diets (Cringan 1957, Simkin 1965, Bergerud 1972, Darby and Pruitt 1984, Edmonds and Bloomfield 1984). Alternately, plants rarely taken by moose form the core winter diet of caribou—arboreal and terrestrial lichens, sedges, and ericoids. On Isle Royale, these typical caribou winter foods are not regularly eaten by moose, although moose do eat some arboreal lichens in the park (R.O. Peterson, pers. comm.). Bogs are scattered all across the main island and surrounding islets, providing patchy supplies of bog ericoids and sedges (Stardom 1975, Brown and Theberge 1990) (Figure 12).

Figure 10. *Savanna habitat near Windigo created by intensive moose browse. Moose have virtually eliminated the shrub layer in some favored habitats on Isle Royale. Photograph: R. Janke, Isle Royale National Park archives.*

Figure 11. *Lightly browsed habitat on Smithwick Island. In the early 1970s, moose had not browsed the vegetation on Smithwick Island. Yet by 1990, when this photograph was taken, favored species such as yew and mountain ash showed signs of browsing, indicating that moose had wintered on this Rock Harbor island in recent years. Still, forage supplies remain abundant on Smithwick Island and other islets that moose do not regularly occupy. Photograph by the author.*

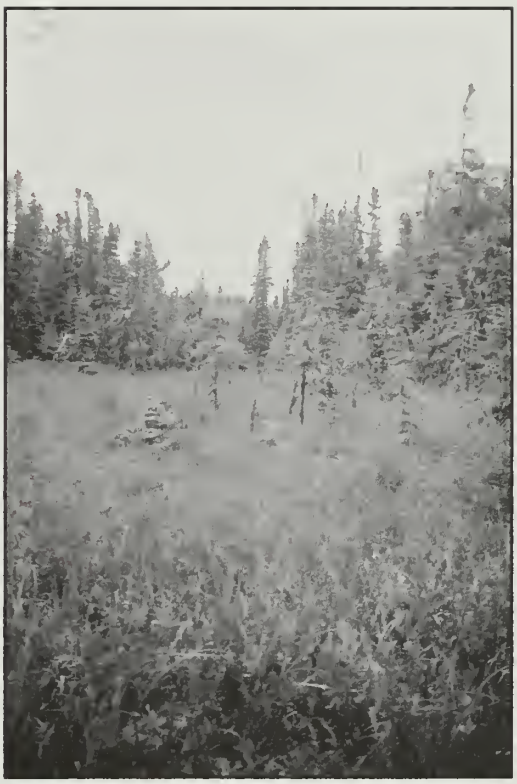

Figure 12. *Bog on Raspberry Island. This bog is typical of Isle Royale's numerous, small black spruce bogs. Photograph by the author.*

Figure 13. *Jack pine stand with ground lichens, Saginaw Peninsula. Isle Royale's only substantial stand of jack pine is on the Saginaw Peninsula. This forest has not burned since the 19th century. Ground lichens are a common ground cover in this forest type. Photograph by the author.*

Ground lichen supplies maybe more sparse on Isle Royale than in northern Ontario. Although widely scattered in rocky openings throughout Isle Royale and especially along south-sloping shorelines, the only extensive ground lichen mats are in the jack pine and black spruce stands on the Saginaw Peninsula (R.O. Peterson, pers. comm.) (Figure 13). In the late 1960s, jack pine forest stands covered only 177 ha (0.32%) of Isle Royale (Hansen et al. 1973). Additional, small outcrops supporting jack pine and ground lichen mats that were not mapped by Krefting et al. (1970) are scattered around the east end of Isle Royale. The Saginaw Point jack pine stands have not burned since the 1890s so ground lichen biomass may be diminished from historical levels. Subsequent burns in this fire-adapted community could eventually improve forage conditions for caribou by restoring the ground lichen cover (Bergerud 1978, Abraham et al. 1990, Schaeffer and Pruitt 1991).

Arboreal lichens are common in the boreal forest type, especially in the cool, moist microhabitats near the lakeshore and on islets (Figure 14). Arboreal lichens are most noticeable in mature balsam and spruce trees and less common in the decadent birch and aspen stands or densely stocked young fir stands.

Summer foods for caribou are abundant on Isle Royale. In particular, thimbleberry, which has become the dominant understory shrub across much of Isle Royale because moose avoid eating it, would provide summer browse for caribou (A.T. Bergerud, pers. comm.). Similarly, caribou could take advantage of the expansive quantities of large-leaved aster, bracken fern, Canada dogwood, twinflower *(Linnaea borealis),* and numerous other herbs as well as mosses and lichens that are not favored by moose. Even shrubs and saplings that are eaten readily by moose, such as the viburnums, *Cornus* spp., mountain maple, mountain ash, and red-berried elder *(Sambucus pubens),* are still present parkwide, especially on islets (Figure 14).

In general, caribou are able to survive in mature forests better than moose, which thrive on the earliest forest successional stages (Abraham et al. 1990). While caribou are not obligate climax forest animals, they are able to exploit foods such as arboreal lichens that are typical of mature, northern coniferous forests.

Figure 14. *Spruce-fir forest on Mott Island. The white spruce and balsam fir forest on Mott Island is typical of the eastern end of Isle Royale. Large-leaved aster is prominent where the understory is partly shaded, while thimbleberry grows best in direct sunlight. Photograph by the author.*

Much of Isle Royale was severely burned during the 19th century (Rakestraw 1965). While these forests have not yet reached climax stages, they are now 100 years old or older (Snyder and Janke 1974). Trees regenerating after the 1936 fire grew out of the reach of moose in the 1960s, and the 1936 burn area has supported their lowest densities on Isle Royale since then (R.O. Peterson, pers. comm.). Similarly, moose bypass the smaller 1948 burn area where minimal browse is available. Herbaceous, summer forage may be adequate for a low density of caribou in these 45–60-year-old birch and aspen stands that cover over 20% of the park.

Predators

Predator densities are a key predictor of habitat suitability for caribou (Bergerud and Elliot 1986, Bergerud and Mercer 1989). On Isle Royale, the predators are wolves and potentially lynx. Coyotes and black bears are absent.

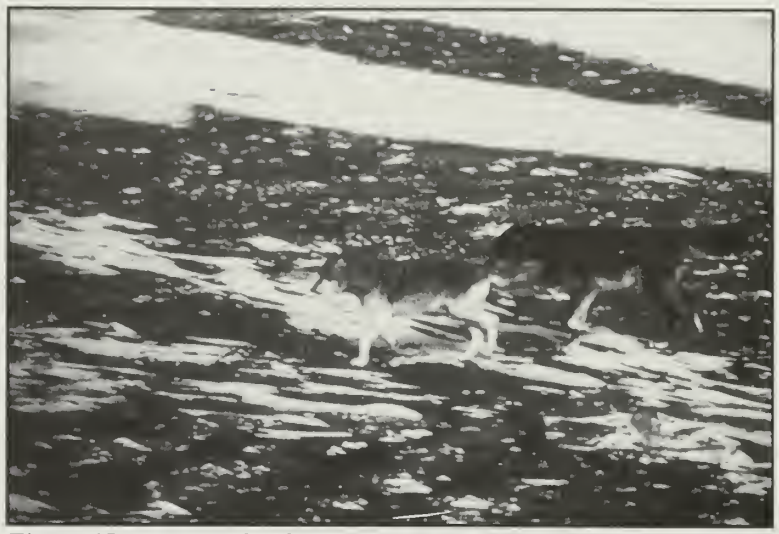

Figure 15. *A pair of wolves on shore ice, Isle Royale. Wolves such as this alpha pair regularly travel on the ice to avoid deep snow and to seek prey on islets. Photograph: R.O. Peterson, Isle Royale National Park archives.*

To generate a "worst case scenario" for caribou restoration, I assumed that wolves would be reestablished if current trends continue and they become extirpated from Isle Royale. In fact, the National Park Service will not decide whether to reestablish wolves until the reasons for their extirpation, presuming they disappear, are understood and a feasibility study and environmental assessment for wolf restoration are completed (R.J. Krumenaker, pers. comm.). If wolves do not recover on their own and are not reestablished, the predictions in this report for caribou restoration, based on high predator numbers, would have to be revised.

Wolves arrived on Isle Royale in the late 1940s (Figure 15) and have numbered between 12 and 50 animals (20-92/1,000 km^2) since 1950 (Peterson 1992, Figure 3). Wolf numbers peaked at 50 in 1980 after a decade of preying on abundant moose. Then suddenly the wolf population crashed by more than 70% in two years. Subsequent research has identified starvation, interpack fighting due to food shortages, and possibly canine parvovirus as the likely causes (Peterson and Thurber 1990). By the mid-1980s wolves had increased again. But in 1985, wolves began another steady decline due to high annual mortality and declining reproduction. Intensive research on the causes of the wolf decline, including radio-collaring and blood assays of wolves, began in 1988.

Isle Royale wolf research has not yet ruled out the possibility that food shortage is responsible for the low wolf reproduction rates in the 1980s (Peterson 1992). Blood assays, however, have indicated that both disease and inbreeding may be factors in the population decline (Wayne et al. 1991). Some wolves sampled on Isle Royale had positive, albeit low, titers for Lyme disease, and this disease appears to cause reproductive problems in some mammal species (ibid). Genetic losses of the magnitude observed in Isle Royale wolves could explain their current low reproductive success through inbreeding depression, although the precise mechanism is unknown (Wayne et al. 1991).

It is difficult to predict whether and how soon Isle Royale wolves would switch to, or actively seek out, introduced caribou, or whether they would continue to rely on moose (A.T. Bergerud, pers. comm.). Wolves search optimally for prey—spending search time where prey are most likely to be encountered (Bergerud 1985, Bergerud et al. 1990, Bergerud and Page 1987, Bergerud and Elliot 1986). When caribou are rare, highly dispersed, or inaccessible across water, wolves continue to seek more numerous moose even though they are individually more difficult to kill (ibid). On Isle Royale, wolf response would depend on individual wolf or pack habits, pack travel patterns, and the demographics and condition of the moose. Despite extraordinary wolf densities, moose densities have

persisted at 1-3/km^2—some three to five times higher than most mainland areas in North America (Peterson 1990).

Despite these uncertainties, Bergerud (pers. comm.) predicts that wolves will restrict caribou to secure escape habitat on Isle Royale. The net effect of high wolf numbers (10/1,000 km^2) is to greatly reduce the carrying capacity for caribou on Isle Royale.

Where caribou range overlaps with moose and wolf ranges, as in northern Ontario and Manitoba, caribou densities average at most 0.01-0.1/km^2, equivalent to 5-54 animals on Isle Royale, compared to 0.3-0.4 caribou/km^2 where moose and wolves are less numerous (see review in Appendix D). Based on the densities of caribou on occupied islets in Lake Nipigon adjacent to high wolf densities, 1.2-1.8/km^2, Isle Royale's islets might support about 10-20 caribou (Appendix D). Bergerud (pers. comm.) predicts that only 20-55 caribou could survive on Isle Royale with wolves present.

Another potential caribou predator on Isle Royale is the lynx. Historically, lynx were common on Isle Royale but disappeared in the 1930s due largely to overtrapping (Martin 1988). Evidence of natural immigration included credible lynx sightings in 1963, 1970, 1981, and 1988; each being a year when regional populations were on the rise and irruptive migrations were recorded on the mainland (Martin 1988; R.J. Krumenaker, pers. comm.). These sightings of individual lynx do not necessarily mean that lynx will eventually recolonize and reproduce to a viable population size. If lynx do not become reestablished on their own, the National Park Service will consider restoration actions (R.J. Krumenaker, pers. comm.).

Important lessons can be learned from the Maine caribou reintroduction program, where the first two years of releases suffered high predation mortality in addition to disease problems stemming from the captive herd (B. Connery, pers. comm.). The Maine investigators concluded that these predation risks could have been overcome by "flooding" the release area with animals until an initial herd became established with the knowledge required to avoid predators (ibid). Since the Maine project was terminated, the final results of that experiment will not be forthcoming. Any plans to release caribou on Isle Royale would be experimental as well, since we cannot fully anticipate the potential for successful restoration on an island archipelago with high wolf densities.

Winter Ticks

During the last few years Isle Royale moose have suffered significant mortality from heavy winter tick *(Dermacenter albipictus)* infestations (Peterson 1990). Across North America, moose die-offs have been linked to winter ticks (Glines and Samuels 1989). Winter ticks were historically a white-tailed deer parasite, to which other cervids are less resistant (W. Samuels, pers. comm.). They spread northward with white-tailed deer after the 1860s, and their range is still extending northward (Samuels 1989). High rates of winter tick infestations are associated with high moose densities and warm, dry spring and fall weather (Welch et al. 1990).

Winter ticks have been collected from a few wild woodland caribou in Alberta. Two captive reindeer harboring extremely high tick densities died (Welch et al. 1990). Although tick infestations have not been observed in woodland caribou populations, Welch et al. (1990) predicted that winter ticks could become a problem for woodland caribou if warm, dry weather conditions continued as in recent years. On Isle Royale, caribou would be exposed to winter ticks due to high moose densities and heavy winter tick infestations on moose (Peterson 1990). Potentially, tick-related caribou mortality could be substantial and additive to predation mortality (W. Samuels, pers. comm.).

Escape Habitat

Categories of potential escape habitat for caribou include islands, shorelines, rocky cliffs, and open bog wetlands. All of these sites afford the caribou greater vision of approaching predators than closed forest habitats. Also, caribou readily flee into the water or sometimes up escarpments or over ice to escape from intruders (see Appendix D). Islands and open wetlands separate caribou from predators that are reluctant to swim in pursuit of uncertain prey resources.

Of these categories, offshore islets are the most likely to provide secure havens for caribou on Isle Royale, except during winter when the water between the main island and some or all islets freezes. The main island of Isle Royale might provide safe sites for a smaller number of caribou and might supply critical habitat in winters with extensive ice on Lake Superior. Due to a lack of concentrated winter food supplies, Bergerud (pers. comm.) predicts that caribou would select winter habitat on Isle Royale based on visibility and snow depth to assure their escape flight potential. A description of each escape habitat type follows.

Low Wolf-Use Habitats. In Pukaskwa National Park, caribou generally avoid high wolf-use areas. Woodland caribou also have been observed to "hide" between pack territories or move away from a territory where wolves have detected them and to "hide" until detected again in a different territory (Bergerud 1984, 1989). On Isle Royale, pack territories have shifted enough between years (R.O. Peterson, pers. comm.) so that caribou probably would not be able to predict relatively safe zones between wolf packs.

The only places on Isle Royale that wolves have not frequented consistently in recent decades are Siskiwit swamp and the 1936 burn area, where moose are uncommon (R.O. Peterson, pers. comm.) (Figure 9). However, these areas may not provide caribou with adequate long-term isolation from wolves, given the wolves' ability to roam and adapt to new prey resources.

Wetlands. In northern boreal forests, woodland caribou find refuge in large bogs or wetlands with small water openings (Bergerud 1978, Abraham et al. 1990). On Isle Royale, wetlands are scattered across the main island and surrounding islets; however, they are typically small or linear and often wooded with black spruce or white cedar. Wetland forest types total only about 1,400 ha (Hansen et al. 1973). When wolf densities are high, Isle Royale's wetlands would probably not be large enough to protect caribou from predation except possibly Siskiwit swamp, which wolves rarely enter in winter (R.O. Peterson, pers. comm.).

Rugged Terrain. On Pic Island, in Lake Superior, caribou escape from predators and human intruders by running up steep cliffs and by fleeing into water (Ferguson et al. 1988). Rocky cliffs are characteristic of northwest-facing slopes on Isle Royale. Along the north shore of Isle Royale, including many of its bays and inlets and most offshore islets, these cliffs are at or near the shoreline. Hence, introduced caribou might learn to use cliffs as an alternative escape route.

Shorelines. The shape of Isle Royale and its islets—long and narrow, striated with long, narrow bays, inlets, and lakes—produces a high shoreline:area ratio favorable to woodland caribou (Bergerud et al. 1990) (Figure 2). Caribou released onto Isle Royale would most likely wander the shoreline until they settled into favorable sites (A.T. Bergerud, pers. comm.). Secure calving sites might be found along stretches of the main island shore where a narrow shelf of land is backed by steep cliffs.

In all but the coldest, and especially the calmest winters, parts of the Isle Royale shoreline remain open except for narrow shelf ice (R.O. Peterson, pers. comm.). When many offshore islets are frozen in, prevailing winds will often keep ice from forming along exposed shorelines of the main island. Only once a decade or so does the wind remain calm enough for ice to completely encircle Isle Royale for a few days or longer (R.O. Peterson, pers. comm.). Thus, shorelines on the main island might provide winter habitat for caribou.

Table 2. Offshore islets, Isle Royale National Park (vegetated islets >0.5 ha).

Islet Group	Number of Islets	Size (hectares) Mean	Range
Rock and Tobin harbors	37	6.2	0.5-61.0
North Shore	23	11.6	0.5-181.2
Malone Bay	9	9.1	1.2-46.9
Washington Harbor	7	34.3	2.1-127.2
Houghton Point	6	4.8	1.5-18.9
Todd Harbor	5	1.4	0.5-2.7
All Islets	87	9.9	0.5-181.2

Note: Vegetation cover determined from aerial photographs; area digitized from topographical maps at the Michigan Technological University GIS Laboratory.

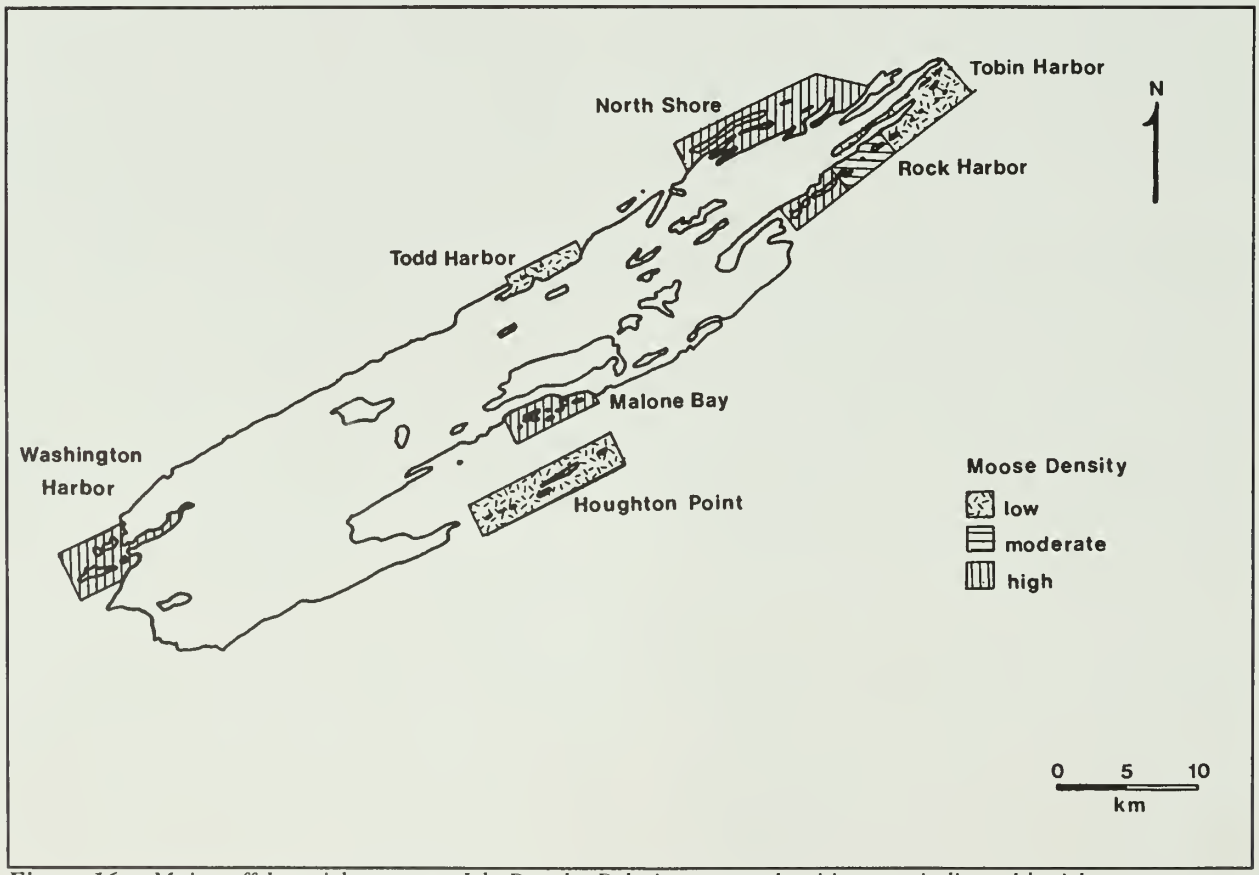

Figure 16. Major offshore islet groups, Isle Royale. Relative moose densities are indicated by islet group, as described by R.O. Peterson (pers. comm.).

Islets. When wolves are present, island archipelagoes are considered the best sites for reintroducing caribou into the southern portions of their former range (Bergerud 1980). "Here, the releases of caribou could 'island hop' to escape wolves." (Bergerud 1980:99). More than 200 islets surround Isle Royale, including 87 vegetated islets 0.5 ha or greater in size (Table 2). Two-thirds of these islets are on the eastern end of Isle Royale in Rock Harbor and Tobin Harbor and along the north shore (Figure 16). Other groupings or chains of islets are at Todd Harbor on the northwest shore, Washington Harbor on the west end, and Malone Bay and Houghton Point on the south shore. Four of the large inland lakes, Siskiwit, Desor, Richie, and Sargent, contain a total of eight large islets.

Figure 17. *Rock Harbor channel in winter with extensive ice cover. When winds are calm during the winter, ice forms between the main island of Isle Royale and its surrounding islets. Islets farther from the main island shoreline rarely freeze in, perhaps only once in 10 years, while closer islets such as Caribou and Mott islands (foreground) are connected to the shore most years. Photograph: R.O. Peterson, Isle Royale National Park archives.*

The 87 islets average 9.9 ha in size (0.5-181.2 ha), with a combined area of about 8.9 km^2, or less than 2% of the park land area. Five islets, Amygdaloid, Mott, Thompson, Washington, and Wright islands, are 0.5 km^2 or larger, and another 15 islets range between 0.1 and 0.5 km^2, half of which are in Rock Harbor and Tobin Harbor. These figures exclude Passage Island, a 0.82-km^2 island located 5.5 km off the northeast tip of the main island, because it is far enough out to discourage caribou crossings from Isle Royale. Moose have not colonized Passage Island, and a draft NPS policy calls for excluding ungulates to protect rare plant resources on Passage Island (R.J. Krumenaker, pers. comm.).

The islets surrounding Isle Royale are typically arrayed in long chains paralleling the main island. Hence, except for the chain of islets off Houghton Point that defines Siskiwit Bay, most of the islets are within 1 km of the main island shore. For example, the 37 vegetated islets in Rock Harbor and Tobin Harbor are, on average, only 430 m from the main island shore (range = 24-1,561 m). Since these islets are close to each other, the distance to the nearest land is much shorter (mean = 49 m, n = 37, range = 12-171 m) than is the distance to the main island.

Distance to shoreline and exposure to prevailing winds are the keys to how frequently and persistently the different islets freeze in (Figure 17). The most sheltered islets are locked in with ice by late December in most years, while islets that are more distant from the main island shore are infrequently icebound. Wind patterns have the greatest influence on where and when ice forms around Isle Royale.

Moose as an Indicator of Islet Habitat Quality. Bergerud (pers. comm.) recommended assessing moose productivity on Isle Royale's offshore islets to determine their relative suitability for caribou. The general suitability of islets as winter refuge habitat is described in Stephens and Peterson's (1984) comparison of winter moose densities, calf percentages, and wolf kill rates between a group of 27 of Isle Royale's larger islets (>10 ha) and the main island. Winter moose densities were four times higher on these islets than on the main island; also,

the highest-use areas on the main island were within 2 km of the shoreline. In January and February, calf percentages were nearly twice as high on islets as the main island.

This wintertime concentration of calves on islets, however, was a residual from the high proportion of calves actually born on islets. In winter, calves were killed at disproportionately high rates on islets, presumably because wolves knew that they were more likely to find calves on the larger islets than they were to find them dispersed on the main island. Stephens and Peterson (1984:23) concluded that the moose's preference for islets in midwinter was "largely attributable to the survival advantage that accrues to very young calves" in their first summer. In another study, restricted to the northeast end of Isle Royale, Edwards (1983) demonstrated that moose cows with calves concentrated on small islets (all islets studied were <10 ha) and along the shoreline of Isle Royale and remained near the lake shore from May through August.

The winter density of moose varies greatly between offshore islets, correlating loosely with the frequency of ice formation, islet size, and forage resources (Snyder and Janke 1974; R.O. Peterson, pers. comm.). For example, Snyder and Janke (1974) found that in the Rock Harbor islet chain, the forest on Mott Island was significantly less browsed than similar forest types on the main island, and the forest on Smithwick Island—farther out on the chain—was barely browsed at all, presumably due to inadequate ice for winter crossings (Figure 15).

Peterson's (pers. comm.) summary of relative winter moose densities, generalized from his observations during the last two decades, provides an index to the quality of winter habitat for caribou by islet group (Figure 16). Wolves regularly cross the ice to access islets with heavy or moderate moose densities—especially the larger islets in Washington Harbor, Malone Bay, the west end of Rock Harbor, and Amygdaloid Island. At the opposite end of the spectrum, moose are largely absent from, and wolves rarely or never, visit the Houghton Point islets and the east end of Rock Harbor and Tobin Harbor. These latter islets would be most suitable for caribou.

Summary of Islet Habitat. In summary, the small islets surrounding Isle Royale would provide summer escape habitat for caribou. Caribou remaining on islets would have a safe haven from wolves for at least 9-10 months of the year. Current forage supplies, especially herbaceous plants, deciduous shrubs, and arboreal lichens, appear to be adequate to support caribou at typical island densities (A.T. Bergerud, pers. comm.). If the islets became heavily browsed, presumably, caribou would be able to survive on depleted food supplies much as they do in Lake Nipigon, the Slate Islands, and Pic Island (as long as they could escape predation during midwinter). If all of the islets and exposed shorelines froze in solidly, however, then caribou would not have sufficient escape habitat and wolves could kill the entire herd.

Summary

Based on this precursory analysis, forage resources and spring-to-early-winter escape habitat appear to be adequate for a small herd of caribou on Isle Royale. The bottleneck for caribou carrying capacity, and mere survival, would be midwinter escape habitat. For caribou to survive on Isle Royale with wolves present, a low frequency of complete ice formation and the availability of alternative escape habitat when ice was widespread would be required. Isle Royale would clearly be most suitable for caribou if and when the wolf population was at low numbers, but wolf recovery would eliminate caribou from most land areas of the park. In the short-term, survival of reintroduced caribou would depend on how quickly they learned to use available escape habitat and the luck of mild winters while the herd became established. The probability of longer-term persistence is evaluated in the following section.

Population Vulnerability Analysis

Population vulnerability analysis is the process of estimating minimum viable population (MVP) sizes for specific populations (Gilpin and Soulé 1986). A minimum viable population is the threshold number of animals required to ensure, at some defined level of risk, that a population will persist for a given time interval at a particular location. Conventional standards for minimum viable populations include (1) greater than 90% certainty of long-term persistence, usually centuries, (2) population maintenance in nature without significant demographic or genetic manipulation, and (3) retaining a replacement level of immediate fitness—vigor, fertility, and fecundity—with sufficient genetic variation to adapt by natural selection to changing environments (Soulé 1987).

In current theory, four kinds of variation independently threaten small populations. These variations are (1) demographics or birth-and-death processes, (2) genetics, (3) environmental stochasticity, and (4) catastrophes (Soulé 1986). Population fragmentation or metapopulation structure, especially systems based on local extinctions and recolonizations, also contribute to MVP estimation (Gilpin 1987). When these elements interact, an extinction vortex, or downward spiral in population size, can result (Gilpin and Soulé 1986).

No single, universal minimum viable population can guarantee that animal populations will persist (Gilpin and Soulé 1986). However, based on theory and empirical observations, ballpark numbers or orders of magnitude of individuals required to maintain minimum viable populations of completely isolated populations have been estimated. For species with "average" reproductive rates and genetic variability, including wild caribou, a population of at least several hundred individuals may be necessary to establish a minimum viable population (Lande and Barrowclough 1987).

Thus, we can predict that a fluctuating population of around 200 caribou in the absence of moose and wolves, such as existed historically on Isle Royale, could not persist indefinitely in isolation from other populations. A population of only 20-55 animals, as Bergerud predicts for reestablishment on Isle Royale, would have a low probability of surviving for many decades, much less centuries.

More accurate and informative predictions can be made by simulating the growth of an introduced population with a computerized model, which I did for a hypothetical Isle Royale caribou herd using Robert Lacy's (1990) VORTEX model (Appendix B). The VORTEX model uses Monte Carlo simulations of demographic events, environmental variation, and catastrophes to calculate population persistence times. Such modeling permits predictions of how long populations established by different reestablishment schemes would survive, or whether the effort is worthwhile. For these simulations, the number of animals released, number of years of releases, mortality rates, and carrying capacities were varied between simulation runs.

VORTEX Results

In preliminary trials with high carrying capacities, so that population size was not immediately truncated below the number of animals initially released, we determined that persistence times were not improved by releasing more than about 75 animals or by extending the release time over more than one year. Subsequent simulations with lower, more realistic carrying capacities reduced to three basic variants: carrying capacity equals 54 with high and moderate mortality, and carrying capacity equals 27 with high mortality (Appendix E). Unfortunately, I was not able to satisfactorily model two release options that might overcome the initial effects of high wolf predation: "swamping" the release site with woodland caribou, and releasing caribou while wolves were absent and subsequently restoring the wolf population (i.e., gradually increasing wolf predation rates as wolf densities

increased). To summarize, a translocated caribou population with fewer than 54 animals and suffering high mortality would not survive for 50 years (Table 3). The mean time to extinction was about 33-44 years. With less severe mortality and a larger mean population size of 54 animals, mean persistence time would increase to 79 years.

Lessons from Elsewhere

Translocating small numbers of ungulates into favorable habitats has frequently succeeded in establishing large populations. Griffith et al. (1989) found that for native game species, just 20-40 founding animals were sufficient to predict high translocation success. Success was defined only as attaining a "self-sustaining population"—long-term persistence was not addressed. Some caribou herds have prospered from initial transplants of fewer than 20 animals into favorable habitats (see history of caribou transplants in Appendix A).

A previous attempt at modeling caribou reestablishment alternatives was part of the Maine caribou reintroduction plan (McCollough 1987). A stochastic model based on Grier (1980) was employed to evaluate six release options for three projected levels of herd survival and fecundity. The Maine simulation predicted only short-term probabilities of achieving the approximately 100 animals believed to be necessary for long-term viability (M. McCollough, pers. comm.). These simulations revealed that only restorations of herds with initial high survivorship and intermediate or high fecundity exceeded the target herd size of 100 animals in 10 years. Releases extending over 5 years and totaling 98-115 animals with heavily skewed adult sex ratios performed better than 3-year releases totaling less than 75 animals. The greatest determinant of success was population survival rate, especially for yearling-only releases.

As it turned out, mortality in the two years of actual releases of woodland caribou to the Baxter State Park region of Maine far exceeded the modeled scenarios, due principally to black bear predation and diseases carried from captivity (McCollough and Connery 1991). Based on this experience, the advisory committee of the Maine project concluded that three releases of at least 40-60 animals would have been necessary to overcome initial high mortality rates and establish a core herd of animals acclimatized to the new habitat.

Several small populations of woodland caribou persist along the north shore of Lake Superior, which could lead to the misleading conclusion that small populations may be viable. These herds have been isolated for only 15-30 years and stray bulls have been recorded moving between some north

Table 3. *Simulated population persistence times (in years) of selected release scenarios for woodland caribou on Isle Royale (50 simulations per 100-year run).*

Runs[1]	Mortality Rate	Carrying Capacity	Persistence Time (in Years) by Percent of Populations Surviving			
			90%	50%	10%	0
1	High	27	21	31	39	50
2-3	Moderate	54	63-64	79-80	93-94	>100
4-6	High	54	31-39	44-50	55-61	70-72

[1] Runs are combined by mortality rate and carrying capacity; number of animals released and occurrence of catastrophes had minimal influence on the results. Number of animals released: run 2 = 52, runs 3-5 = 78, run 6 = 104. Catastrophes were omitted from run 5. See Appendix E.

shore herds in the last 15 years (Bergerud 1985, 1989*a*; Darby et al. 1989). Furthermore, the prognosis for all the Lake Superior herds is bleak. Bergerud (1989*a*), for example, predicted a high probability of extinction for the Pukaskwa herd within 25 years. Fluctuations in the size of the Slate Islands herd, characterized by periodic widespread starvation, have been increasing in amplitude (A.T. Bergerud, pers. comm.). This fluctuation suggests that total population collapse is possible despite a mean population size of 250-400 animals. Thus, I conclude that historic Lake Superior populations, including Isle Royale, were probably part of a regional metapopulation with regular gene flow between groups and ready recolonization of islands from the mainland.

Summary

The prospects for caribou restoration on Isle Royale can be viewed on two time scales. In the short run, a small release of 12-24 animals might be sufficient to establish a nuclear herd given adequate escape habitat and assuming wolves are present. If the released caribou learned how to avoid wolves (find and exploit secure habitat), then initial population growth should be good. But as the herd grew it would be subject to high mortality rates—10-22% annual adult mortality—and the population probably could not exceed a density of 0.1/km^2 (K = 54), with wolves numbering six or more. Under these conditions, the VORTEX model predicts that the caribou herd would not survive for 40-60 years.

When a proposed restoration site is too small to support a minimum viable population at carrying capacity, restoration may be possible by managing several small populations as a single "metapopulation." A metapopulation consists of a constellation of small subpopulations that interact loosely through differential dispersal, establishment, growth, and extinction (Gogan and Cochrane 1994). Managing several small populations as a metapopulation could involve providing movement corridors for individuals to naturally disperse among subpopulations and to directly relocate, as well as including captive individuals at zoological parks as a subpopulation (Gogan 1990).

I conclude that releasing a reasonable number of caribou, approximately 100 animals, would not result in an independently viable population on Isle Royale or any population at all without follow-up releases beginning as soon as 10 years. This result is not surprising based on MVP theory and given assumptions of high mortality rates, high variance in mortality, and a carrying capacity of no more than 54 animals. Historically, caribou on Isle Royale did not have to contend with wolves, and movements to and from the mainland would have prevented inbreeding and recolonized the island after infrequent catastrophic declines. Replicating the natural functions of this historic link to mainland caribou populations would be essential to any restored Isle Royale population. Hence, as long as wolves are present on Isle Royale, successfully restoring woodland caribou may only be possible by managing a regional metapopulation.

Reestablishment Methods

The goal of this section is to evaluate whether translocation of caribou to Isle Royale is feasible. Analysis of the logistics, costs, and relative benefits of specific alternatives is left to the restoration plan and environmental assessment if the NPS pursues the project in the future.

The Maine woodland caribou reintroduction plan (McCollough 1987), Selkirk Mountains, Idaho, herd supplementation plan (Summerfield 1985*a*, 1985*b*), and subsequent program reports (McCollough and Connery 1990; Servheen 1988, 1989) provide a thorough review of alternative caribou capture and release procedures. Release options can also be gleaned from a proposal for reintroducing caribou to Minnesota (Karns and Lindquist 1986). Recent translocation projects in Ontario add to the

wealth of examples from which Isle Royale could draw, especially in transporting caribou between Lake Superior islands.

Alternative Reestablishment Strategies

Reestablishment strategies vary principally in how long the animals are held before release and whether they are caught in the wild or captively reared (Summerfield 1985*b*; McCollough 1987; McCollough and Connery 1990; G. Eason, pers. comm.). Caribou may be raised in nursery herds either with adult animals or by humans. Direct translocation approaches include (1) capture and release of calves only, (2) delayed release with holding for a few months, (3) quick release with holding for a few days to three weeks, and (4) immediate release. Target sex and age ratios for releases depend upon initial project goals. Population growth is maximized by releasing prime breeding-age animals. The average sex ratio in nonhunted caribou herds is about two males:three females (Bergerud 1980). Caribou are polygynous, however, and a typical breeding male:impregnated female ratio is about 1:5 (R. Page, pers. comm.). Given the risks of high initial male mortality and logistical constraints on selective captures, a practical release goal for caribou is around one male:two-three females (Summerfield 1985*b*; McCollough 1987; G. Eason, pers. comm.).

Release Timing

In their study of translocation success rates, Griffith et al. (1989) found that multiyear releases were not significantly more successful than onetime releases. In our simulations, multiyear and single-year releases of the same number of animals performed similarly.

The best time to release caribou and presumably to capture them for quick or immediate release strategies depends on whether deterring dispersal is the major goal, or if the caribou would gain by learning the new terrain at particular seasons. Logistical constraints might dictate release timing, such as when the animals could be caught at the source area and when transportation is available. Some release times used by other projects include (1) early fall/prerut when animals are in good condition and congregated in groups, (2) early winter/postrut when females are pregnant and dispersal from the release site may be limited by snow, (3) late winter before females are ready to calve and when caribou may be using more open habitat to facilitate capture, and (4) spring, just before calving, to allow calving in and summer adjustment to the new location.

A few techniques have been suggested to help retain caribou at release sites and to deter wolf predation during the first year (A.T. Bergerud, T. Kreeger, R. Page, L. Rogers, pers. comm.). These techniques include (1) salt licks, (2) penning, (3) chasing swimming caribou back to islets, (4) stationing monitoring staff at the release site over winter, (5) hand-rearing calves at the release site, and (6) conditioning the caribou with dogs to be wary of predators.

Disease and Parasite Screening

Since wild caribou would be translocated from Canada, U.S. Department of Agriculture (USDA) requirements for live animal importation and U.S. Fish and Wildlife Service permit regulations would have to be met (Summerfield 1985*b*; McCollough 1987; S. Schmidt, pers. comm.). These regulations require testing for tuberculosis (TB) and brucellosis, and possibly Bang's disease, before animals may be shipped across the international border. Specific USDA requirements are determined in each case by the state veterinarian and the USDA Washington office. Since the TB test takes 72 hours, animals have to be held at the capture site, a

source of stress and potential mortality. Wild caribou and moose are not known to carry TB, and, in fact, the standard TB testing procedure was developed for cattle and may not be valid for cervids (S. Schmidt, pers. comm.).

Caribou captured in Newfoundland for rearing and release in Maine were held for exhaustive disease and parasite testing (McCollough 1987, McCollough and Connery 1990). The Maine project's primary concern was to prevent potentially importing *Elaphostrongylus cervi*, a nematode parasite of European reindeer. This parasite infects caribou herds in central Newfoundland.

In the Idaho translocation program, captured animals were treated with a single dose of Ivermectin as a general worming agent at the same time they were tested for TB and brucellosis (G. Servheen, pers. comm.). *E. cervi* has not been detected in the Canadian source herd, hence, no treatment or quarantine was prescribed for that parasite.

Sources of Caribou—the Slate Islands

The closest source of caribou for transfer to Isle Royale is the Slate Islands herd in Ontario, 112 km northeast of Isle Royale. Because of the high density of caribou on the Slate Islands, this herd has been used for transplants around Lake Superior in Ontario (Appendix A). Ontario Ministry of Natural Resources policy (WM.2.10.U5, dated 10 August 1988) permits transferring live animals out of Ontario for legitimate and well-documented reestablishment programs. Removing caribou from the Slate Islands to restore extirpated populations elsewhere is approved in the Slate Islands Provincial Park management plan. Beyond the Slate Islands, the nearest source of caribou for transfer at this time is either Manitoba or far northwestern Ontario (H.R. Timmermann, pers. comm.), which would be an exponential increase in transport time and costs to Isle Royale.

Caribou have been captured on the Slate Islands with permanent drive traps and bait traps (G. Eason, pers. comm.). Before transport, the caribou have been sedated with Atravate, then tied to stretchers and flown by Twin Otter float plane directly to the release sites (Figures 18 and 19). A maximum of six animals were transported at a time with a total flight time of less than two hours. The entire capture and transport effort required four to eight people. Since disease testing was unnecessary for transfers within Ontario, the animals were released immediately and generally fared well (G. Eason, H.R. Timmermann, pers. comm.). Recent transfers off the Slate Islands were done in the fall, primarily because government planes were available then (G. Eason, pers. comm.). Long-distance dispersal was not an issue for the Canadian island release sites and was not a major problem for the 1989 release on the Gargantua Peninsula (G. Eason, pers. comm.).

Potential drawbacks of transferring animals from the Slate Islands herd would include inbreeding, nutritional stress, and no predator wariness. Due to isolation, the animals are inbred, with reduced heterozygosity and fewer alleles than North American averages for caribou (A.T. Bergerud, pers. comm.). Delayed breeding and delayed antler growth in Slate Islands caribou may be genetically linked (A.T. Bergerud, pers. comm.), but these conditions may also result from prolonged nutritional stress. Females from the Slate Islands released into better environments have reproduced normally (G. Eason, pers. comm.).

Another concern about Slate Island's caribou is that they lack conditioning for escaping predators. This lack of conditioning may have contributed to high predation losses in the first months after release on the Gargantua Peninsula, as indicated by caribou that left the offshore islands (where they had been released) for vulnerable mainland sites (G. Eason, pers. comm.). However, Slate Islands caribou are still wary of humans and flee readily to water (H.R. Timmermann, pers. comm.). Thus, Slate Islands

Figure 18. *Capturing woodland caribou on the Slate Islands. Caribou are captured on the Slate Islands singly in traps baited with salt. They are then blindfolded, sedated, and tagged or radio-collared before transport. Photograph: H.R. Timmermann, Ontario Ministry of Natural Resources.*

Figure 19. *Preparing caribou for transport off the Slate Islands. In the first Slate Islands translocations, shown here, caribou were loaded into crates and transported by barge. Recently, transportation has been improved by placing the animals on stretchers and moving them by float plane. Biologists ride with the animals—no more than six at a time—and massage their legs during the one-hour flight to maintain blood circulation and keep the animals calm. Photograph: H.R. Timmermann, Ontario Ministry of Natural Resources.*

caribou apparently have the basic predator avoidance instincts but need to learn site-specific escape habitats.

Freutel and Lankester (1989) found nine species of gastrointestinal parasites during extensive tests on Slate Islands caribou, most of which are host-specific to caribou (M. Lankester, pers. comm.). Of the four Elaphostrongyline species, only *Parastrongylus andersoni* has been found in Slate Islands caribou, and then only in 4% of the herd (Lankester and Hauta 1989). *P. tenuis* and *E. cervi* are most certainly absent (ibid).

Thus, the Slate Islands caribou appear to be comparatively free of contagious diseases and parasites that could spread to other animals. Yet additional testing would be required to assess any potential risks to Isle Royale moose posed by introduced Slate Islands caribou, particularly from *P. andersoni*. Caribou captured for transport to Isle Royale would have to be screened and possibly treated for parasites and diseases before release.

One final caveat: The Slate Islands herd is not immune from extirpation, even within the next decade or two. Bergerud (pers. comm.) predicts that the caribou are likely to crash below a sustainable level in one of the next population cycles. Ultimately, caribou cannot persist in the Lake Superior region if they are isolated in small populations. The Slate Islands herd will not persist indefinitely unless it is managed as part of a regional meta-population.

Summary

In conclusion, Slate Islands caribou are a relatively inexpensive and easily captured nearby source of caribou for an Isle Royale transplant. These animals would be the logical source for initial releases on Isle Royale. Potential problems with the condition, wariness, and availability of Slate Islands animals would need to be addressed further as part of a detailed release plan. Further study of diseases and parasites in Slate Islands caribou and their potential impacts on Isle Royale moose would be required for the plan's environmental assessment.

Impacts and Management Implications

Potential impacts of caribou on Isle Royale resources are suggested here to provide guidance for an environmental assessment if restoration is pursued. I have not attempted to quantify impacts such as browse depletion.

Caribou restoration would prompt changes in a number of Isle Royale National Park management practices—both temporary and permanent. In addition to evaluating and planning caribou restoration to minimize impacts on other park resources, managers would have to consider altering existing management programs such as visitor and fire management policies to facilitate caribou restoration. Bergerud (1989*a*) recommended a number of steps to protect caribou in Pukaskwa National Park that might be applicable to Isle Royale.

All but 1% of Isle Royale National Park's land area is legally designated as wilderness. Park management strives to provide a high-quality "wilderness experience" for park visitors. Thus, park resources potentially affected by caribou include not only natural resources—plants, animals, and natural systems—but park cultural resources, visitor use facilities, and wilderness aesthetics.

Vegetation

Given a scenario where wolves confined caribou for the most part to offshore islets and adjacent shorelines, caribou would have little impact on vegetation resources on the main island. In contrast, vegetation on occupied islets could be altered significantly, as shown by the Slate Islands, Pic Island, and islands in Lake Nipigon (Euler et al. 1976, Ferguson et al. 1988, Bergerud et al. 1990). If 20-50 caribou spent much of the year browsing on Isle Royale's islets, roughly 9 km^2 (excluding Passage Island) of forage supplies would be affected. Through selective foraging, the composition as well as abundance of islet plant life would be altered. In the absence of countervailing influences such as fire, spruce budworm outbreaks, or climate change, heavy browsing would intensify or accelerate the natural successional trend from mixed deciduous forest to a more pure conifer forest.

Endangered Species and Rare Plant Communities

Slavik and Janke (1987) reviewed rare and unusual plant occurrences on Isle Royale. Arctic and alpine plant communities on the rocky, Lake Superior shoreline include numerous postglacial relics, and eight state-listed threatened species and two state-designated special-concern species. Altogether, 39 state-listed threatened and endangered species and 16 special-concern species have been found on Isle Royale; for some, Isle Royale is the species' only site in Michigan (Slavik and Janke 1987). Caribou should not be released onto Isle Royale until their likely impacts on these species are considered. A rare plant survey focusing on the rock shore communities of offshore islets would be especially relevant to a caribou restoration environmental assessment.

Other Animals

Competition between moose and caribou for food supplies has not been reported, but is possible (A.T. Bergerud, pers. comm.). Moose and caribou are generally segregated either by food preferences or habitat selection (Bergerud and Page 1987, Bergerud and Elliot 1986, Abraham et al. 1990). However, on an archipelago like Isle Royale where dispersal is not possible and moose are abundant, these two cervids could compete for winter foods (Peterson 1977).

Introduced caribou would provide wolves with a second alternative prey to moose—in addition to beaver—that is easier to kill but possibly harder to find than moose. Yet, if projected caribou densities are correct, total prey biomass would not increase much on Isle Royale. Hence, predation rates on moose might not change much either. The role of caribou as alternate prey for wolves would depend on how closely moose and caribou vulnerabilities were linked (e.g., if vulnerability of both animals was tied to weather, snow depth, etc., or if vulnerability was based on independent population demographics such as moose population age structure).

Another predator that could be affected by caribou restoration is lynx. While presently extremely rare on Isle Royale, lynx could increase either naturally or through reestablishment actions. Caribou calves could provide an alternate prey for lynx during low numbers of snowshoe hare (Bergerud 1971).

Caribou restoration would complicate the decision process for wolf reestablishment if the wolves become extirpated. Given the current uncertainties of wolf recovery, whether natural or artificial, a caribou restoration plan would have to conservatively assume that wolves would be present on Isle Royale in the long run. In other words, a realistic. worst-case scenario for caribou on Isle Royale includes high wolf numbers.

The current record-low number of wolves and projections of additional decline would appear to foster caribou restoration on Isle Royale in the short run. The probability that caribou reestablishment would succeed increases if it was delayed until after wolves had declined to five or fewer animals. However, given the potential for wolf population recovery, the long-term prospects for a self-sustaining caribou population appear to be poor as long as wolves are present.

Diseases and Parasites

The potential for introducing new diseases and parasites to Isle Royale's isolated animal populations must be a major concern for any proposed introductions. While caribou were once native to Isle Royale, their absence for more than 60 years may have left alternative hosts in the park free of pathogens carried by caribou. Also, introduced animals may carry different parasites or diseases from those carried by Isle Royale's native caribou, particularly pests that have invaded or spread to the Great Lakes region during this century. Moose would be vulnerable to cross-species transfer of pathogens from caribou, especially since the Isle Royale moose herd has apparently been isolated from mainland environments for many decades.

Lankester and Fong (1989) published a thorough review of the distribution of the four species of Elaphostrongyline parasites carried by caribou, which are *P. tenuis*, *E. cervi*, *P. andersoni*, and *P. odocoilei*. The intermediate hosts for all four species are gastropods. Any abundant and mobile native species of snails and slugs are probably suitable hosts (Lankester and Hauta 1989).

The meningeal brainworm is common in white-tailed deer, its normal definitive host, across eastern North America. The parasite causes severe neurologic disease in other cervid species. Woodland caribou infected with this parasite usually die (Anderson and Strelive 1968, Anderson 1971). Meningeal brainworm is widespread in Michigan white-tailed deer (T. Cooley, pers. comm.). A previous report of meningeal brainworm larvae from Isle Royale moose pellets (Karns and Jordan

1969) has since been discounted (Lankester and Hauta 1989). Given the similarity in appearance, the larvae collected on Isle Royale may have been *P. andersoni* but could also have resulted from collecting equipment contamination (M. Lankester, pers. comm.).

The muscleworm, *P. andersoni*, is also common in white-tailed deer in North American (Anderson and Prestwood 1981, Pybus and Samuel 1984) and woodland caribou in Labrador and Ontario (Lankester and Hauta 1989). *P. andersoni* and another muscleworm, *P. odocoilei*, found in caribou and deer in western North America, are not considered lethal cervid parasites, although they can cause verminous pneumonia and severe myositis in their hosts (M. Lankester, pers. comm.). The potential impact of *P. andersoni* on moose is unknown. Since moose on Isle Royale are already heavily infested with both hydatid tapeworms *(Echinococcus granulosus)* and winter ticks, they may be especially vulnerable to other new parasites (R.O. Peterson, pers. comm.).

Introduced to North America through reindeer imported to Newfoundland, *Elaphostrongylus cervi rangiferi* also causes neurologic disease in caribou. Experimental infestations of moose with *E. cervi* caused pathological changes and paralysis (Lankester 1976). A parasite resembling *E. cervi* was identified in woodland caribou in Ontario (Lankester 1976, Lankester and Northcott 1979). Subsequently, this parasite was positively identified as the muscleworm, *P. andersoni* (Lankester and Hauta 1989).

The greatest risk to Isle Royale moose is the introduction of elophostrongyline nematodes, particularly *E. cervi* and *P. andersoni*. In North America, *E. cervi* has only been found in introduced reindeer and in caribou from Newfoundland. The muscleworm *P. andersoni* is present at low densities in Slate Islands caribou, as well as white-tailed deer and caribou in some other parts of the Lake Superior region (Lankester and Fong 1989; M. Lankester, pers. comm.). Additional studies should be conducted to determine the effects of *P. andersoni* on moose and whether it is present on Isle Royale.

Slate Islands caribou could also import intestinal parasites to Isle Royale (Fruetel and Lankester 1989). To date, no sampled Slate Islands caribou have carried the tapeworm *Taenia krabbei*, which requires the wolf as a final host (M. Lankester, pers. comm.). *T. krabbei* is not present on Isle Royale (R.O. Peterson, pers. comm.). The tapeworm's introduction should be avoided, even though it has little impact on moose populations where it is common (M. Lankester, pers. comm.). Finally, botfly species carried by caribou are host-specific (M. Lankester, pers. comm.), so they would not be expected to transfer to moose.

In summary, extensive parasite and disease screening on the Slate Islands or other source herd and Isle Royale would be necessary before woodland caribou were translocated between these parks. Imported caribou would have to be certified free of infectious diseases by Canadian and American veterinarians before being released on Isle Royale. A protocol for parasite testing and, if necessary, treatment would have to be included in a caribou restoration plan. Risks of parasite and disease introduction should be weighed carefully in decisions about restoration.

Wilderness

Intensive browsing would affect the appearance of vegetation on offshore islets. However, many visitors would not notice until conditions were severe; the dramatic effects of moose browse have to be pointed out to most summer visitors (pers. obs.). Negative reactions might be outweighed by the perceived bonus of seeing or knowing about caribou in the park.

Monitoring activities would also impact the wilderness character of Isle Royale. Radio collars on animals might be objectionable to some visitors.

These concerns were raised when the National Park Service agreed to radio-collaring moose in 1983 and wolves in 1988, but the debate has remained largely philosophical because few visitors actually see the collared animals (R.O. Peterson, pers. comm.; pers. obs.).

A much more intrusive element of radiotelemetry monitoring is low-level overflights. By regulation, float planes cannot land outside of three designated sites in Isle Royale National Park, except at the discretion of the park superintendent. The National Park Service also attempts to restrict flight intrusions over the wilderness by imposing restrictions on government and concessionaire flights.

Caribou monitoring would have to be even more intensive than the current wolf telemetry studies to provide accurate information on calving and sources of mortality. If caribou were concentrated on offshore islets, much of the summer monitoring might be done from boats. Although more time and labor consuming, this option would be much less expensive and intrusive than airplane flights. Other alternatives to extensive monitoring flights include satellite telemetry and attaching antenna to existing radio or fire towers.

The visitor's park experience could also be affected by campground and trail closures and other restrictions on boat or foot travel implemented to protect caribou. Restrictions on undesignated backcountry camping have already been instituted largely to protect wolves, without appreciable concern from the public (R.J. Krumenaker, pers. comm.). Caribou protection would probably be focused on offshore islets, most likely on the northeast end and south shore, which are already closed to undesignated camping.

Caribou readily become accustomed to routine human activities such as logging (A.T. Bergerud, R. Page, pers. comm.). Moose are not only habituated to Isle Royale's campgrounds and settled areas, but some cows with calves actually seek out these human-use areas as a refuge from wolves and have higher calf survival as a result (Stephens and Peterson 1984). Thus, other than trying to prevent curious visitors from directly harassing caribou, "visitor management" for caribou on Isle Royale would be primarily educational.

Summary

This review highlights potential impacts and management concerns with attempting to restore a caribou herd on Isle Royale. Any proposal to reestablish caribou in the park would require a thorough environmental analysis, including quantitative impact analysis. Studies would be needed to illuminate the risks of caribou introducing diseases or parasites to Isle Royale's insular moose herd and the susceptibility of caribou to winter tick infestation. Rare plant distribution and threats from caribou trampling and browsing would also have to be investigated. Another study topic would be visitor attitudes about caribou restoration.

The scale of a caribou restoration project as projected in this study would be unprecedented for resource management on Isle Royale. The interagency, public, and private effort required to plan, fund, and implement caribou reestablishment would far exceed the ongoing peregrine falcon *(Falco peregrinus)* restoration project and perhaps even the moose and wolf research effort. Park managers would have to be committed to a lengthy program requiring considerable logistical support, regardless of the source of project funding and staff. The initial translocation would be followed by at least three to five years of intensive population monitoring and require flexibility to deal with complications.

Yet the odds of successful woodland caribou restoration on Isle Royale are linked most directly to the fate of wolves in the park, and hence, to decisions about managing the wolf population. In the long-term, population viability goals for caribou are probably not attainable as long as wolves are in the park, hence, "artificial immigration" or periodic imports of new caribou would be required to

maintain a caribou herd. Managing a caribou herd under these circumstances would necessarily be experimental and does not fit strictly under NPS policies for native species restoration (see the Introduction).

Conclusions

We cannot say definitively whether caribou restoration would succeed on Isle Royale. This report shows that conditions on Isle Royale could be suitable for caribou—except that with high numbers of wolves, escape habitat would not be secure in severe winters. We do not know the frequency of winters severe enough to eliminate all water-related escape havens. More importantly, how caribou would adapt to Isle Royale and whether wolves would learn to seek out caribou is uncertain. These questions could only be answered experimentally. But assuming that five or more wolves were present (0.01/km^2) and restricted caribou to no more than 54 animals (0.1/km^2), the VORTEX model predicts that the herd would persist for less than 40-60 years.

Logistically, translocating caribou from Ontario would not be difficult. Complications might arise from disease and parasite screening and treatment. While logistically feasible, the project would be expensive. Including the expense of diligent monitoring, the total bill for caribou restoration would far exceed previous projects in the park—up to $100,000 per year.

Woodland caribou inhabited Isle Royale for thousands of years, coevolving with the island's unique biotic resources. Yet the island ecosystem has changed since caribou were extirpated and caribou restored with wolves present are unlikely to behave and disperse as they did historically. Thus, potential impacts of caribou on present park resources would need further study before restoration could be approved. Issues that would need to be resolved include the caribou's potential effects on rare plants and the effects of caribou diseases and parasites on moose.

Addressing the NPS management policies on page 1, I conclude:

1. Adequate proof exists that caribou lived on Isle Royale and that they disappeared or were substantially diminished as a direct or indirect result of human-induced change to the species and ecosystem.

2. Adequate foraging habitat exists on Isle Royale for caribou. Secure winter escape habitat may not be adequate to protect caribou from wolf predation during severe winters. Also, translocated caribou might not learn to use the available escape habitat before they were extirpated by wolves. If predictions for wolf predation are correct, then the caribou would not achieve a self-perpetuating, viable population size.

3. Caribou would not pose a threat to the safety of park visitors or to persons or property outside park boundaries. They might, however, threaten rare plants in the park or carry diseases or parasites threatening to moose. Further study would be needed to assess these potential threats.

4. Assuming five or more wolves were present at the time of release, caribou would likely encounter problems with predation either at the release site or more likely as they subsequently wandered on the main island.

5. Caribou attained from Ontario near or in Lake Superior would nearly approximate the caribou subspecies extirpated from Isle Royale.

6. The prospects for natural (unassisted) reestablishment are virtually nil. Restoration has a poor chance of success (measured in decades) unless either wolves are nearly or

totally extirpated, or restoration is defined to include "artificial," periodic infusions to the caribou herd.

7. A restoration action plan has not been developed and is not proposed currently.

Ironically, the only "natural" system that has been proven to work on Isle Royale, by surviving for more than 3,500 years of prehistory, is a caribou-lynx-snowshoe hare-Native American community. Yet it is clear that this "primitive vignette" (Leopold et al. 1963) of Isle Royale cannot be replicated simply by translocating caribou to the island. The chief obstacles to caribou restoration on Isle Royale would be wolves and moose—two species that arrived on the island in this century as a result of human-induced changes on the mainland.

Barring regular management intervention, the odds are high that wolves would eliminate caribou from Isle Royale within a few decades. In other words, interjecting caribou into the present wolf-moose system is unlikely to establish a self-sustaining caribou herd. I based this prediction on knowledge of wolf and woodland caribou population dynamics in Canada and my assessment that secure winter escape habitat is limited on Isle Royale. The prediction's accuracy might be improved with additional population and habitat suitability modeling or with an experimental release.

The questions posed by caribou restoration are not unique; wolves may never be a self-sustaining species on Isle Royale either, being unable to reach a 100-year or longer minimum viable population. The challenge is to determine how important these large animals are to the island ecosystem and how important the island is to regional population viability of these species. The answers may determine how aggressively species are managed. Wright et al. (1933) anticipated that "not one park is large enough to provide year-round sanctuary for adequate populations of all resident species . . . [or to] guarantee against the invasion of external influences." While they promoted restoration of species to achieve an "original, natural state" in national parks, they also cautioned that "due care must be taken that management does not create an even more artificial condition in place of the one it would correct" (ibid).

Reflecting recent trends in biodiversity conservation, Soulé (1986:7-8) presents a case for aggressive management of large, rare species:

> Viability, in the strict sense, will be impossible for some populations in certain situations, but wise management may still be able to insure the persistence of a relatively 'natural' community or system. Probably the majority of nature reserves in the world are too small to contain more than a few family groups of primates or herds of large ungulates. Such tiny groups in vest pocket reserves may contribute virtually nothing to the viability of the species as a whole, but their survival may be important, nonetheless, for ecological and social reasons. . . . When such groups die out, therefore, they should simply be replaced from whatever source is available.

If maintaining regional biodiversity is a goal, management of isolated nature reserves and national parks will increasingly require coordination outside reserve and park boundaries. Perhaps more than any other mammal on Isle Royale, woodland caribou were historically part of a regional metapopulation. Thus, the value of restoring caribou on Isle Royale should be assessed not only from the park's perspective but also as part of a regional effort to preserve the subspecies at the southcentral boundary of its range.

Translocating woodland caribou from the Slate Islands to Isle Royale and other regional sites—if practical—would disperse the genetic stock of Lake Superior caribou and help to reduce the chances of a catastrophic loss of this ecologically and genetically unique subgroup. But sustaining these small herds, isolated from each other by human-altered landscapes, would require periodic intervention. Isle Royale, a national park and designated wilderness supporting unique floral and faunal communities, may not be an appropriate setting for this type of biodiversity management. Based on the NPS

management policy that restored populations be "self-perpetuating," Isle Royale would not be an appropriate site for caribou restoration under current conditions.

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Postscript

"I saw caribou when I was young. One spring, we came down on the steamer *America*, oh, it was in April, about the 20th of April, and there was still a lot of ice in Rock Harbor channel. And you know, those animals, there'd usually be a lot of them together. There'd be maybe seven, eight or more. And then this one time across from Anderson's place, up, right across from Caribou Island, there were 10 or 12 of 'em walking along the ice. It was still strong enough to walk on, for caribou. And since then, I only seen occasional, you know, not very many. But finally they disappeared altogether. The moose came in, they seemed to leave." (Milford Johnson, interviewed by Lawrence Rakestraw, 1965; Isle Royale Oral History No. 5.)

"The [visitors] ask me if there's caribou on this island. . . . And I says they were there till about 1919. And, boy, they were some of the most beautiful animals that you ever saw; they had big white neck yokes on 'em, and they had the longest and the most beautiful horns you ever saw. Boy, we had horns here till three years ago, that they had shed; somebody had found them . . ." (Pete Edison, unknown interviewer, no date; Isle Royale Oral History No. 3.)

". . . [in 1919 or 1920, we were fishing herring out by Saginaw Point] . . . and we were coming in, and there was a caribou, and that was the last one that I seen. He was standing in that beach, just on the outside of Mine Point, and he was standing there, and he had the finest neck yoke on 'em. Oh, he was a beautiful animal. And they were big animals. They reminded me a whole lot of the reindeer in Norway. They were, on, eh, practically the same build. And that is the last I remember of the caribou." (Pete Edison, interview with Lawrence Rakestraw, 3 September 1965 at Edison Fishery Isle Royale; Isle Royale Oral History No. 22).

Female woodland caribou. Females typically grow antlers, although they are smaller than males' antlers. Populations near Lake Superior have a higher proportion of anterless females than more northern woodland caribou populations. Photograph: S. Stewart, courtesy of H.R. Timmermann, Ontario Ministry of Natural Resources.

Appendix A
Summary of Caribou and Selected Reindeer Translocation Attempts

Location	Date(s)	Techniques Used	Results	Reference(s)
Caribou Island (Lake Superior), Ontario	1904 or 1905	6 released on small island	Success, then shot or removed	Lankester and Fong 1989
Michigan (Grand Island?)	1922	60 reindeer released	Failure, P. tenuis	Johnson 1962
Red Lake Refuge, Minnesota	October 1938 and 1942	1 male released with 3 wild females, 9 (1 male, 8 calves) held 4 years then released with (6-11) progeny	Failure, predation, poaching, P. tenuis	Swanson et al. 1945, Karns 1978
Liscombe Game Sanctuary, Nova Scotia	April 1939	5 females released immediately; 4 females held, then released with 3 males	Failure, P. tenuis	Tufts 1939, Benson and Dodds 1977
Adak Island, Alaska	July 1958 and 1959	23 hand-reared calves released at 2 months old (no predators)	Success	Jones 1966, Burris and Knight 1973
Baxter St. Park, Maine	December 1963	19 females, 5 males (adults) released immediately	Failure, dispersal, and P. tenuis?	Dunn 1965
Kenia Peninsula, Alaska	May 1965 and April 1966	38 females, 6 males released immediately (adults and yearlings)	Success	Burris and Knight 1973
Southampton Island, Ontario	1967	52 adults released	Success	Miller 1982
Cape Breton Highlands, Nova Scotia	1968 and 1969	51 released	Failure, P. tenuis?	Dauphine 1975
Great Cloche Island, Ontario	May 1970	12 held in enclosure	Failure, P. tenuis	Anderson 1971, 1972
Central Wisconsin	1971-72	14 from captive herd released into enclosure	Failure, P. tenuis	Trainer 1973
Laurentide Park (Grand Jardin), Quebec	1966-72	82 captive herd progeny released	Success	Vandal 1984, Vandal and Barrette 1985

Continued

Location	Date(s)	Techniques Used	Results	Reference(s)
Newfoundland (coast and islands)	1961-82	22 separate sites (384 caribou), immediate release, all age/sex classes	Failure at 5 sites, dispersal and harassment; 17 successes	Bergerud and Mercer 1989, Bergerud 1978
Michipicoten Island (Lake Superior), Ontario	Fall 1982	1 bull, 4 cows, 3 calves released immediately	Success	H. Timmerman, Pers. comm.
Montreal Island (Lake Superior Provincial Park), Ontario	Fall 1984	1 bull, 6 cows, 1 calf released immediately	Success	H. Timmerman, Pers. comm.
Bowman Island (Lake Superior Provincial Park), Ontario	October 1985	6 released immediately	Failure, predation	Bergerud and Mercer 1989
Leach Island (Lake Superior Provincial Park), Ontario	Fall 1986	1 bull, 1 cow, 1 calf released immediately, joined 1 cow	Result unknown (bull left island)	H. Timmerman, Pers. comm.
Selkirk Mountains, Idaho	March 1987-88 and 1990	60 adults (1:3 sex ratio) released after 72 hours near wild caribou	Result unknown; high predation mortality	G. Servheen, pers. comm.
Northern Maine	March 1989, 1990	59 animals (captive herd and progeny) released after holding period	Failure, predation, disease, dispersal	McCullough and Connery 1990; Connery, pers. comm.
Gargantua Peninsula (Lake Superior Provincial Park), Ontario	Fall 1989	10 bulls, 26 cows, 3 calves released immediately	Result unknown; few survivors, predation	H. Timmerman, Pers. comm.

[1] "Success" means the herd has persisted to date and is reproducing. Likely causes for failures are listed after "Failure."

[2] This table was compiled from Summerfield 1985, McCollough 1987, Bergerud and Mercer 1989, Lankester and Fong 1989, and personal communications.

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Appendix B
VORTEX: Simulation Model of Stochastic Population Change

Stochastic Simulation of Population Extinction

Life table analyses yield average long-term projections of population growth or decline, but do not reveal the fluctuations in population size that would result from variability in demographic processes. When a population is small and isolated from other populations of conspecifics, these random fluctuations can lead to extinction even of populations that have, on average, positive population growth. The VORTEX program is a Monte Carlo simulation of demographic events in the history of a population. Many of the algorithms in VORTEX were taken from a simulation program, SPGPC, written in BASIC by James W. Grier of North Dakota State University (Grier 1980*a*, 1980*b*; Grier and Barclay 1988).

Fluctuations in population size can result from any or all of several levels of stochastic or random effects. First, demographic variation results from the probabilistic nature of birth and death processes. Thus, even if the probability of an animal reproducing or dying is always constant, we expect that the actual number of caribou reproducing or dying within any time interval to vary according to a binomial distribution with mean equal to the probability of the event (p) and variance given by Vp = p * (1 - p)/N. Demographic variation is thus intrinsic to the population and occurs in the simulation because birth and death events are determined by a random process (with appropriate probabilities).

Environmental variation is the variation in the probabilities of reproduction and mortality that occur because of changes in the environment on an annual basis or other time scales. Thus, environmental variation impacts all individuals in the population simultaneously, changing the probabilities—or means of the above binomial distributions—of birth and death. The sources of environmental variation are thus extrinsic to the population itself due to weather, predator and prey populations, parasite loads, etc. VORTEX models population processes as discrete, sequential events, with probabilistic outcomes determined by a pseudo-random number generator. VORTEX simulates birth and death processes and the transmission of genes through the generations by generating random numbers to determine whether each animal lives or dies, whether each adult female produces broods of size 0, 1, 2, 3, 4, or 5 during each year, and which of the two alleles at a genetic locus are transmitted from each parent to each offspring. Mortality and reproduction probabilities are sex-specific. Fecundity is assumed to be independent of age, after an animal reaches reproductive age. Mortality rates are specified for each prereproductive age class and for reproductive age animals. The mating system can be specified as either monogamous or polygynous. In either case, the user can specify that only a subset of the adult male population is in the breeding pool, the remainder being excluded perhaps by social factors. Those males in the breeding pool all have equal probability of siring offspring.

This description of VORTEX was taken from an unpublished manuscript entitled, "VORTEX: Simulation Model of Stochastic Population Change," Version 8.0, by R. Lacy, Chicago Zoological Park, Brookfield, IL, 60513, dated 20 August 1990.

Each simulation is started with a specified number of males and females of each prereproductive age class, and a specified number of breeding-age males and females. Each animal in the initial population is assigned two unique alleles at some hypothetical genetic locus, and the user specifies the severity of inbreeding depression, expressed in the model as a loss of viability in inbred animals. The computer program simulates and tracks the fate of each population and outputs summary statistics on the probability of population extinction over specific time intervals, the mean time to extinction of those simulated populations that went extinct, the mean size of populations not yet extinct, and the levels of genetic variation remaining in any extant populations. A population carrying capacity is imposed by a probabilistic truncation of each age class if the population size after breeding exceeds the specified carrying capacity. The program allows the user to model trends in the carrying capacity as linear increases or decreases across a specified number of years.

VORTEX models environmental variation simplistically by selecting at the beginning of each year the population age-specific birth and death rates and carrying capacity from normal distributions with means and standard deviations specified by the user. Thus, environmental variation is simulated by sampling a normal distribution, with the standard deviations specifying the annual fluctuations in probabilities of reproduction and mortality and in carrying capacity. Unfortunately, we rarely have sufficient field data to estimate the fluctuations in birth and death rates and in carrying capacity for a wild population. Lacking any data on annual variation, a user can try various values, or simply set environmental variation to equal 0.

VORTEX can model catastrophes, the extreme of environmental variation, as events that occur with some specified probability and reduce survival and reproduction for one year. A catastrophe is determined to occur if a randomly generated number between zero and one is less than the probability of occurrence (a binomial process). If a catastrophe occurs, the probability of breeding is multiplied by a severity factor specified by the user. Similarly, the probability of surviving each age class is multiplied by a severity factor specified by the user.

VORTEX also allows the user to supplement or harvest the population for any number of years in each simulation. The numbers of immigrants and removals are specified by age and sex. VORTEX outputs the observed rate of population growth (mean of N[t]/N[t-1]) separately for the years of supplementation/harvest and for the years without such management, and allows for reporting extinction probabilities and population sized at whatever time interval is desired (e.g., at five-year intervals).

Overall, the computer program simulates many of the complex levels of stochasticity that can affect a population. Because VORTEX is a detailed model of population dynamics, often it is not practical to examine all possible factors and all interactions that may affect a population. The user must specify those parameters that can be estimated reasonably, leave out those that are believed not to have a substantial impact on the population of interest, and explore a range of possible values for parameters that are potentially important but very imprecisely known. Still, VORTEX is a simplified model of the dynamics of real populations that may under- or overestimate extinction rates due to the artificial representation of population stochasticity.

VORTEX is not copyrighted or copy protected. The program can be a useful tool for exploring the effects of random variability on population persistence, but the results should be interpreted with due caution and an understanding of the program's limitations.

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Appendix C
The History of Caribou in the Lake Superior Region

Mainland Michigan (Excluding Isle Royale)

Baker (1983) summarized accounts of caribou in Michigan. Prehistoric records of caribou extend as far south as Lake St. Clair in the southeastern lower peninsula, farther south than in Wisconsin or Ontario. The last record for caribou in the lower peninsula is in 1853 on Beaver Island in Lake Michigan. Caribou were still hunted by Native Americans in the upper peninsula in the mid-19th century. The last records for Michigan's upper peninsula are from 1906 in Dickinson and Luce counties and 1910 or 1912 in Chippewa County.

Baker (1983) speculated that caribou may have been only winter migrants to Michigan, based on four lines of evidence: (1) a lack of summer observation records in Michigan or Wisconsin; (2) observations of caribou moving on ice; (3) findings of antlers, indicating presence when antlers were shed; and (4) the close correlation between the disappearance of caribou in the eastern upper peninsula and the adjacent Sault Forest District, Ontario, and between Isle Royale and the adjacent Port Arthur and Geraldton Forest districts in Ontario. Baker (1983) also cited Mech's (1966) and Stoll's (1926) speculations that Isle Royale caribou were migratory, but a number of summer records show clearly that they were year-round residents on Isle Royale.

None of Baker's evidence proves that caribou were absent from Michigan in the summer. Further, I do not see what advantage caribou would have gained by migrating completely out of Michigan to summer in Canada. Older literature on historic caribou abundance is typically biased by seasonal shifts in distribution and density. Bergerud (1989*a*) pointed out that observations of local wintering congregations give an impression of abundance. Alternately, in summer, woodland caribou disperse to calve and, if seen at all, are solitary or with calves. Further, while woodland caribou frequently move to seek more favorable winter habitat, these migrations are typically much shorter than the movements of barren ground caribou; for example, the maximum seasonal migration near Lake Nipigon was 80 km (Cumming and Beange 1987), and, in Ontario, seasonal movements average only 10-40 km (Goodwin 1990). Thus, despite a lack of recorded observations, caribou may have summered in Michigan, particularly in the upper peninsula.

Northeastern Minnesota

Before 1800, caribou ranged across most of northern Minnesota, including the entire Lake Superior coast (Swanson 1940). However, records of the American Fur Company (AFC), Northwest Company (NWC), and Hudson's Bay Company (HBC) indicate that the region west of Lake Superior was severely "trapped out" by the 1830s (see also Lytwyn 1986, Hickerson 1974). Traditionally, caribou were a subsistence staple for the north shore Ojibwa, and the caribou totem or clan name was preeminent among area bands. For example, Joseph Caribou was chief at Grand Portage in the 1890s, according to government censuses. By the 18th century, caribou were also a trade good.

Both the means of efficient harvest, firearms, and demand for meat and hides escalated significantly due to the fur trade. However, caribou were not a major trade item. Post returns indicate that caribou meat and hides were traded for local consumption rather than shipment to European markets. Trading records are incomplete, and exchanges are mentioned only occasionally in NWC and AFC trader's logs or letters to headquarters (copies at the Minnesota Historical Society in St. Paul). For example:

1795 Trade for caribou skins was reported at "Sagina" [Lake Saganaga?] (C. Chaboillez);

1824 Minnesota Indians traded "caribou" at the competitive HBC post at Fort William (Trader B. Chapman);

1833 Traders received smoked caribou meat at the Savanna Portage [Minnesota] post (Trader Ely).

Early explorer Henry Schoolcraft wrote in 1831 that caribou inhabited the forested country at the western end of Lake Superior (Schorger 1942). But descriptions of game depletion date back to John Tanner (in James 1956), who reported in 1791 that "game was not plentiful around Grand Portage." William Keating, "the journalist of an expedition to the Northwest in 1823 led by Major Stephen H. Long of the U.S. Topographical Engineers, described the country between Rainy Lake and Fort William as being utterly destitute of game animals" (Hickerson 1974:143). A history of the Grand Portage, Minnesota, Ojibwa summarizes this period: "most of the Chippewa complained that both beaver and otter were scarce. Moose, deer, and caribou were almost extinct and the Indians depended on rabbits and partridge for winter food still they were often without food and had to get corn, fish, and potatoes at Fort William" (Blackwell et al. 1983:39).

After 1820, fur trade correspondents and then the annual reports of the Commissioner of Indian Affairs (COIA) persistently refer to the poor condition of the Indians from Fond du Lac (Duluth) to Fort William (Thunder Bay) due to game shortages. For example (from HBC trader's logs, copies at the Minnesota Historical Society in St. Paul):

1822 " . . . the country between Fort William and Lake of the Woods has few caribou or moose, too few for clothing" (J. McLouch-lin).

1824 Referring to the country north of "Mille Lac": "no moose, caribou scarce, Indians can't get enough for clothes" (J. Haldane).

1824 The chief at Grand Portage killed "4 caribou, 1 moose, and 7 bears," plus 150 beavers and 100 martens, yet his band was reportedly starving (B. Chapman).

1831 "The land between Fort William and Fond du Lac has few large animals" (McIntosh).

1834 " . . . the country west of Fort William is destitute of game for food" (Anonymous).

The situation near Lake Superior had not improved by the 1850s, when COIA reports show that natural resources were "greatly depleted" in 1851 and "game [is] gone" in 1853. The Ojibwa "are miserably poor [from Pigeon River to Rainy Lake, Minnesota]. . . . They rely for their winter's support upon the rabbit and the reindeer" (COIA annual report for 1850, copies at the Minnesota Historical Society in St. Paul). Reports from other posts farther inland, Leech Lake and Vermillion Lake, claimed that game was more abundant until the severe winter of 1869 left these Indians "destitute" for at least three years (COIA annual report for 1871, copies at the Minnesota Historical Society in St. Paul). I did not find additional specific references to caribou taken or traded west of Lake Superior after 1870, although hunting and fishing remained part of the reserve Indians' mixed economy.

I could not determine how far caribou numbers recovered from the recorded depletion of the 1820-50s. Surber (in Swanson et al. 1945:24) described caribou as "comparatively abundant in the northern

border counties clear across the state from the Pigeon River on the east to very close to the Red River Valley on the west" around 1870. Yet Fashingbauer (1965) believed caribou numbers were below their original abundance in the 1880s in this region. Herrick (1892 in Fashingbauer 1965) found that caribou were "not rare" in 1884 along the Whiteface and St. Louis rivers and he observed them in upland meadows along the north shore.

In the late 1880s, caribou were "comparatively common" in Lake and Cook counties; some inhabited the Pigeon River watershed in 1887 (Swanson 1940). According to C.A.A. Nelson of Lutsen, "the animal was still present along the north shore of Lake Superior in 1890, but it soon disappeared" (Breckenridge 1949). Karns and Lindquist (1986) reviewed Minnesota sources and concluded that heavy subsistence hunting by settlers and natives decimated caribou populations in the 1890s. Hunting caribou was prohibited from 1893 to 1897, and again after 1905 (Fashingbauer 1965). A north shore newspaper (*Cook County Herald*, 6 April 1895, in Swanson 1940) reported that "one animal was seen floating on the ice out in Lake Superior in April 1895." And 11 caribou were seen on the ice in the direction of Isle Royale near Grand Portage in the early 1900s (Adams 1909). Timm (1975) described a band of 20 caribou that was seen regularly along Gunflint Lake from 1916 to 1925 but reported no documented sightings after 1925.

Grand Marais-Grand Portage resident Richard Anderson (1988) recalled that reindeer were raised on a game farm near Devil's Track Lake on the Gunflint Trail before 1920. In 1928 or 1929, Anderson and his father saw a group of animals near Devil's Track Lake that they presumed to be surviving escapees from the game farm, but these could also have been native caribou.

The last free-ranging, indigenous caribou observed in Minnesota was captured in the Red Lake country in 1940 (Swanson et al. 1945, Fashingbauer 1965, Bergerud and Mercer 1989). Bergerud and Mercer (1989) reviewed the failure of the caribou introductions north of Red Lake between 1938 and 1942 and concluded that the released animals lacked the tradition of migrating from the northwestern Minnesota bog country to calve on the islands of Lake of the Woods and Rainy Lake, Ontario. Since then, occasional migrants may have wandered into Minnesota from Ontario, such as the pair of caribou that were observed in the vicinity of Hovland during the winter of 1981-82 (Mech et al. 1982).

Northwestern Ontario

According to de Vos and Peterson (1951), the woodland caribou was the only cervid species found in northwestern Ontario before 1900; moose and white-tailed deer ranges remained farther south and west Moose were present at low densities in the Minnesota-Ontario borderlands. The most impressive, albeit suspect, early account of caribou numbers in Ontario came from Nicholas Perot. Perot reported that the Indians snared 2,400 animals on Manitoulin Island in northern Lake Huron during the winter of 1670-71 (Blair 1911). Hickie (n.d.) reported the exact citation as 2,400 "elans," a French word for European elk that has been translated from North American references variously as elk, deer, moose, or caribou, and Hickie assumed the Manitoulin reference was to moose.

In the spring of 1769, Alexander Henry found a band inhabiting Caribou Island, a predator-free island in Lake Superior, 35 km east of Michipicoten Island and 62 km from the closest mainland. Henry's party found moss-covered caribou bones littering the ground and killed 13 animals over three days (Quaife 1921).

From 1780 to 1820, the negative impact of the fur trade described for Minnesota also extended across northwestern Ontario. Lytwyn (1986) provides a detailed analysis of the fur trade north of Lake Superior. The fur trade in Canada's "Little North" began in the 17th century and gradually escalated after 1720 as the Montreal Canadians of the Northwest Company built posts in the interior. In 1777, Hudson's Bay Company began to build

trading posts inland from their traditional base on Hudson's Bay to compete directly with the Montreal traders. Competition for furs at the local level increased dramatically and peaked in 1805, when the fur resource began to show signs of collapse. By 1821, when the Northwest Company was taken over by Hudson's Bay Company, overhunting was an acknowledged problem. The interior forts were closed after the merger in 1821, partly to "help to conserve fur bearers" (Lytwyn 1986:161). The fur trade was not intensively pursued after 1821, and the demand for beaver plummeted in the early 1840s.

Lytwyn (1986) includes a few references to big game hunting and trade in his study. These references include the use of firearms to hunt moose and caribou along the Albany River in 1780 and trade for moose and deer (caribou) in 1818-19, north of Lake of the Woods. The decline in big game is illustrated with the returns from the area southeast of Lac Seul, which show the average number of moose traded per year by period: 1796-1800: 39; 1805-10: 56; 1819-21: 0.

Lytwyn (1986) concluded that the impacts of the fur trade in northwestern Ontario was profound on both the native human and wildlife populations, a circumstance that had been largely overlooked in traditional histories because the resources recovered substantially by the mid-1800s.

Miller (1897) reported that caribou were "very abundant on the north shore of Lake Superior" in the 1890s. He found caribou bones at the north shore sites of White River (now in Pukaskwa National Park), Peninsula Harbor, Schreiber, and Nipigon. Caribou were reported to be plentiful in the Pigeon River watershed in 1900 (Cringan 1956). The pre-1900 caribou population of the Sibley Peninsula (280 km^2), due north of Isle Royale, was estimated at more than 500 by J.G. Cross, a local resident and trapper (de Vos and Peterson 1951).

The range of woodland caribou retracted gradually northward away from Lake Superior between 1900 and 1950 (Cringan 1957). Caribou disappeared from the western shore of Lake Superior between 1905 and 1912 (Riis 1938). Once the only cervid in the Lake Nipigon area, caribou became uncommon soon after the Canadian Pacific Railway was constructed across the north end of the lake around 1910. Caribou were declining and scarce on the Sibley Peninsula by 1914 (Cringan 1956). When a Michigan sportsman visited St. Ignace Island in 1905 he found caribou tracks; upon his return in 1917, he found that caribou were gone and that moose had become abundant (Hickie n.d.). Sport hunting of caribou was finally banned in Ontario in 1929, but populations continued to diminish in subsequent years (Cumming and Beange 1987).

De Vos and Peterson (1951) produced a detailed review of postsettlement caribou range changes in Ontario, with a district-by-district chronology of the decline: caribou disappeared from the Fort Frances District around 1900, from the Kenora District around 1913, and from around Lake of the Woods by 1930. In the Port Arthur District, caribou decreased on the Sibley Peninsula around 1907, but remained common on the adjacent Black Bay Peninsula into the 1940s. Currently, about 300 caribou live in the Lake Nipigon area (Bergerud et al. 1990). Farther east in the White River District caribou range was still continuous south to Lake Superior in 1950 and possibly as late as the 1960s to what is now Pukaskwa National Park (Bergerud 1989*a*).

The current southern boundary of continuous caribou range crosses Ontario at about 50° latitude (Figure 5) (Darby et al. 1989, Abraham et al. 1990). This line bisects the boreal coniferous forest, but closely follows a line of reduced abundance of moose and wolves. North of the line, moose density averages 0.049/km^2 and wolf density averages 1 wolf/260-500 km^2, compared to higher densities south of the line (0.148 moose/km^2 and 1 wolf/130-160 km^2) (Darby et al. 1989, Bergerud 1989*a*). Darby et al. (1989) list only six native herds

remaining south of Lake Nipigon: the Slate Islands, Pic Island, Pukaskwa National Park on Lake Superior, and three inland bands.

Caribou have also been successfully transplanted to Michipicoten Island and to two islands in Lake Superior Provincial Park. The success of a 1989 transplant to the mainland in this park has not been determined; however many of the released caribou were taken by wolves or bears (G. Eason, pers. comm.) (see Appendix D). The long-term persistence of these relict and released populations is tenuous due to small population sizes, isolation, high surrounding wolf densities, and predicted global warming trends fostering the range expansion of white-tailed deer (Bergerud 1989*a*). Gene flow between the remnant Lake Superior herds is limited to occasionally wandering young bulls (ibid).

Isle Royale

Archeological research has clearly demonstrated that caribou were the dominant, and probably the only, large mammal hunted on Isle Royale in prehistory (Cleland 1966, 1968; Martin and Maulis 1989; Martin 1989; C. Clark, pers. comm.). Caribou remains have been found at Archaic and Woodland period sites dating back to 1500 B.C. (Crane and Griffin 1965; C. Clark, pers. comm.). While a few moose bone fragments have also been found, they were associated with historic artifacts and are likely of recent origin (Martin 1989; C. Clark, pers. comm.).

Historic records of caribou on Isle Royale begin with John Tanner's narrative of his "captivity and adventures with the Indians" (James 1956). Tanner reported that two caribou were killed on a trip to Isle Royale in 1794. He was invited to spend the winter on Isle Royale, where sturgeon and caribou were "abundant." HBC post returns for Fort William include two notes of an Ojibwa hunter, the Bete, killing caribou on his frequent trips to Isle Royale:

> 28 July 1834: "The Bete and son payed us a visit and brought a little dryed caribou meat which he killed on Isle Royale."

> 2 August 1836: "The Bete and family arrived from Isle Royale. He killed only 3 Rein deers [caribou]."

By this time, caribou had been nearly eliminated from the mainland shore and killing "only 3" on Isle Royale was sufficiently unusual to merit a note in the trader's log. Isle Royale's reputation as a source of caribou was also recorded in the AFC's papers, in a letter from Lyman Warren to Ramsey Crooks dated 16 October 1834 (Warren 1834):

> Among . . . [the crew at La Pointe, Wisconsin] there is an old man who tells me the he knew the place [Isle Royale] well, he says the island is large, say 50 or 60 miles, the Indians used to make their hunts there on account of the great quantity of beaver and reindeer. It is the place where the N West Co. used to make their fishing for Fort William. . . .

The American Fur Company operated a commercial fishing station on Isle Royale from 1837 to 1841, staffed largely with Metis fishermen and their native wives (Karamanski et al. 1988).

The 1840 annual report of the U.S. Indian Service (1840:354) reported that Isle Royale was a "barren rock island...destitute of game, with the exception of a solitary herd of reindeer [caribou]." This report reads like a deliberate attempt to downplay Isle Royale's value just before treaty negotiations. Given the great demand for meat and hides in the early 1800s, the availability of firearms, the tradition of hunting on Isle Royale, and the close proximity of the island to the two largest trading posts in the region, Grand Portage and Fort William, I conclude that hunting on Isle Royale was likely heavy in the early to mid-1800s.

Isle Royale was ceded by the Ojibwa Nation to the United States in the treaty 1842, signed at La Pointe (Kapler 1904). Cession sparked the first wave of Euro-American mineral exploration. Three mining surges followed in the 1850s, the early 1870s, and

the early 1890s (Rakestraw 1965). Records from each occupation period offer clues to caribou abundance after 1850.

Despite extensive exploration across Isle Royale in the 1840-50s, aided by burning much of the forest cover and a large settlement of miners in Rock Harbor in the 1850s, references to caribou on the island during the mid-1800s are limited. Foster (1851:1), who explored the island for mineral deposits in 1850, reported that caribou antlers "were picked up by our party on Isle Royale, Lake Superior. It is not unusual to find horns on this island and on the Canada coast." One antler from this trip was placed in the Smithsonian Museum's collection as *Rangifer caribou* No. 900. From the same survey, Foster and Whitney (1850:375-376) reported that "fires have swept over large tracts.... The caribou, the lynx, and the rabbit [snowshoe hare] are among the few animals that roam over [Isle Royale]."

Charles T. Jackson (1852:234) reported:

> Occasionally, in severe winters, the ice does extend from the Canada shore to Isle Royale, which is from fifteen to twenty miles distant; so that the caribou and moose cross over on it to the island, whither the Indian hunters sometime follow them over the same treacherous bridge. . . .

Indians would probably not chance a 15-mile ice crossing, and moose were not recorded on Isle Royale until the turn of the century. However, Jackson had spent time on Isle Royale and his reports of caribou crossings are reasonable. A typical summer visit by Ojibwas coming from Fort William was recorded by a Rock Harbor mine investor in 1851 (Myers 1851), but without reference to them hunting on Isle Royale.

Two former residents recalled a severe shortage of provisions at the Rock Harbor mining location in the winter of 1852, yet no hunting by the miners (Master 1913, La More 1923). William Henry La More (1923) was born at the Siskiwit Mine site (Rock Harbor) in 1852. Years later, when asked about the food shortage and near starvation, "Mr. LaMore . . . [could] not give the reason why deer etc. were not killed to furnish food. He . . . [could] only speculate that ammunition must have given out early in the autumn." Another possible explanation is that the miners did not encounter caribou because these animals were already scarce or found only at the opposite end of the island. Elsewhere, subsistence hunting by miners and settlers, as well as by natives, was widespread throughout the 19th century and would have been commonplace on Isle Royale if game was available.

When the Island Mine operated in the 1870s, residents reported both an Indian camp and resident trappers on Isle Royale but not personal caribou sightings. A typical story only hints at caribou hunting. Mrs. Henry Conary (1939) said the Indians stayed all winter in 1873 and gave her family fish and game. She wore moccasins all winter, obtained from the Indians, but she did not know what hide they were made from.

In the summer (1873-74), the Indians came over for brief periods to obtain maple syrup, hunt, and fish (Jeffrey 1942). One Island Mine resident (Jeffrey 1942) said moose were not on Isle Royale at that time but there were "probably caribou," although he never heard of any or saw any. He also reported lynx trapping and the slaughter of passenger pigeons that "darkened the sky" at Island Mine.

As many as 500 people lived on Isle Royale around 1875, with a herd of about 300 cattle kept to feed the community at Island Mine (Phillips n.d.). The only direct evidence of caribou at that time came from Gillman (1873:751), who found caribou antlers during a May 1873, visit and wrote that "such specimens, often of great size, are frequently discovered of late at this isolated place," presumably by observers less restricted to the Island Mine settlement.

Another source confirms that caribou were rare, at best, in the 1870s. Emmet H. Scott (1924) wrote to Albert Stoll, Jr.:

> In 1876, when I explored the northeasterly part of the island pretty thoroughly, I met the representative of the old Island Copper Company, an English concern, who had cruised the whole island and had charge of it for many years. He told me that there were no moose or caribou on the island at that time, but that there used to be a great many.

When the third wave of miners came to Isle Royale, to the Wendigo mine in the 1890s, caribou had apparently recovered enough to be seen or at least recorded more often. Dr. W.P. Scott (1925:9), who taught at the Wendigo one-room school in 1890-92, recounted a rare caribou sighting:

> In the summer time the only animal track I recognized, and followed for a mile or more, was that of a large caribou who wandered into our upper camp . . . and startled the sole occupant left in charge, our diamond setter, old Billy May, who when asked what he did when he saw the animal, said 'I he'd a stone at un.' I was sorry not to have had a chance to see a real live caribou. We had heard, what we had considered something of a fairy tale, about caribous being present on the island, and this was the only real evidence we had been able to get. The same animal was seen once or twice later and was likely a straggler from the north shore which had come over to us on the ice. When one reads in the daily papers of late [1925] of the herds of caribou and moose present on Isle Royale, we who have lived there . . . can't help but be suspicious . . . if [the caribou] have increased to any considerable number, we in Houghton do not hear much about it and certainly to not hear of many successful caribou hunts from local sportsmen.

A common bias is reflected in Dr. Scott's observations—extrapolating to the entire island based on observations in a restricted, "settled" area. This report contrasts with one from respected geologist and mineral prospector Jacob Houghton, who wrote to the chairman and directors of the Wendigo Copper Co. Ltd. on 10 October 1892:

> In the west side of section 25 . . . [between Lake Desor and Little Todd Harbor] . . . is a little pond about 1/2 mile long and from 300 to 500 feet in width and almost entirely surrounded by an open marsh, were numerous caribou tracks. It is a particularly secluded and protected spot. These facts seem to point to the occupation of the place by a sizeable herd of these animals. We also saw a few tracts [sic] along the summit ridge. Recently a caribou was seen on the Wendigo property. Also tracks were seen by Mr. Hay in the Huginin [sic] Cove. Also a camper reported having seen a caribou at Rock harbor during the past summer. I have come to the conclusion that there is a great number of caribou on the island than has heretofore been imagined.

Fred Dustin (1946:688), self-appointed historian of Isle Royale place names, was told that "in the nineties, many caribou were on the island, especially at the southwest end [Siskiwit swamp]." Fishermen provide two more observations from the 1890s. Raymond (n.d.) reported that his fishing party "found marks of caribou, of which the island has many, on the shores of Malone Bay in June, 1897." Finally, resident fisherman Mike Johnson (1942) recalled that in the "early days" (he came to Isle Royale in 1892) he saw "two bunches of caribou come out from the forest across from Pete Edisen's place [in Rock Harbor and Mike's own place at the time] and start across the ice. They [the fishermen] did not have rifles but a Finlander [another fisherman] crippled and then killed a cow with a load of buckshot." This caribou was the first fresh meat they had of any large animal on the island that year although they frequently shot "rabbits" (they kept a gun in their boat). Again, the implication is that hunting was so commonplace as to be taken for granted by subsistence fishermen and trappers in the 1800s, but sightings of caribou and, hence, opportunities to hunt them, were rare. Presumably, the lack of sightings was due to caribou being scarce, but also, perhaps, because most fishermen did not venture inland from Isle Royale's shoreline.

Turn-of-the-century records include more indications of the connection between Isle Royale and mainland caribou herds. J.G. Cross, of Ontario's Sibley Peninsula, wrote the following in a letter to wolf biologist Dave Mech (1966:16):

> Previous to 1900, when caribou were abundant, they were often observed on the outside of Silver Islet singly, or in small herds . . . these animals often could be observed traveling back and forth, apparently to Isle Royale, or following the shoreline in both directions.

In the early 1900s, John Erickson observed 11 caribou on the lake ice in the direction of Isle Royale while fishing approximately five miles off Pigeon Point, Minnesota (Adams 1909). And on 27 March 1904, Isle Royale fisherman John Anderson saw two caribou near Blake Point, when the island was connected to the Canadian mainland by an ice bridge (ibid).

Numerous individual sightings of caribou were reported by Isle Royale fishermen and visitors between 1902 and 1928. A chronological summary follows. Oral history interviews are from the Isle Royale National Park archives, Mott Island, unless noted otherwise.

1902-05 Ingeborg Holte, daughter of fisherman Sam Holte, recalled seeing caribou while her family lived year-round at Chippewa Harbor (Holte 1980).

1902-05 Glen Merritt, summer resident since 1902, recalled that "our family never saw the caribou, but talk to the fishermen and they . . . would tell about . . . the big herds of caribou they would see on the shore in the early spring when they [the fishermen] came down [walking on the ice to get to their fisheries in the spring]. . . . they were there in such large numbers, according to the fishermen. I don't know when they disappeared . . . but it must have been just before the moose arrived. . . . by that time most of the caribou had left the island." He also heard of a fisherman who saw caribou about 1925 (Merritt n.d., 1974).

1904-26 NPS biologist James Cole (1956 in Mech 1966) reported (secondhand) caribou observations on Isle Royale in 1904, 1915, 1920, 1921, and 1926.

1904 On 27 March, Victor Anderson saw two caribou on the ice between Moskey Basin and Middle Islands, and his son, John, saw two caribou at Blake Point (Mech 1966).

1905 The Andersons saw nine caribou on the ice near Rock Harbor lighthouse on 16 April (ibid).

1906-25 Milford Johnson was one of the fishermen who would see the caribou in the spring in the Rock Harbor channel. He reported usually seeing 7, 8, or more, and once saw 12 in a group on the shore ice (Johnson 1965).

1912-13 Violet Miller recalled that her father saw caribou during his first winter on Isle Royale, at Chippewa Harbor (Miller 1986).

1915-22 John Skadberg, who fished with the Seglems then on his own at Hay Bay, recalled seeing a few caribou and tracks of a pair on Siskiwit Lake in his early years (Skadberg 1987). He also recalled the Seglems trying to rope the swimming bull at Fisherman's Home to "capture it"—but having to cut the rope when the animal got it's feet caught on a reef.

1916-20 Fisherman Pete Edisen was fond of telling stories about or his early caribou sightings, especially the last bull he saw near Conglomerate Bay around 1920, or later (Mech 1966, Oikarinen 1979, Edisen and Edisen 1965, Edisen 1975).

1918 or 1919 Ohio newspaper editor and Isle Royale visitor W.P.F. Ferguson wrote of caribou sightings on Isle Royale in a series of articles published in the *Detroit News* promoting the national park movement. In 1918 or 1919, while hiking on the Greenstone Ridge, he saw three bulls at the Island Mine spring and a band of 13 adults and 7 or 9 calves swimming from a Lake Desor

island to shore. Whether these sightings occurred on the same or different trips is unclear (Ferguson 1922*b*, 1922*c*).

1922 Fisherman Holgar Seglem tried to ride a bull caribou that he and his brother, Olaf, roped while it was swimming across the harbor at Fisherman's Home (Anonymous 1928, Erskine 1922).

1922 W.P.F. Ferguson saw caribou at the Hidden Lake salt lick, a favorite for moose today. He reported he had never seen caribou "so near the human playground" (Ferguson 1922*c*).

1926 Summer resident Frank Warren (1926) observed an antlered caribou on a beach at Caribou Island.

1926 James MacGillivray reportedly photographed a cow with twin calves at McCargoe Cove in the summer of 1926 (Hickie n.d.). A print of this photograph is located in the *Detroit News*' Isle Royale papers in the Michigan Historical Collections, Ann Arbor. The caption on the photograph, written by Albert Stoll, Jr., reads:

> So far as is known this photograph of a female caribou and twin fawns, taken by James MacGillivray of Oscoda, Michigan, in 1926, is the last evidence of the presence of woodland caribou on Isle Royale. Mr. MacGillivray, at the time the photograph was taken, was official photographer for the Michigan Department of Conservation and he submitted this evidence to Frank M. Warren of Minneapolis, who was also interested in uncovering evidence of the presence of these animals on the island and stated that undoubtedly these were the last of the species remaining on Isle Royale.

In an article for American Forests and Forest Life, Stoll (1926) wrote:

> . . . two years ago [1924?] we photographed a cow caribou with twin calves in the marshy wastes of MacCargoes [sic] Cove, a stamping ground for moose and caribou. Those who later viewed the photographic results were skeptical of this parental possession for twin calves are considered more than a rarity.

The photograph was taken from behind the animals at some distance and when I saw the print it was clear to me that the cow and calves were moose, not caribou.

1926 W.P.F. Ferguson (1926:472) thought "caribou are not numerous and live chiefly, I think, in the big hills behind Siskiwit Lake."

1928 Hugh E. Green, chief conservation officer of the Michigan Department of Conservation, visited Isle Royale in 1928 and saw "few deer" and "but one caribou" (Anonymous 1928).

1928 G.A. West (1929), subsequent director of the Milwaukee Public Museum, reported that on a guided hike up the Little Siskiwit River from Hay Bay in 1928, resident warden Bill Lively informed him that a number of "upland caribou" still lived in the extensive swamp they were passing about three miles above Lake Superior. Indian guide John Linklater was along on the trip. Both Lively and Linklater were knowledgeable outdoorsmen with extensive experience in the Isle Royale woods.

1929 Finally, Fred Dustin (1946) was "informed" that caribou may still have survived in the Siskiwit swamp area "as late as 1929," but he did not list his sources. Tobin Harbor resident Frank Warren (1929) wrote to Albert Stoll, Jr., that tracks of caribou were no longer seen by 1929. Dr. Frank Oastler (1929) reported to the National Park Service that deer and caribou "seemed to have disappeared in recent years." And a 1934 NPS report on fauna in the National Parks stated that "Isle Royale once had a band of caribou, but it disapeared many years ago" (Wright and Thompson 1935).

In summary, caribou were seen on Isle Royale as late as 1928 and may have persisted on the west end of the park a few years later. Observations ranged from 1 to 22 animals at a time and occurred during winter, spring, and summer.

Reports from Michigan game wardens provide the best estimates of caribou abundance on Isle Royale. Warden C.S. Pierce reported that at least two large herds were on Isle Royale in 1911 (Wood and Dice 1924 in Martin 1988). After a winter of trapping over the western two-thirds of Isle Royale in 1916-17 and talking with trappers on the east end, warden Foster (1917) estimated that 30 caribou, indicated by "track signs," and 150-200 moose and 20 white-tailed deer were in the park. Foster also recorded that at least 67 lynx and 60 coyotes were taken on the island that winter; he thought only 12 coyotes and one lynx were left.

Albert Stoll, Jr., was the source of the highest caribou estimates. For example, the 1921-22 Biennial Report of the Michigan Department of Conservation (Stoll 1924*a*) estimated that 225-300 caribou had been on Isle Royale before 1920. On 13 February 1924, Stoll wrote the following to the Hon. Hubert Work, secretary of interior: " . . . moose estimated conservatively at 1,800, in addition to being the home and breeding range of approximately 400 woodland caribou." These figures were repeated verbatim one month later in a memorandum to the press from the U.S. Department of the Interior (copy available in the Michigan Historical Collections in Ann Arbor). Elsewhere, Stoll (1926) was more candid: "There must be hundreds of caribou but no official census has been made that approaches accuracy."

The debate over the protection of Isle Royale as a state or national park was at its peak in the mid-1920s, fueling hyperbole on the grandeur of Isle Royale's resources. For example: "Where in the States could one find a thriving, contented herd of roving woodland caribou . . . shrouded in mystery and uncertainty" (Stoll 1926). Early predictions of the impending moose population irruption had begun by 1923 (Willebrands 1923), inciting some to object to park status because hunting would not be allowed and causing others to downplay the numbers of game animals and their impacts. Thus, all sources must be weighed together to provide an accurate sense of caribou numbers and the potential effects of moose overbrowsing and coyotes on the last caribou.

References cited in this section appear in the Literature Cited section starting on page 43.

Appendix D
Caribou Ecology

Habitat Use

Where predators are numerous, caribou select habitats foremost to avoid predators, then they select sites with optimal forage resources or to escape deep snow or biting insects, or both (Bergerud et al. 1990). Observations of this predator-driven habitat selection include the following: (1) avoiding habitat preferred by predators (Bergerud and Page 1987, Jakimchuk et al. 1987); (2) avoiding habitat used by alternate prey and hence greater predator densities (Bergerud and Page 1987); and (3) selecting good escape habitat regardless of predator densities (Bergerud 1989*a*). These patterns apply especially in the spring and summer when caribou are most vulnerable. Elsewhere, woodland caribou select habitats primarily for optimal forage and secondarily for suitable snow conditions in winter (Schaeffer and Pruitt 1991).

Caribou that calve in open habitats—barren ground caribou and woodland caribou in coastal or interior tundra-like habitats—aggregate into large herds and migrate, sometimes great distances, presumably as an antipredator strategy (Bergerud 1978, Darby et al. 1989). In contrast, forest-dwelling woodland caribou migrate short distances or not at all and remain widely dispersed from each other for most of the year (Fuller and Keith 1981, Shoesmith and Storey 1977, Cumming and Beange 1987, Edmonds 1988, Darby and Pruitt 1984, Bergerud 1989*a*, Bergerud et al. 1990). This spacing strategy is an adaptation to minimize contact with predators in forested habitat (Bergerud 1983, Bergerud et al. 1990). Bergerud (1980) calculated that woodland caribou typically need 2.6 km^2 per animal to minimize contacts with predators (to "space out"), but only 0.25 km^2 per animal to find adequate food supplies in typical boreal forest habitats (see also Bergerud et al. 1990).

Abraham et al. (1990:9-18) provide an excellent summary of forest-dwelling woodland caribou habitat use in northern Ontario:

> *Winter Habitat.* Large areas of mature coniferous forest, particularly open jack pine or black spruce lichen-rich stands, are desirable winter habitat because they have an abundant winter food supply and a relatively low suitability for moose, and thus relatively low populations of bears and wolves. . . . These stands generally have an open canopy, are shrub poor and have an abundant supply of ground lichens and ericaceous shrubs. . . .
>
> In autumn and winter, woodland caribou feed on arboreal and terrestrial lichens, sedges and bog shrubs; woody browse in not a dietary staple (Simkin 1965, Bergerud 1972, Darby and Pruitt 1984, Edmonds and Bloomfield 1984). In northern Ontario caribou feed primarily on terrestrial lichens in late winter (Simkin 1965, Cumming and Beange 1987, Bergerud 1989*b*).
>
> Early winter (October to January) habitat of woodland caribou is generally lowland black spruce-muskeg where caribou feed on sedges, shrubs and arboreal lichens, often in open bogs (Fuller and Keith 1981, Darby and Pruitt 1984, Bergerud 1989*b*). In the absence of abundant lowland lichen mats, caribou move into upland coniferous forest when snow depths in lowlands exceed about 50 cm (Stardom 1975, Fuller and Keith 1981, Darby and Pruitt 1984, Bergerud 1989*b*). Snow depth is usually shallower in such uplands in late winter (January to March) (Stardom 1975, Darby and Pruitt 1984). Caribou then seek open jackpine and black spruce uplands (less than 70% canopy closure) where they can dig feeding craters for terrestrial lichens. . . .

The amount of area occupied by woodland caribou in winter depends on the number of animals in a herd, forage availability, snow conditions and predators. Studies of woodland caribou occupying boreal forest year-round show that individual caribou may occupy 30 to 780 km^2 in winter, 250 km^2 on average (Shoesmith and Storey 1977, Fuller and Keith 1981, Darby and Pruitt 1984, Edmonds and Bloomfield 1984). However, mean monthly group size in winter varies from 2.8 to 11.4 (Shoesmith and Storey 1977, Fuller and Keith 1981, Darby and Pruitt 1984, Brown et al. 1986, Cumming and Beange 1987, Bergerud 1989*b*). The wintering areas occupied by individual caribou in these groups are largely overlapping. . . .

[Based on . . .] the size of wintering areas reported for various herds of woodland caribou occupying boreal forest year-round . . . the mean wintering area required per caribou on a "herd" basis is 16.2 km^2 [range 1.5-40.0 km^2/caribou, from Stardom 1975, Darby and Pruitt 1984, Edmonds and Bloomfield 1984, Wepruk 1986, Cumming and Beange 1987, Bergerud 1989*a*]. Behaviour may vary, but the main factors affecting area occupied in winter are snow conditions and predators. For example, some caribou make long distance movements in mid-winter (Fuller and Keith 1981, Edmonds and Bloomfield 1984), sometimes in response to deep snow (Brown et al. 1986) or to predators (Bergerud 1989*a*). Other caribou wintering areas may be restricted in size due to predators as is the case in Pukaskwa National Park in Ontario (Bergerud 1989*a*). . . .

Calving Areas. Calving occurs in sites where security from predation is maximized (Bergerud and Page 1987). For forest dwelling caribou, these areas include islands in lakes, lake shorelines (especially those with rugged topography and/or peninsulas), and isolated or secluded mainland bogs and fens (Bergerud 1974*b*, Shoesmith and Storey 1977, Darby and Pruitt 1984, Brown et al. 1986).

On a continuum of behaviour and grouping among forest dwelling caribou, island or island/shoreline calving situations probably represent those animals with the greatest degree of gregariousness, cohesion and visibility. This permits some "herd" identification and has led to a preponderance of data on island and shoreline calving locations. . . . In contrast, mainland calving sites may represent the calving habitat of more dispersed cows. Identification of a "herd" or even association with a specific wintering area is difficult. Widely dispersed calving sites in isolated or secluded bogs or fens are more difficult to identify, and less likely to attract human attention. . . . However, a much higher proportion of Ontario's caribou give birth to calves in this type of site and collectively they may be more important than island/shoreline sites. . . .

Summer Range. Summer home range is generally the smallest seasonal home range for both sexes (compared to fall and winter). In some cases, females with calves stay on calving islands all summer. In other cases, they move to the mainland in July and August. Much of their activity occurs within 100 m of shore, whether on mainland or island sites, possibly because of the potential security of escape to water when predators threaten. There is a significant risk of predation of calves and adult females at the time of this move (Shoesmith and Storey 1977). These habitats may also provide some relief from insect harassment. Caribou seek rapidly growing green plants in spring and summer, and their diet is probably most varied during this period. . . .

[*Seasonal Shifts*]. Forest dwelling caribou are essentially solitary from just prior to calving in May until just prior to the rut in late September. They form small groups during and after rut until late April. Maximum group size seldom exceeds 50 animals, and usually averages less than 10 throughout the September to April period. Average group size from May to September is less than two animals. . . .

Woodland caribou sometimes . . . migrate . . . long distances between seasonal ranges from year to year. In . . . [the Lake Nipigon region] movement from summer calving habitat to winter range averaged 46 km (range 26-80 km) (Cumming and Beange 1987). Migration distances between summer and winter ranges reflects the juxtaposition of shoreline, summer habitat (anti-predator strategy) and winter lichen supply (Bergerud 1989*b*).

> Spring movements of females from wintering to calving areas generally occurs in April prior to mid-May peak calving. Travelling at this time of year often requires little effort since lakes, streams and bog areas remain frozen with minimal snow cover. . . . Fall shifts to wintering areas occur at any time between late October and early January (Shoesmith and Storey 1977, Cumming and Beange 1987).

The importance of lichens in woodland caribou diet and range selection has been rated high by some observers (Bergerud 1972, Bergerud 1974*a*, Euler et al. 1976). Caribou confined to the tiaga biome of northern Canada in winter are by necessity restricted to a diet of lichens (Skoog 1968). While caribou have evolved the ability to subsist on lichens as winter forage, unlike other cervids, they may select lichen-rich habitats principally because these habitats are used little by moose and deer and, thus, support fewer predators (Abraham et al. 1990). The persistence of remnant and transplanted woodland caribou herds on Lake Superior islands illustrates that caribou can persist on ranges poor in ground lichens. These herds survive where lichens are browsed out on the Slate Islands and Pic Island (Euler et al. 1976, Bergerud 1983, Ferguson et al. 1988) and in deciduous forest with few lichens on Michipicoten Island (G. Eason, pers. comm.).

The relationship between woodland caribou, ground lichen abundance, and fire has been poorly understood. *Cladina* lichen stands, typically in jack pine and black spruce forests, are now known to be fire dependent, although fire temporarily reduces lichen abundance (Abraham et al. 1990). For example, woodland caribou use of burned tiaga habitats in southern Manitoba declined some five years after a forest fire as deadfall obstructions increased and lichen stands decreased (Schaeffer and Pruitt 1991). Ground lichen biomass peaks 40-100 years postfire, when the tree canopy is relatively open (Bergerud 1978, Abraham et al. 1990). In contrast, snow conditions improve for woodland caribou as the forest reverts to a climax closed canopy (Schaeffer and Pruitt 1991).

While woodland caribou are generally associated with mature, northern boreal forests, they will readily exploit young deciduous forest foods where predation risks are low. For example, in the Slate Islands and islands in Lake Nipigon, early-to-midsuccessional mixed deciduous forests are used as much or more often than mature coniferous forest (Euler et al. 1976, Bergerud et al. 1990). Mixed deciduous forest is also used by caribou in southeast Manitoba, but less so than mature coniferous forest (Darby and Pruitt 1984).

Woodland caribou shift between seasonal ranges in response to predator movements, winter snow depths, biting insect activity, and food availability (Shoesmith and Storey 1977, Fuller and Keith 1981, Darby and Pruitt 1984, Edmonds and Bloomfield 1986, Cumming and Beange 1987, Bergerud et al. 1990). In a typical annual cycle, woodland caribou move from calving and summering habitat on islands and adjacent shores, or in remote bogs, to gather on fall rutting habitat on islands or open bogs. After the rut, woodland caribou remain in open bog habitat until snow depth exceeds 50 cm, then they switch to more exposed ridges or jack pine habitat in mid- to late winter (Abraham et al. 1990). Bergerud (pers. comm., 1989*a*) has hypothesized that open habitats are selected primarily for ease of predator detection or escape; secondarily, caribou are able to survive on the plants available there, bog shrubs and sedges, and ground lichens. In forested habitats, topography that provides relief from biting insects is coincident with prime escape habitat in open areas and shorelines (Bergerud et al. 1990).

Home Range and Density

The range size of woodland caribou in forested habitats can vary 10- or 20-fold within a year. Home ranges of individual woodland caribou vary from 13 km^2 in summer to 335 km^2 in winter (Shoesmith and Storey 1977, Fuller and Keith 1981, Darby and Pruitt 1984). Seasonal ranges of entire herds have been calculated in southern Manitoba (95-140 km^2 in winter and 175-190 km^2

in summer) and the Lake Nipigon area, Ontario (390 km² in winter) (Darby and Pruitt 1984, Cumming and Beange 1987). In general, individual ranges are smallest in the summer but herds are most dispersed at this time.

Bergerud (1983:48) calculated an average of 0.4 woodland caribou/km² as a "synthesis of boreal populations, frequently in joint equilibrium with self-sustaining wolf populations (2-4 wolves/1,000 km²)." Bergerud (pers. comm.) would now revise this estimate downward to 0.3/km². Where moose are also present and wolf numbers are higher (7-15 wolves/1,000 km²), caribou densities are typically lower (<0.2/km²) (Bergerud 1983). Densities of the remnant population at Pukaskwa National Park have varied from 0.05 to 0.12/km² (Bergerud pers. comm.). Densities across Ontario vary from 0.006 to 0.05/km² in areas ranging from 4,300 to 293,000 km², where much of the area is not occupied by woodland caribou (Ontario Ministry of Natural Resources 1986, Darby et al. 1989, Cumming and Beange 1987, Bergerud et al. 1990). Much of the wide variation in density estimates reflects differences in the resolution of the area censused: from a region, to a study area, occupied polygons, subsets of prime habitat, or seasonal ranges. For example, densities for the Lake Nipigon woodland caribou herd have been reported as 0.006/km² for a 32,000 km² study area, 0.07/km² for the area actually occupied by caribou, and 1.8/km² for small islands in summer (Cumming and Beange 1987). In another study, this same herd's density was estimated at 0.05/km² for an area including the waters of Lake Nipigon (Bergerud et al. 1990).

These density figures apply to mainland ranges; woodland caribou densities on islands are generally higher (A.T. Bergerud, pers. comm.). The Slate Islands caribou population has varied from 6.9-11.0/km² (Bergerud 1980). On the Slate Islands and Pic Island, populations averaging 2-5/km² for many decades continue to be highly productive despite food shortages (Bergerud 1983; Ferguson et al. 1988; A.T. Bergerud, pers. comm.). Yet, in general, food resource depletion can be detected by the time caribou populations reach 5/km² (Bergerud 1980). Overgrazing is evident on islands in Lake Nipigon with a current average density of 1.8 caribou/km² (Bergerud et al. 1990).

Escape Habitat and Predator Densities

Woodland caribou cows do not defend their young against predators and rely on lack of detection by "hiding in space" or dispersing, running, or escape features such as water and steep cliffs to avoid predation (Bergerud 1980, 1985; Bergerud et al. 1984; Bergerud and Page 1987; Cumming and Beange 1987; Ferguson et al. 1988; Bergerud et al. 1990). During open water seasons, islands fulfill this function well by separating caribou from mainland predators and providing close access to water escape. Thus islands are frequented in summer in most regions and for year-round refuge where they do not freeze in (Simkin 1965, Bergerud 1974*a*, Shoesmith and Storey 1977, Cumming and Beange 1987, Ferguson et al. 1988, Bergerud 1989*a*, Bergerud et al. 1990).

Woodland caribou will continue to seek refuge on islands when forage resources are greatly depleted, even if abundant forage is available nearby on the mainland (Ferguson et al. 1988, Bergerud et al. 1990). At Lake Nipigon, timing of migration is tied to ice development and melt, not insect or vegetation cycles (Bergerud et al. 1990). Woodland caribou use the shoreline as escape habitat by remaining within 100 m of shore at Lake Nipigon, Pic Island, in Pukaskwa National Park, and at Reed Lake, Manitoba (Shoesmith and Storey 1977, Bergerud 1985, Cumming and Beange 1987, Ferguson et al. 1988, Bergerud 1988, Bergerud et al. 1990). On Pic Island, both cows and bulls select feeding sites near steep, rocky cliffs and retreat up the cliffs when threatened (Ferguson et al. 1988).

Bergerud (1983) proposed that predation is the most consistent regulator of woodland caribou populations in the boreal forest. Continentally, many North

American caribou populations have declined in regions shared with moose, where wolf densities are high (7-15 wolves/1,000 km^2) (Bergerud 1983). Bergerud and Elliott (1986:1525) reviewed caribou population dynamics in numerous North American herds and concluded that "caribou cannot coexist [with wolves] away from refuge habitat when moose biomass allows wolf numbers to increase to high levels [>6.5/1,000 km^2]." Based on the history of caribou introductions in eastern North America, Bergerud and Mercer (1989:118) predicted that "caribou introductions will fail in northern Minnesota and southern Ontario, even in the absence of deer, when wolf numbers exceed 10/1,000 km^2."

Relict herds of woodland caribou persist in the face of high wolf populations only where excellent escape habitat is available for young calves (Bergerud 1980, 1985). For instance, woodland caribou presently survive at Lake Nipigon, where wolf densities are commonly 10-14/1,000 km^2, by calving and summering on wolf-free islands (Cumming and Beange 1987, Bergerud et al. 1990). The small band at Pukaskwa National Park follows a similar strategy to persist where wolf densities average 13-14/1,000 km^2 (Bergerud 1989*a*).

Diet

Woodland caribou browse a wider variety of vascular plants than other North American cervids (Bergerud 1978). Bergerud (1977 *in* Bergerud 1978) cataloged more than 62 lichen species and 282 kinds of seed plants eaten by caribou. Their staple summer diet of deciduous foliage is supplemented by sedges, grasses, herbs, mushrooms, and lichens (Ahti and Hepburn 1967, Bergerud 1978). In early spring caribou seek any newly sprouting greens (Bergerud 1978). When fall frosts kill deciduous forage, caribou prefer lichens, sedges, and broadleaved evergreens (Darby 1979). Terrestrial lichens and arboreal lichens are heavily used during the winter, but evergreen and deciduous shrubs are browsed as well, along with lesser amounts of various sedge, grass, and herb species, depending on what is available through the snow (Cringan 1957, Ahti and Hepburn 1967, Bergerud 1972, Darby and Pruitt 1984). Relative availability is the prime factor in plant species use (Bergerud 1978). In essence, caribou "will eat any green plant in escape habitat" (A.T. Bergerud, pers. comm.).

The diets of caribou on other Lake Superior islands may be especially relevant to an Isle Royale population. On the densely populated Slate Islands, where appreciable quantities of terrestrial lichens are not available and arboreal lichens remain only above the 1.5-m caribou browse line (Bergerud 1978; A.T. Bergerud, pers. comm.), Cringan (1956) found that mountain maple, American mountain ash, red osier dogwood, arrowwood *(Viburnum rafinesquianum),* and various willows together composed 75% of their winter diet. By late winter, Slate Islands caribou subsist entirely on windblown arboreal lichens—a near-starvation diet (A.T. Bergerud, pers. comm.). For unknown reasons, they do not eat sedges or leatherleaf in the winter on the Slate Islands (ibid). Ferguson (1983) found that on Pic Island, alder (*Alnus* spp.) and maple stems were highly preferred, as were ferns (*Dryopteris* spp.), raspberries (*Rubus* spp.), and currants (*Ribes* spp.) in the spring diet of the resident band. Although somewhat less severe than on the Slate Islands, the Pic Island caribou survive despite facing starvation some winters due to poor food supplies (Ferguson et al. 1988).

Population Dynamics

Compared to other cervids, caribou have a low reproductive rate due to slow maturity and single births. Typically, female caribou become sexually mature at 2.5 years, although they may be able to breed as yearlings under ideal conditions and some do not breed until 3.5 years or older (Bergerud 1974*a*, 1978, 1980). Pregnancy rates for females 2.5 years or older average 84% (Bergerud 1980) and 96% for females 3.5 years or older (R. Page, pers. comm.). These rates are consistent within herds from year to year, with annual variation in

productivity deriving from the proportion of non-parous two-year-olds in the population (Bergerud 1980; R. Page, pers. comm.).

Caribou are polygynous, and males suffer higher mortality from at least four years old and in some populations from birth (Bergerud 1971, 1980, 1989*a*; Thomas et al. 1989). Although sex ratios typically favor males at birth (Bergerud 1980, 1983), adult sex ratios average 39:61 (Bergerud 1980). The preponderance of females among adults means that calves, at birth, compose 27-30% of the population (ibid). Caribou bulls form harems of 5-50 females, fewer in forested habitats. In an average year only 20% of mature bulls breed, siring six to eight calves (R. Page, pers. comm.). However, the turnover in dominant males between years is high due to the stress and high mortality rates associated with dominance (ibid).

Woodland caribou calf mortality rates are often high, especially in the first month to six months of life. In the first year, mortality averages 50% and sometimes reaches 80-90% (Bergerud 1980, 1983; Bergerud and Page 1987). Natural annual adult mortality in the absence of predation averages 5-6%; with predation, annual adult mortality averages 10% (7% for females, 13% for males) (Bergerud 1983) or as high as 20-30% in declining populations (Bergerud, pers. comm.; 1989*a*). Thus, across North America, calf recruitment to one year will average 10-15% in stable populations (Bergerud 1980, 1983; R. Page, pers. comm.). Female caribou may live to 17 years, while males do not survive past 13 years (Bergerud 1980). Dominant, breeding bulls rarely live through the winter of their fifth or sixth year (R. Page, pers. comm.).

Under ideal conditions such as release onto predator-free islands, caribou populations grow at an intrinsic rate of 0.30-0.35 per year (Bergerud 1980). Observed population growth rates in mainland herds averaged 0.28/year without wolf predation and 0.02/year with "normal" wolf densities (1 wolf/259 km^2) (ibid).

References cited in this section appear in the Literature Cited section starting on page 43.

Appendix E
Summary of VORTEX Modeling Runs

After numerous trial runs of the VORTEX program, I refined the basic population characteristics for a hypothetical caribou herd on Isle Royale (Tables 4 and 5). Then I ran six final simulations using these population characteristics, but varying the mortality rate, carrying capacity, number of animals released, and number of years of releases (Table 6). Table 7 provides a sample of VORTEX output, for the run with high mortality, carrying capacity at 54 animals, and 78 animals released. I also attempted a sequence of four runs to simulate a release of woodland caribou with wolves absent, then reintroduced and gradually increasing; however, the results were inadequate for presentation in this report. Future work on this scenario would be worthwhile. In addition, I had planned five "control" runs to test the hypothetical Isle Royale population characteristics. By running VORTEX with release numbers from Canadian restoration projects (the "controls"), I could have compared the results of VORTEX simulations with actual data from the surviving herds. Unfortunately, I was not able to complete these runs for this report.

In the six simulations I completed, I used moderate-to-high mortality rates and low carrying capacities to represent the "worst case" scenarios for caribou on Isle Royale with wolves present. Moderate mortality was used only if carrying capacity was 54 animals. Otherwise I assumed annual productivity would be good due to ample summer forage and summer escape habitat on the island (see "Habitat Suitability" in the Results and Discussion section).

Large releases are a strategy to overcome high initial mortality while the herd adjusts to its new surroundings. VORTEX, however, will not run with initial population sizes or release numbers in excess of carrying capacity. In VORTEX, carrying capacity works as a population ceiling rather than long-term sustainable average, as wildlife biologists define the term. Thus, I could not model scenarios with high release numbers when carrying capacity was at 54 animals or less, despite numerous attempts. While introducing numbers of animals in excess of carrying capacity was possible with multiyear releases and carrying capacity at 54 animals, these "extra" animals were "killed off" immediately by the VORTEX program, so the results were virtually the same as introducing fewer animals.

VORTEX is sensitive to changes in mortality rates. Deriving good estimates for average mortality rates was difficult because these rates vary considerably between years in the wild. In the Isle Royale simulations, a high mortality rate exceeded the level of mortality that a normally reproducing population could sustain indefinitely. Estimated calf mortality was the exception, with moderate rates reflecting excellent calving habitat on Isle Royale. With these high mortality rates, the simulated populations would inevitably expire; the VORTEX simulations estimated when.

One trial was run without catastrophes, but this run resulted in only slightly longer persistence times than the equivalent run with catastrophes set to occur once every 50 years. In the end, the six trials I ran represented three low carrying capacity scenarios, with the number of animals released having a minimal effect on the results. The three scenarios follow: (1) carrying capacity = 54, high mortality; (2) carrying capacity = 54, moderate mortality; and (3) carrying capacity = 27, high mortality.

Table 4. Population values in VORTEX simulations[1] (listed in order of input).

Variable	Value for All Runs
Inbreeding depression model[2]	Heterosis
Number lethal equivalents/diploid genome[3]	3.0
Age first breed[4]: female	3.0
Age first breed: male	4.0
Sex ratio (percent males) at birth[5]	0.52
Maximum number of young per litter	1.0
Percent adult females with litter of 0 young[6]	17.0
Percent adult males with litter of 1 young	83.0
SD[7] in percent females with 0 young	2.0
Breeding system	Polygynous
Do all males breed equally?	No
Average number of litters/year/successfully breeding male[8]	3.0
Frequency of catastrophes[9]	1.0
Effect of catastrophes on reproduction[10]	0.8
Effect of catastrophes on survival[11]	0.6
Initial population[12]:	
females 2 years old	2
females 3+ years old	18
males 2 years old	1
males 3 years old	2
males 4+ years old	3
Number of years simulated	100
Number of simulations per run	50

[1] I selected the population values for a hypothetical Isle Royale herd to be representative of North American caribou, especially herds in the Lake Superior region living in conditions similar to Isle Royale.

[2] VORTEX offers two models for inbreeding depression: RECESSIVE LETHALS and HETEROSIS. HETEROSIS is a general model in which selection against homozygotes does not remove the genetic load, but which allows for a user-defined number of lethal equivalents. This model was recommended by R. Lacy (pers. comm. with T. Kreeger) for caribou populations.

[3] 3.0 lethal equivalents per diploid genome is a conservative estimate for caribou based on values from other mammals (R. Lacey, pers. comm. with T. Kreeger).

[4] Average age of the parents at the time the young are born (e.g., on the adult female's third birthday and adult male's fourth birthday).

[5] North American average (see Appendix D).

[6] North American average; also average for Pukaskwa National Park herd (see Appendix D).

Table 5. Mortality rates by sex and age class[13].

Sex	Age (Years)	Percent Mortality			
		Moderate	(SD)[14]	High	(SD)
Female	0-1	40.0	(8)	50.0	(10)
	1-2	10.0	(2)	12.0	(2)
	2-3	5.0	(1)	10.0	(2)
	>3	7.0	(1)	14.0	(2)
Male	0-1	45.0	(8)	50.0	(10)

[7] The standard deviation (SD) is an estimation of the effect of environmental variation on reproductive success.

[8] The average number of litters sired per successful male in a year is probably closer to 5.0 than 3.0 (R. Page, pers. comm.), but using the high value in the VORTEX model results in an underestimate of the number of males in the breeding pool (e.g., less than 17% of adult males, given the sex ratios and mortality rates input). In actual populations, the turnover in dominant males is so high between years that closer to 30% of adult males are in the breeding pool, especially in small populations such as we expect on Isle Royale. Using the value of 3.0 litters/successful male/year results in a better representation of the male contribution to the gene pool in the VORTEX simulations.

[9] VORTEX models catastrophes as explained in Appendix B. I used 1.0% frequency of occurrence for catastrophes based on advice from R. Lacy and trial and error in early runs. In preliminary runs using a slightly different version of VORTEX, T. Kreeger found that the model was sensitive to higher values for frequency of catastrophes, so we used 1.0 in all of the final runs.

[10] 0.8 is the severity factor assigned for the effect of catastrophes on the probability of breeding, based on suggestions by R. Lacy (pers. comm. with T. Kreeger).

[11] Severity factor for the effect of catastrophes on survival (R. Lacy, pers. comm. with T. Kreeger).

[12] I used the estimated first year's translocation as the initial population. In runs with annual supplements, I used the same age and sex distribution and total number released as in the first year.

[13] Woodland caribou mortality and reproductive rates, and population densities are described in Appendix D, Caribou Ecology. The range of carrying capacities used in our simulations is discussed in "Population Vulnerability Analysis," in the Results and Discussion section of the text. The composition of annual releases is explained in "Reestablishment Methods," in the Results and Discussion section of the text (for simplicity, supplemental annual releases were set the same as the first-year releases).

[14] SD is the estimated standard deviation in mortality rate.

Table 6. *Woodland caribou population simulations run in VORTEX.*

Run	Mortality Rates	Carrying Capacity[16]	Released Animals[15]		
			Total Number	Years	Catastrophes
1	High	27	26	1	Yes
2	Moderate	54	52	2	Yes
3	Moderate	54	78	3	Yes
4	High	54	78	3	Yes
5	High	54	78	3	No
6	High	54	104	4	Yes

[15] Total number of animals released over the specified number of years. The first year's release is the same as the "initial population"; see composition of the initial population in Table 4.

[16] Carrying capacities were calculated by multiplying the land area of Isle Royale, 544 km^2, by an average density for woodland caribou living near high wolf densities in Ontario, 0.05 caribou/km^2, and a "maximum possible" density near high wolf densities, 0.10/km^2 (see Appendix D).

Table 7. *Sample VORTEX results, run number 4 (K = 54; mortality = high; released 78 caribou = 26 per year for three years; 50 simulations; 100 years). Results: female r = 0.005; male r = - 0.070; mean lambda before K = 0.98. Mean time to extinction = 45.2 years (standard deviation = 8.6 years).*

Year	Mean Population Size	SD in Population Size	Mean Heterozygosity	Mean Number Alleles	Percent Population Extinct
1	30.0	03.5	01.000	46.4	0
2	53.4	04.4	01.000	86.9	0
3	54.8	06.9	01.000	90.6	0
5	50.2	07.2	00.999	63.2	0
10	44.6	08.5	00.995	38.3	0
15	40.5	09.5	00.987	27.5	0
20	35.5	12.0	00.979	20.8	0
25	27.9	11.6	00.965	15.8	0
30	23.0	11.1	00.956	12.9	4
35	17.6	09.9	00.948	10.3	15
40	13.0	08.6	00.9333	08.1	31
45	10.4	07.0	00.924	06.7	54
50	08.4	05.5	00.943	05.7	73
55	06.7	03.6	00.938	05.4	90
60	03.8	02.1	00.775	04.5	96
65	04.0	00.0	01.000	05.0	99
70	00.0	00.0	00.000	00.0	100

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