A photograph of a snowy mountain landscape. In the foreground, two wolves are walking away from the viewer on a snow-covered slope, leaving tracks. The background features a large, snow-covered mountain peak with a deep crevasse. The sky is a pale, hazy blue. The overall scene is serene and wintry.

Ecological Studies of Wolves on Isle Royale

1997-1998

Durward L. Allen

1910 - 1997



Dedicated to the memory of
Durward L. Allen
who founded and directed
studies of wolves and moose
on Isle Royale, 1958-1975.

Ecological Studies of Wolves on Isle Royale

Annual Report 1997–98*

by

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(Results reported here are preliminary and, in some cases, represent findings of collaborators; please do not cite without consulting the author.)



Ecological Studies of Wolves on Isle Royale



“The larger the island of knowledge, the longer the shoreline of wonder.”

Ralph W. Sockman

Personnel and Logistics

In summer 1997 Rolf Peterson directed ground-based field work, aided by Edith N. Greene, Melinda Jones, Christine Kornylak, Krista Markovic, Carolyn C. Peterson, Trevor S. Peterson, Marcel Potvin, and Børge Wahl. Field work continued from May 17 through August 30.

In 1997 the annual winter study extended from

January 13 to February 22. Peterson and pilot Don Glaser participated in the entire study, assisted in the field by volunteers Cynthia D. Carter, Edith N. Greene, Ann Mayo, Leah Vucetich, and the following personnel from Isle Royale National Park—Larry A. Kangas, Jack G. Oelfke, David C. Soleim, and Robert K. Whaley.

Summary

After several years of steady population increase, wolves unexpectedly declined to just 14 individuals in 1998, down from 24 in 1997 (figure 1). Only three of ten pups observed in 1997 survived until winter, and over half of the older wolves also died before the 1998 winter study. Decomposed remains of six wolves were recovered, but causes of death were unknown. Acute food shortage arising from the moose die-off in 1996 is a likely cause of the wolf decline, and the possibility of disease outbreak will be evaluated after wolves are live-captured in 1998. All the wolves remaining alive are less than five years old.

The wolf population contained three territorial packs, each with a breeding pair in 1998, plus one nonterritorial pair. Most of the moose now reside within the territory of one pack, which was very

active in tracking and expelling foreign wolves from its territory. Moose kill rates in winter 1998 were relatively low, and wolves killed primarily moose calves as well as taking frequent advantage of warm conditions to hunt beavers.

The moose population was buoyed up by average calf production in 1997, bringing moose numbers up to an estimated 700 animals. To date, remains of 273 moose that died in 1996 have been examined. Calves and old moose were most vulnerable during this record-severe winter, but many young adults also succumbed. Moose calves born in 1997 were quite numerous and noticeably larger than in 1996, indicating that cow moose surviving the nutritional deprivation of 1996 had largely recovered their condition in one growing season.

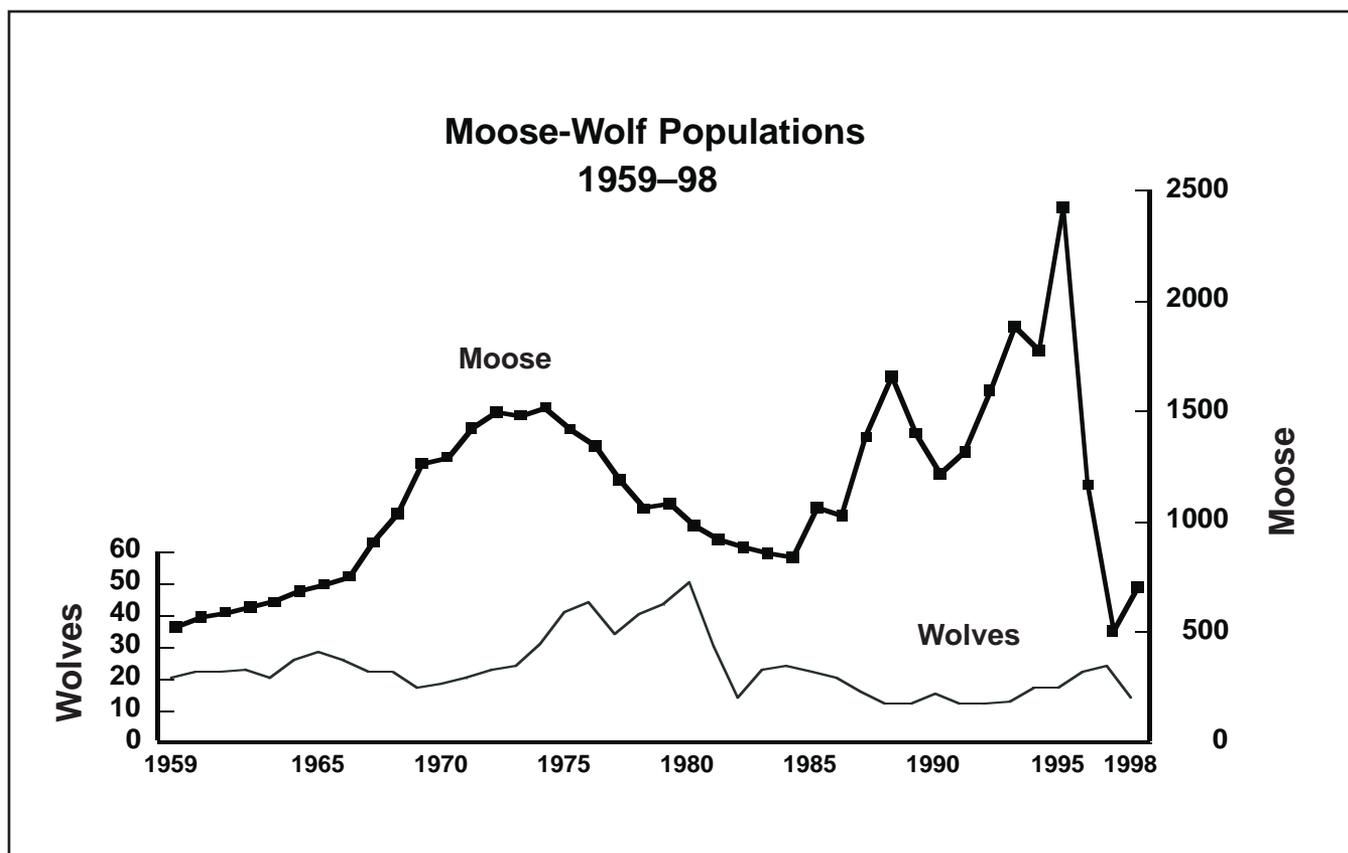


Figure 1. Wolf and moose population fluctuations, Isle Royale National Park, 1959–98. Moose population estimates during 1959–85 were based on population reconstruction from recoveries of dead moose, whereas estimates from 1986–98 are based on aerial surveys.

The Wolf Population

In 1998 the wolf population was organized as follows (figure 2):

East Pack III.	5
Middle Pack II.	4
West Pack II.	2
Northeast duo.	2
Singles.	1
Total.	14

All wolf groups were reduced in size by high mortality and most adult wolves were found paired with a mate. At least four of the six breeding wolves identified in 1997 died before the 1998 winter study, and the other two could not be identified with certainty (females in Middle Pack and East Pack). Only one collared wolf remained from the five present the year before. The population of 14 wolves in 1998 contained six males, five females, and three wolves (two pups and one single) of unknown sex. Mortality in the past year was the highest ever observed for this population (figure 3). The wolf population has again been reduced to a level where random fluctuation in sex ratio (coupled with other risks) can become a survival issue for the population.

Skeletal remains of six wolves that died in 1997 have been recovered, including three that died in spring and three that died in autumn (figure 4). Causes of death for all these wolves were uncertain.

Aside from three territorial (scent-marking) packs,

one male-female pair was found at the eastern end of the island, residing entirely within East Pack territory. The East Pack tracked down the pair in January but stopped a few hundred meters short of making contact. In February, however, the pair was discovered by the East Pack as the two wolves cautiously approached a kill of the pack. The East Pack gave spirited chase for several kilometers, but the pair outran their pursuers.

The East Pack territory is particularly attractive as it now contains about half the moose population, at an average density more than three times higher than in the adjacent pack's territory. The Middle Pack trespassed twice into East Pack territory, each time killing a moose calf and remaining to consume the prey. The East Pack chased the Middle Pack from the first kill, but this didn't dissuade the Middle Pack from returning, when they killed and consumed a calf without being detected by the East Pack.

At the west end of the island, the West Pack consisted of a new breeding pair of uncertain origin. A nonterritorial pack (female and two pups in 1997) disappeared from the west end, and it is very possible that the current West Pack consists of the sole offspring of the former West Pack (a male) and the female from the nonterritorial pack present in 1996 and 1997. Indeed, one might wonder if the aging breeding female in the West Pack might have allowed the foreign female to remain in this territory for two years as a potential mate for her only son; such happenings are known in other wolf populations.

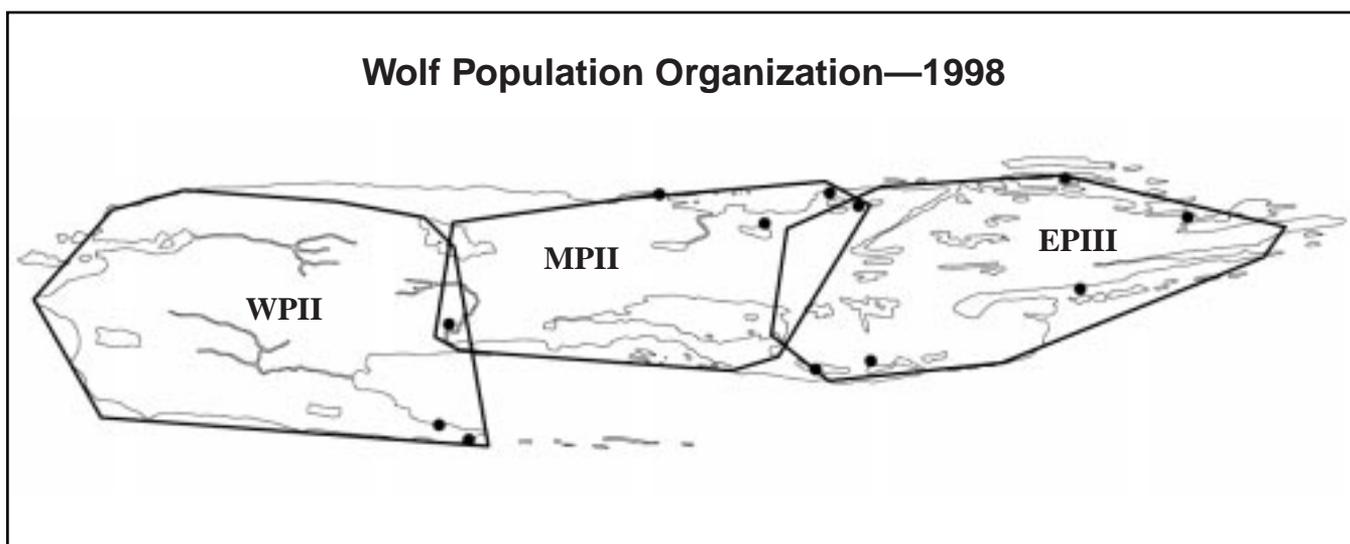


Figure 2. Wolf pack territories (polygons) and moose carcasses (black dots) during the 1998 winter study.

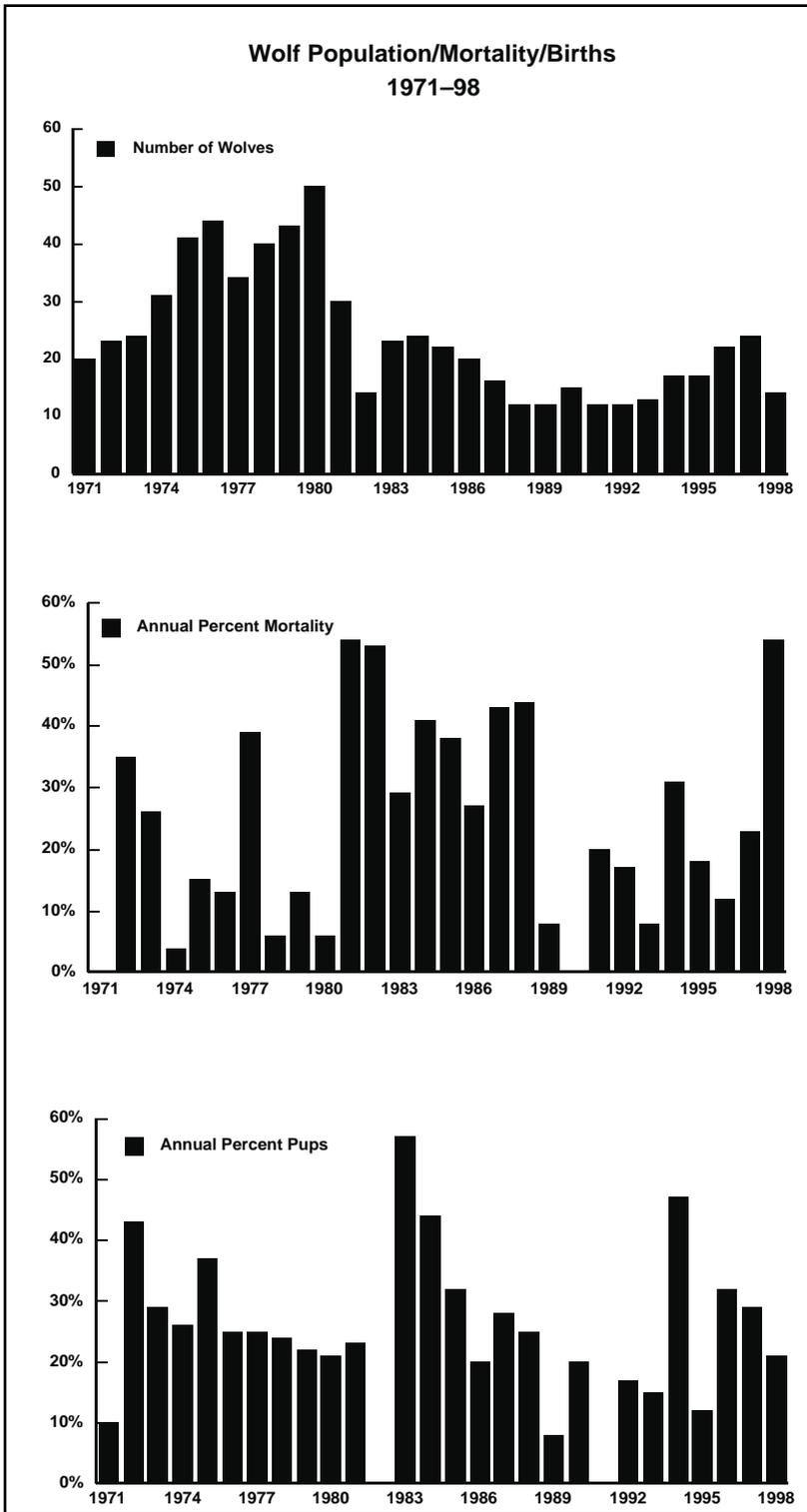


Figure 3. Wolf population size (top) is explained by patterns of mortality (middle) and reproduction (bottom). The decline in 1998 was caused by unusually high mortality in the preceding year.

There has been much discussion among scientists and in the media about the genetic viability of the highly inbred wolf population on Isle Royale. The expected consequence of such inbreeding is reduced reproductive success, based on data from captive populations of many species. Direct counts of five pups each in the East and Middle packs during summer 1997 provided evidence that wolves on the island still have the capacity to produce litters of average size for the species (figure 5). Although genetic variability continues to be lost with each passing generation, there is as yet no convincing evidence that reproductive fitness has been compromised by inbreeding.

Three breeding pairs leading territorial packs appear to have an opportunity to reproduce in 1998. A fourth male-female pair was also present, but it had no exclusive territory and was not seen scent-marking.

Wolf predation rate on moose was relatively low in 1998, primarily because wolf numbers were so low (figure 6). Only 12 wolf-killed moose (8 calves, 12 “adults”) were recorded during the 1998 winter study. The Middle Pack and, particularly, the two-member West Pack spent considerable time hunting beavers in thawing conditions during mid-February.



Figure 4. Well-cleaned skull of dead wolf found on Inner Hill Island at the eastern end of Isle Royale in May 1997. The wolf evidently died on the ice, and scavengers left the skull on this small island.



Figure 5. Middle Pack alpha female (foreground) stands near pup (prone) and alpha male (rear) in February 1998.

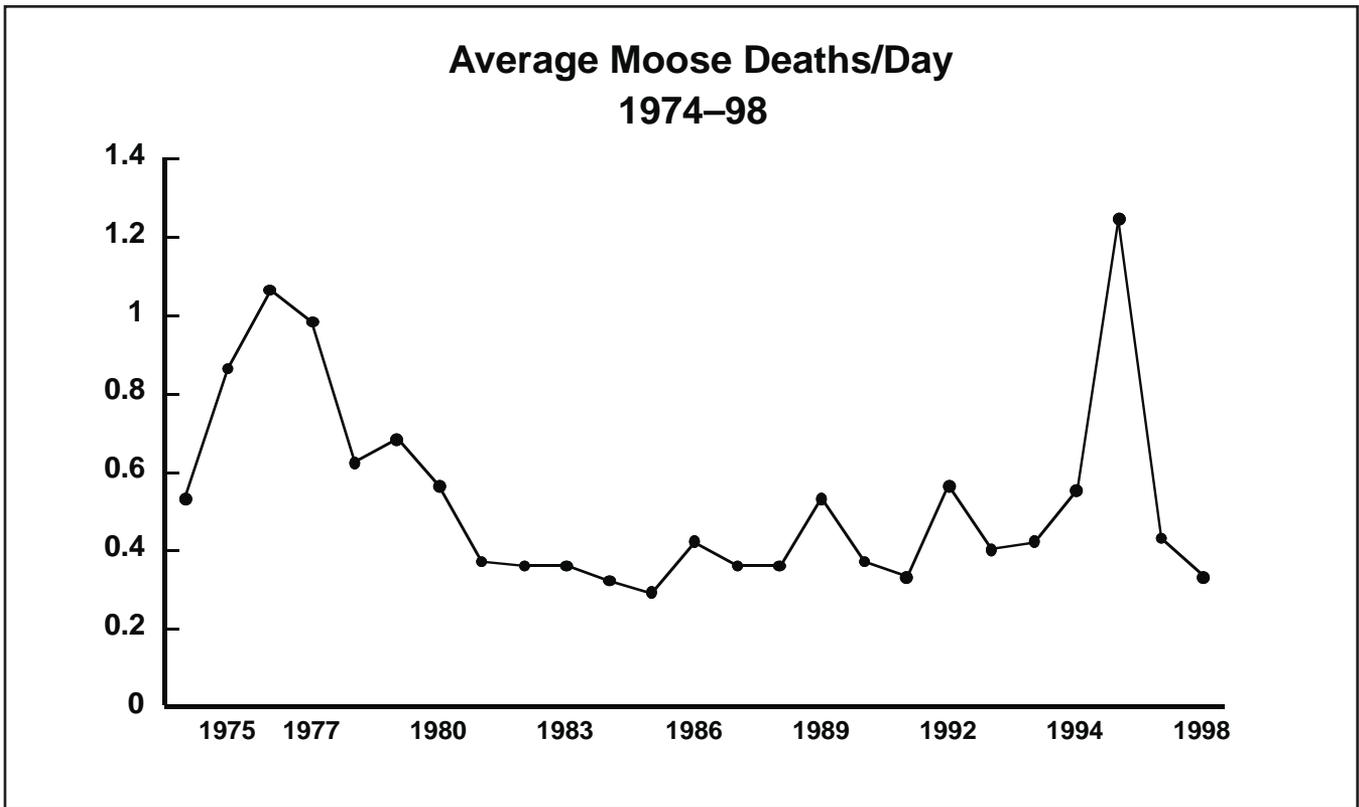


Figure 6. Moose mortality rate in winter 1998 was relatively low.

The Moose Population

After reaching a historic peak of almost 2,500 animals in 1995, Isle Royale moose were reduced by starvation to an estimated 500 after the severe winter of 1996. Although still at a relatively low level, the moose population is now slowly rebuilding (figure 7). From a midwinter aerial census in February 1998, in which 17 percent of the island was intensively searched, it was estimated that 700 moose were present (figure 8). The 95-percent confidence interval for this estimate was calculated to be ± 144 moose.

Moose calves born in 1997 were relatively abundant early in 1998, comprising 13 percent of the moose on census plots. This percentage is near the long-term average level for this population and much higher than calf levels in the previous two years (figure 9). Evidently cow moose that survived the die-off in 1996 recovered in condition in one growing season (summer 1996) to produce calves at normal frequency in 1997. Calves in winter 1998 were strikingly larger in body size than in recent winters, again an indication of improved nutrition for moose (figure 10). Finally,

bone marrow fat for dead moose in 1998 ranged from 40 percent to 80 percent, even for calves, a dramatic increase from the mid-1990s (figure 11).

Food plants for Isle Royale moose have had two growing seasons, 1997 and 1998, to begin to recover from extremely high herbivory by moose earlier in the 1990s (figure 12). It would probably take at least a decade of reduced moose numbers, particularly at the west end of Isle Royale, before forest tree species could escape moose herbivory and grow into the canopy. At the east end of the island, a major release of balsam fir occurred when the moose population was low in the late 1970s and early 1980s. However, height growth of fir at the west end has continued to be suppressed by moose browsing, resulting in a large break in the height structure for this species—except for fir trees in the canopy, most stems are less than a meter tall. The canopy fir trees, the only source of seed for the species at the west end, are steadily disappearing because of senescence-related mortality (figure 13). If the rate of mortality for canopy fir remains



Figure 7. The physical condition of moose on Isle Royale improved dramatically after the 1996 die-off.

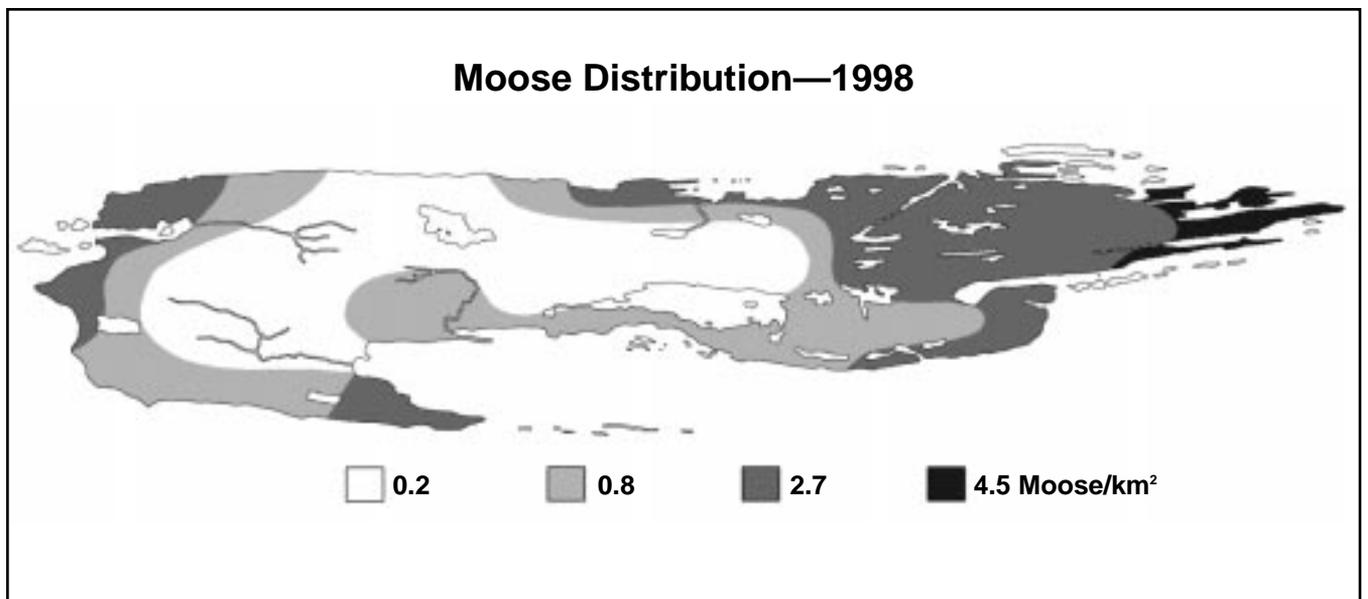


Figure 8. Moose distribution on Isle Royale during the aerial census in February 1998.

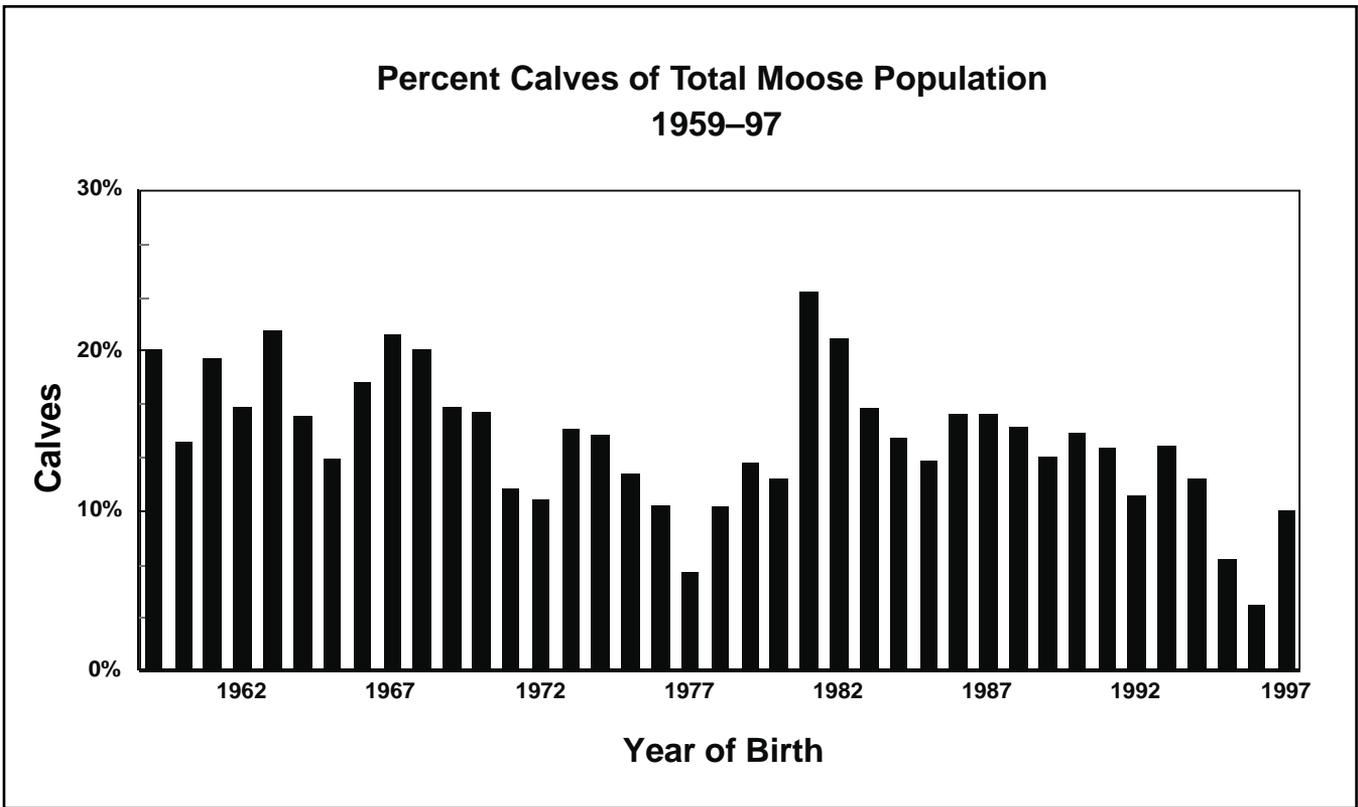


Figure 9. Moose calf abundance (at approximately six months of age) on Isle Royale, as a proportion of the total population. These are single best estimates, the mean of all available counts for each cohort (summer ground observations and aerial counts in autumn and winter).



Figure 10. Body size for moose calves approached normal in the 1997 cohort, after several years of growth retardation. This cow and calf were drinking at a sodium spring at Hidden Lake in February 1998.

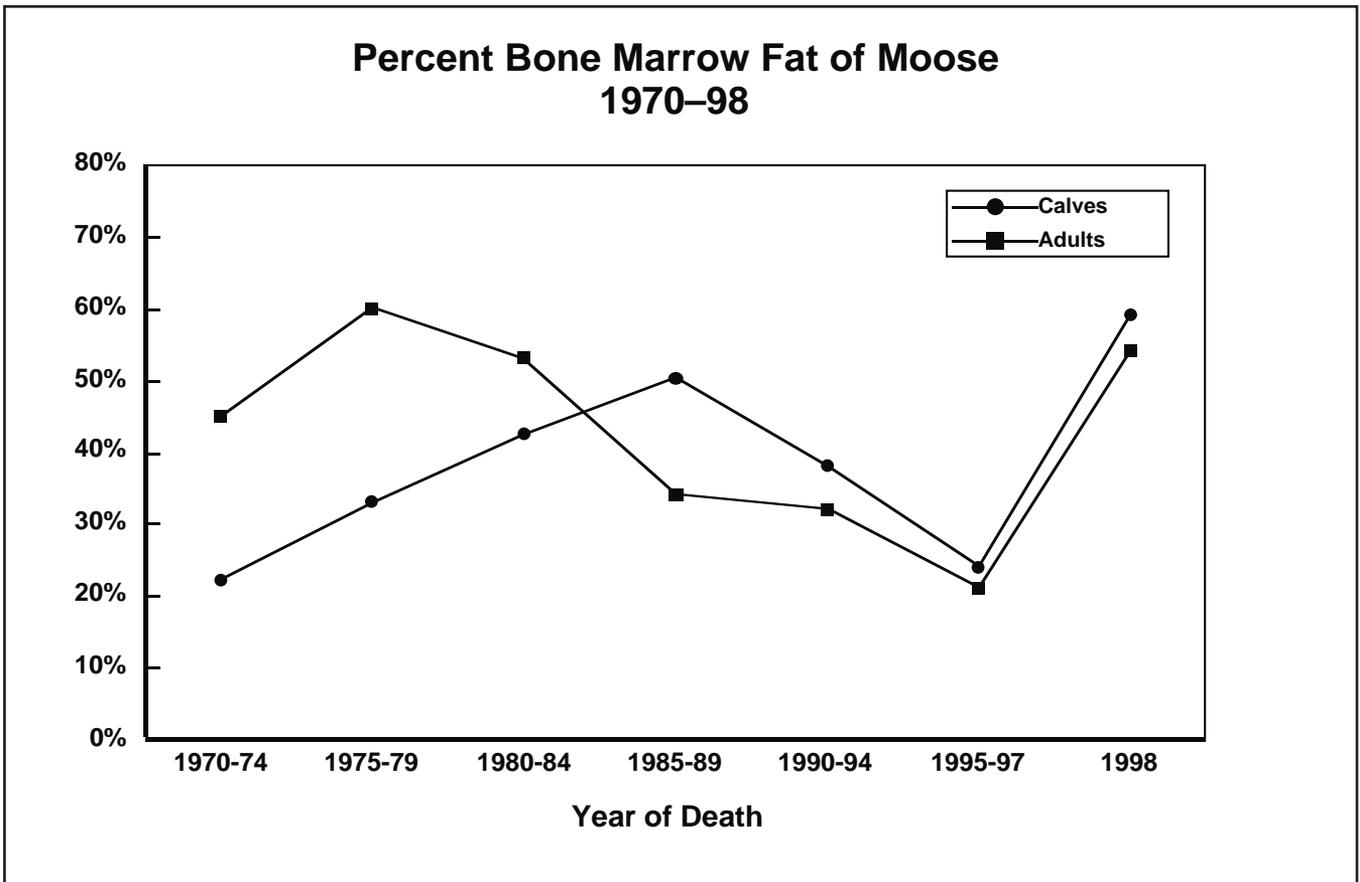


Figure 11. Long-term trends in moose bone marrow fat. Data for calves (which best reflect current conditions) represent mean levels, whereas data for adults is the proportion with >70% marrow fat.

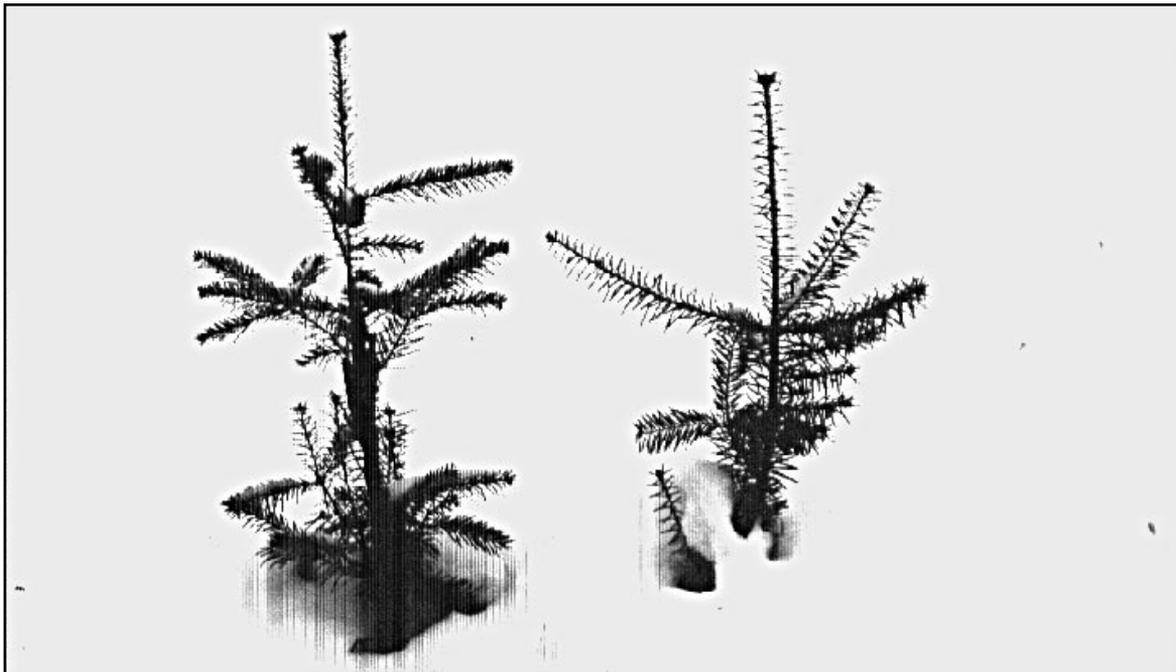


Figure 12. These balsam fir trees were formerly heavily browsed by moose in winter. But after the moose die-off, there have been two growing seasons of uninhibited growth.

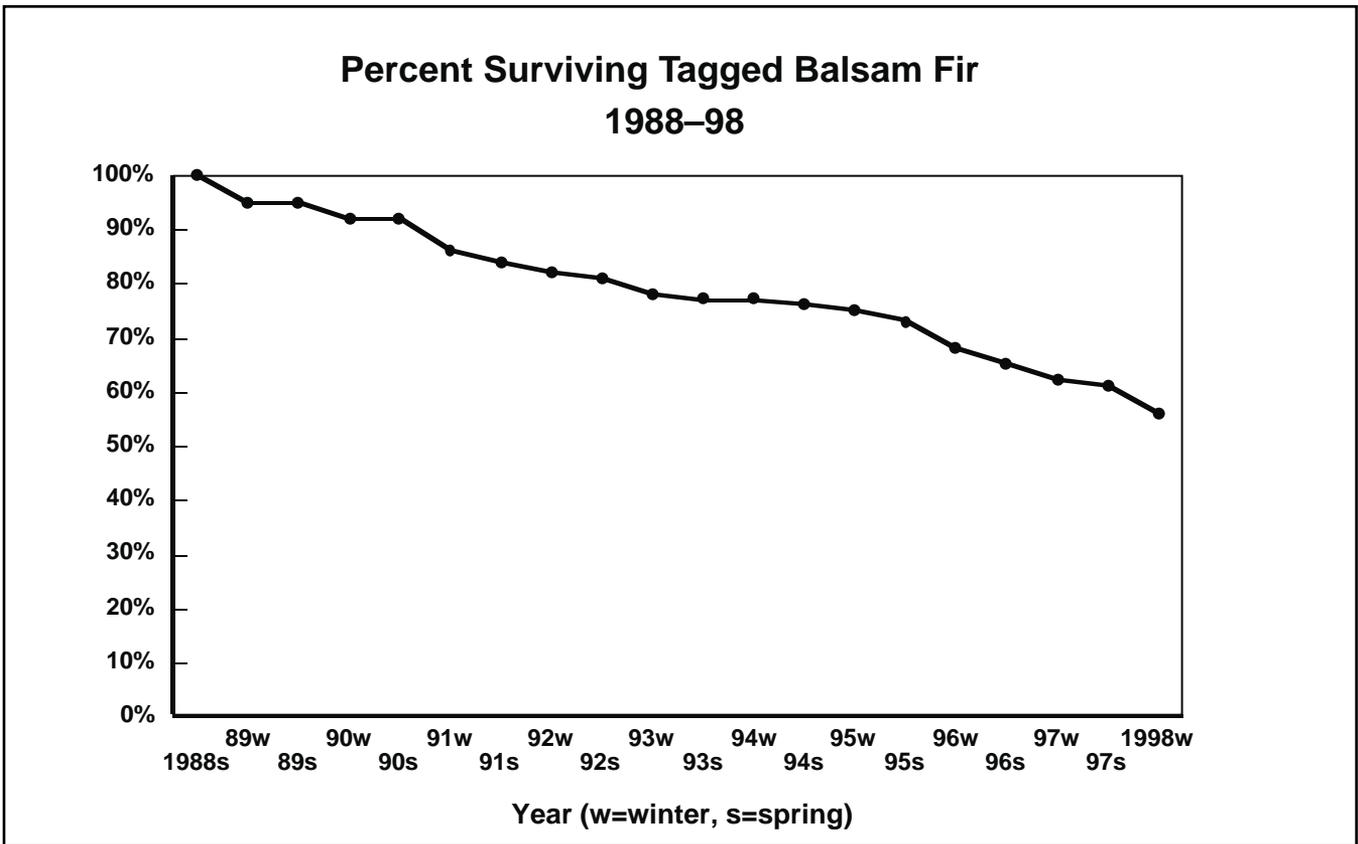


Figure 13. Survival of tagged, balsam fir trees in the canopy at the western end of the island, where there has been no successful recruitment of fir since the initial increase of moose around 1915. If the rate of mortality continues at the same rate as in the past decade, this tree species will virtually disappear from the forest canopy at the west end of Isle Royale by the year 2011.

the same as during the past decade, this important species will virtually disappear from the canopy in about 13 years. While the suppressed fir trees in the forest understorey usually survive well, they were browsed severely during the mid-1990s when moose density was high and about 15 percent of these stems died during 1992–98.

The striking differences in moose habitat between the east and west ends of Isle Royale have led to divergence in moose population status at the two ends of the island after the 1996 die-off. During that severe winter, moose at both ends of the island were restricted to shoreline areas where balsam fir provides much of the available forage. Because of higher stem density and unsuppressed growth form at the east end, available forage there was 16 times higher than at the west end. This forage difference, plus the greater mobility afforded moose at the east end with its convoluted shoreline, allowed a higher proportion of the moose on the east end to survive starvation in 1996.

These habitat differences for moose are now manifested in the status of wolves across the island, as all but two of the wolves were found on the east half of the island in 1998.

During field work in 1996 and 1997, carcasses or skeletal remains of 273 moose that died in 1996 were examined. Almost all of these moose starved to death in 1996. The age distribution of these moose when they died (figure 14) revealed that moose calves almost one year old were most susceptible to starvation mortality. A surprisingly high number of young adult moose (1–6 years old) also died; moose of this age usually show higher survival than older moose (age 7 years or more) that have begun to lose cutting edges on their teeth and exhibit other signs of senescence. Widespread deaths among young adults in 1996 illustrates the severity of nutritional stress resulting from an exceptionally long winter and a moose population at the absolute limits of winter forage.

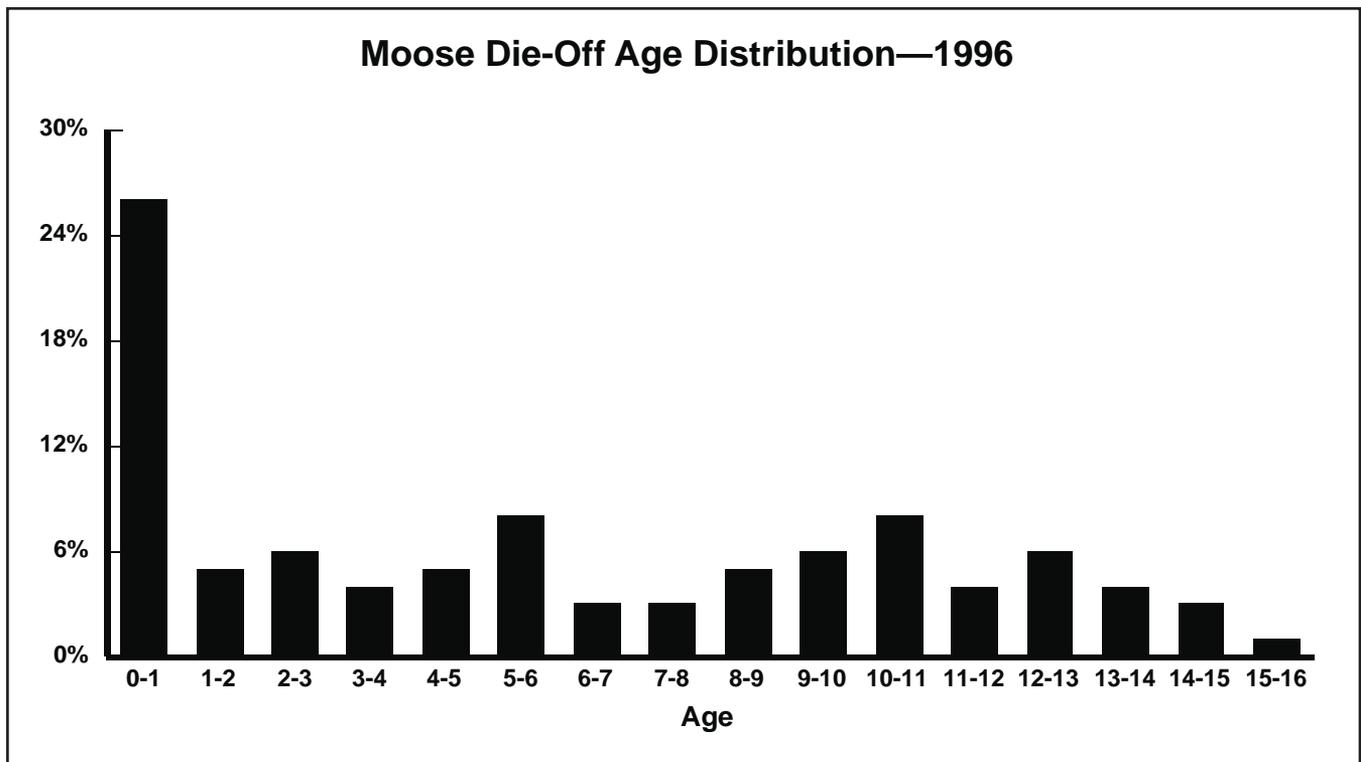


Figure 14. The age distribution of 273 moose that died in 1996 reveals that calves were particularly vulnerable, and a surprisingly large number of young adult moose also died.

Other Wildlife

Beginning in 1995, the deer mice of Isle Royale have been studied by PhD student Leah Vucetich in the field and in the lab as a model system to investigate the relationships between population size, genetic diversity, and fitness in a natural population. Of course, this is a matter of great interest for the wolves of Isle Royale, but it is more feasible to evaluate these relationships in other species. The deer mouse is the only small mammal on Isle Royale (figure 15). Its small size facilitates multiple captures and easy handling, while its short generation time increases the probability of observing demographic and genetic effects of small population size. The main island supports a large, contiguous population of deer mice, while the offshore islets support many small, isolated populations.

During 1995 we surveyed the Rock Harbor chain of islands for mouse populations. Deer mice were present on Cemetery, Rabbit, East and West Caribou, Mott, Davidson, and Inner and Outer Hill islands and were absent from Star, Shaw, Smithwick, Raspberry, Bat, Passage, and North and South Government islands. The presence or absence of deer mice on the Rock Harbor chain of islands seems to be related more to the degree



Figure 15. The woodland deer mouse, the only species of small rodent on Isle Royale, is now the subject of a study evaluating population viability and genetic variability.

of isolation from other islands than to island size (figure 16). In three years of observation, we have detected two population extinctions and one recolonization event. The Cemetery Island population went extinct in summer 1997. Star Island, which had mice in 1969 during a study by Wendell Johnson, had no mice in 1995–96; however, we captured one lone male in the fall of 1997. Once the presence of deer mice was established, several populations were chosen for closer study.

Live-trap grids for deer mice were established near Bangsund Cabin (summer headquarters near Daisy Farm Campground) on the main island and on Inner Hill island in 1995. Grids were added on Davidson Island in 1996, and Rabbit, Cemetery, and Outer Hill islands in 1997. We live-trapped and ear-tagged mice in the island populations. From these observations, we estimated population size, survival, and recruitment rates; all are critical components of population fitness. Genetic variability is assessed by taking a small tissue sample from each mouse, amplifying the DNA via polymerase chain reaction (PCR), and separating the PCR product by gel electrophoresis. As the study progresses, we will be analyzing patterns among population size, genetic diversity, survival, and recruitment.

The frequency of snowshoe hare observations during summer ground travel provides an index of snow-

shoe hare density on Isle Royale (figure 17). Data from 1997, together with long-term patterns of fluctuation, suggest that hares are currently in decline, for the fourth time since the mid-1970s. The irruption of hares in 1988 appears to be a unique event, perhaps resulting from the coincidence of mild winter weather and low fox density.

Red fox observations were relatively low in winter 1998, as they were less-frequent scavengers on moose carcasses, and there was no mountain ash fruit available along the shoreline, as in 1997 (figure 18).

Reproduction of bald eagles recovered in 1997 after 1996, a bad year due to the late winter. National Park Service surveys revealed 13 fledged eagles in nine nests in 1997, and at least five osprey nests with 9 fledglings. Both species are slowly increasing after reaching a very low level in the Lake Superior region in the 1960s and 1970s.

In winter 1998, tracks of marten were identified in several areas near Windigo at the island’s west end. Tracks of this mammalian predator, absent from the island for most of the 20th century, have been recorded sporadically during the 1990s. In 1998 Larry Kangas (NPS) also found marten tracks at Houghton point, some 15 kilometers distant, suggesting increased numbers and distribution for this new arrival.

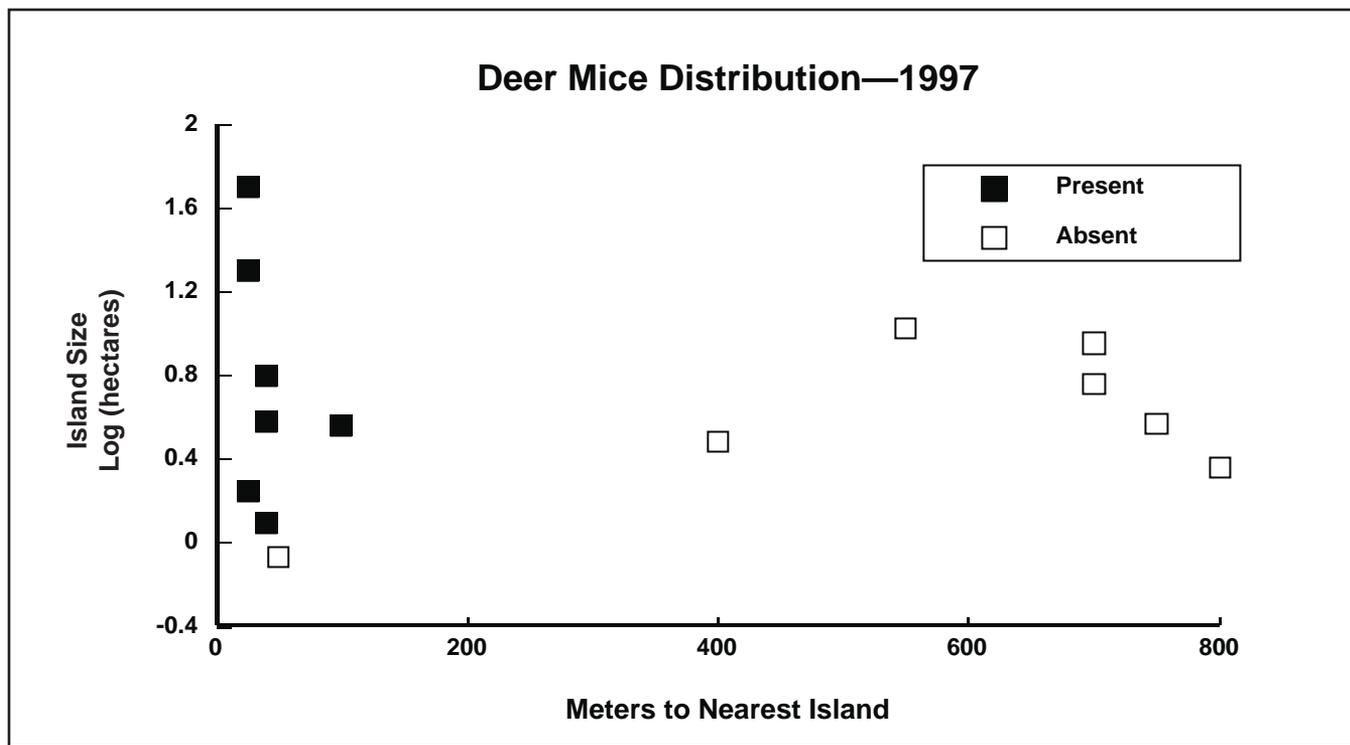


Figure 16. The occurrence of deer mice on small islets at Isle Royale seems to be explained more by distance to adjacent populations than the size of the islets.

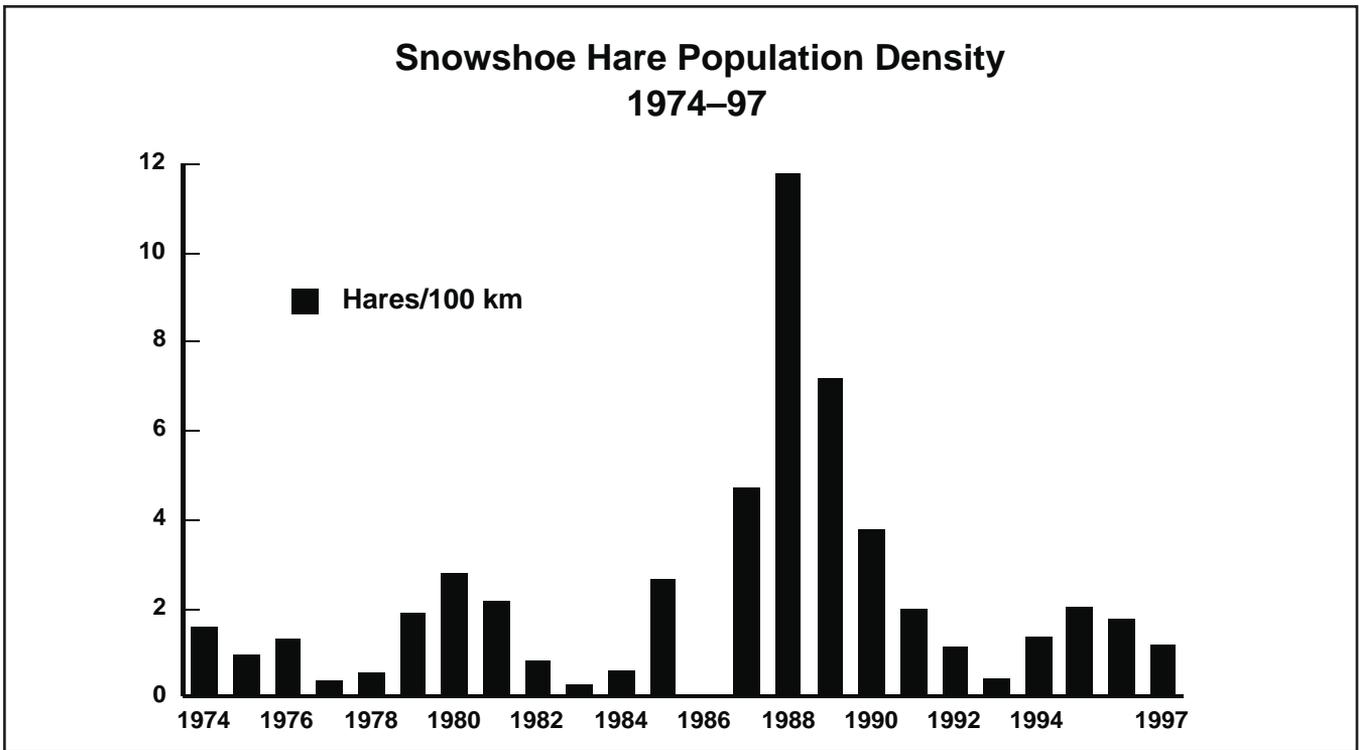


Figure 17. Snowshoe hares on Isle Royale seem to be in decline again, showing little indication of repeating the unusual population high observed in 1988. Index is the number seen per 100 kilometers hiked in summer.

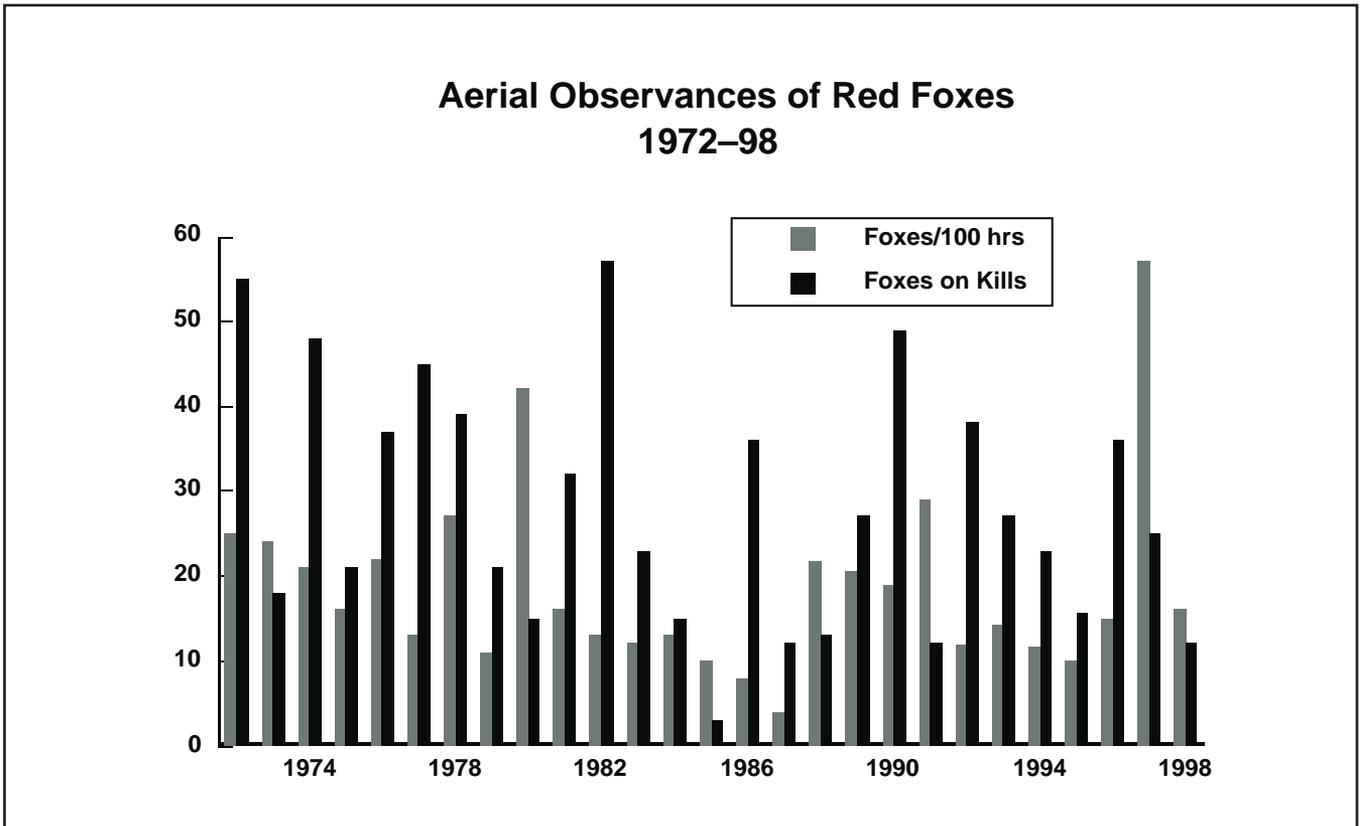


Figure 18. Relative abundance of red foxes from aircraft observations in winter 1972–98. Gray bar is the number of foxes seen away from moose carcasses/100 hours, while the black bar is the number of foxes seen on carcasses.

Weather, Snow, and Ice Conditions

Weather was most unusual at Isle Royale during winter 1998, as it was in much of North America. El Niño warming prevailed through the entire winter, and deteriorating ice conditions forced closure of the winter study 10 days early, the first early termination in 40 years (figure 19). Our landing field at Washington Harbor held for only about six weeks in midwinter, and there was very little shoreline ice (figure 20). At no time was there an ice bridge to the mainland during the winter of 1997–98 (figure 21). Temperatures during the winter study were warm, although not



Figure 19. U.S. Forest Service pilot Wayne Erickson (left) conferred with research pilot Don Glaser (right) while a fox inspected the plane that evacuated research personnel after a February thaw threatened the ice landing field.

unprecedented (figure 22), but what was most unusual was the total lack of any cold weather in early winter, prior to the winter study.

Snow depth was only 20 centimeters until shortly before the 1998 winter study began in January (figure 23). Maximum snow depth of 60 centimeters was attained only briefly in mid-January before snow depths steadily declined through the winter. For moose, the winter of 1997–98 will rank as probably the least severe of the past four decades, only two years after the worst winter of the century.



Figure 20. When the 1998 winter study was terminated by receding ice, the only suitable landing field was at the head of Washington Harbor at the island's west end.



Figure 21. The south shore of the island near Hay Point revealed the almost total lack of shoreline ice that was typical in 1998.

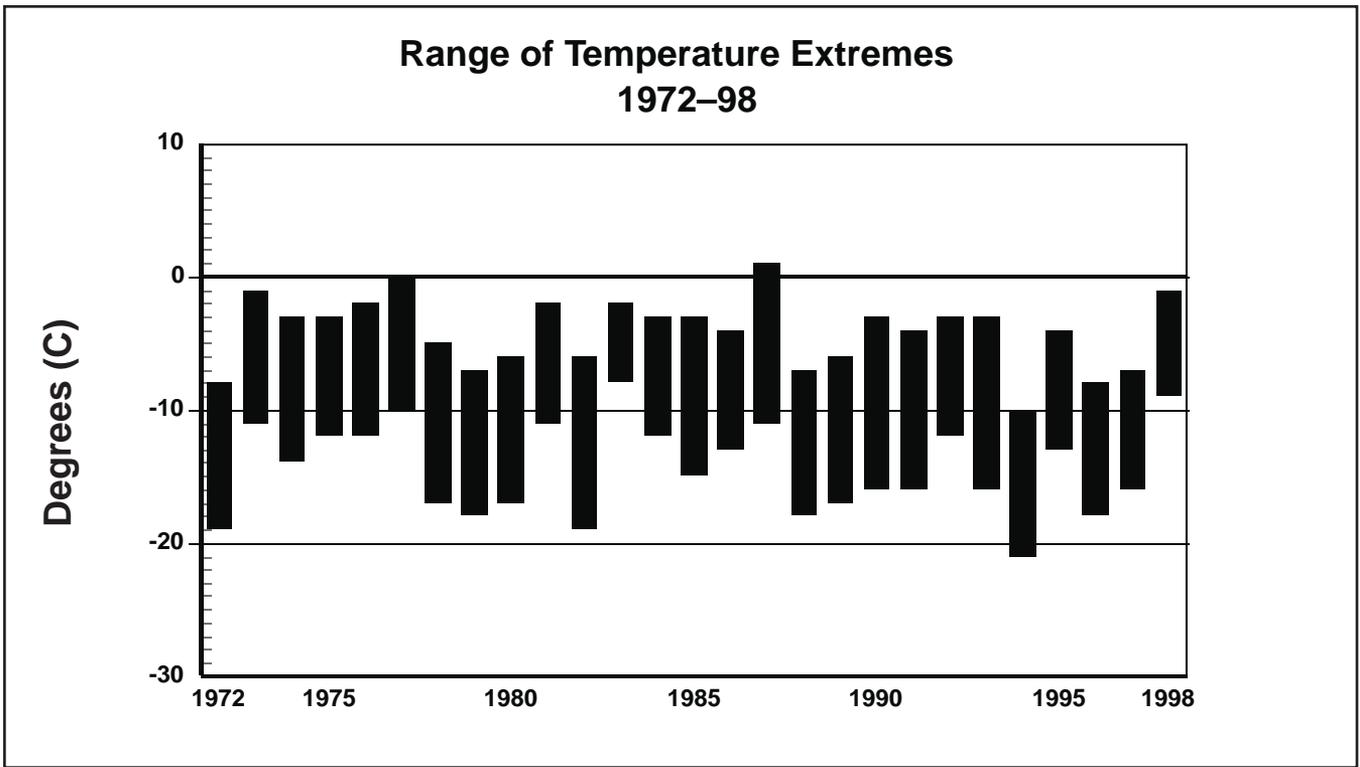


Figure 22. Range of average daily maximum and minimum temperatures during annual winter studies at Isle Royale, 1972-98. Unusually warm temperatures prior to the 1998 winter study contributed to unprecedented lack of snow and ice.

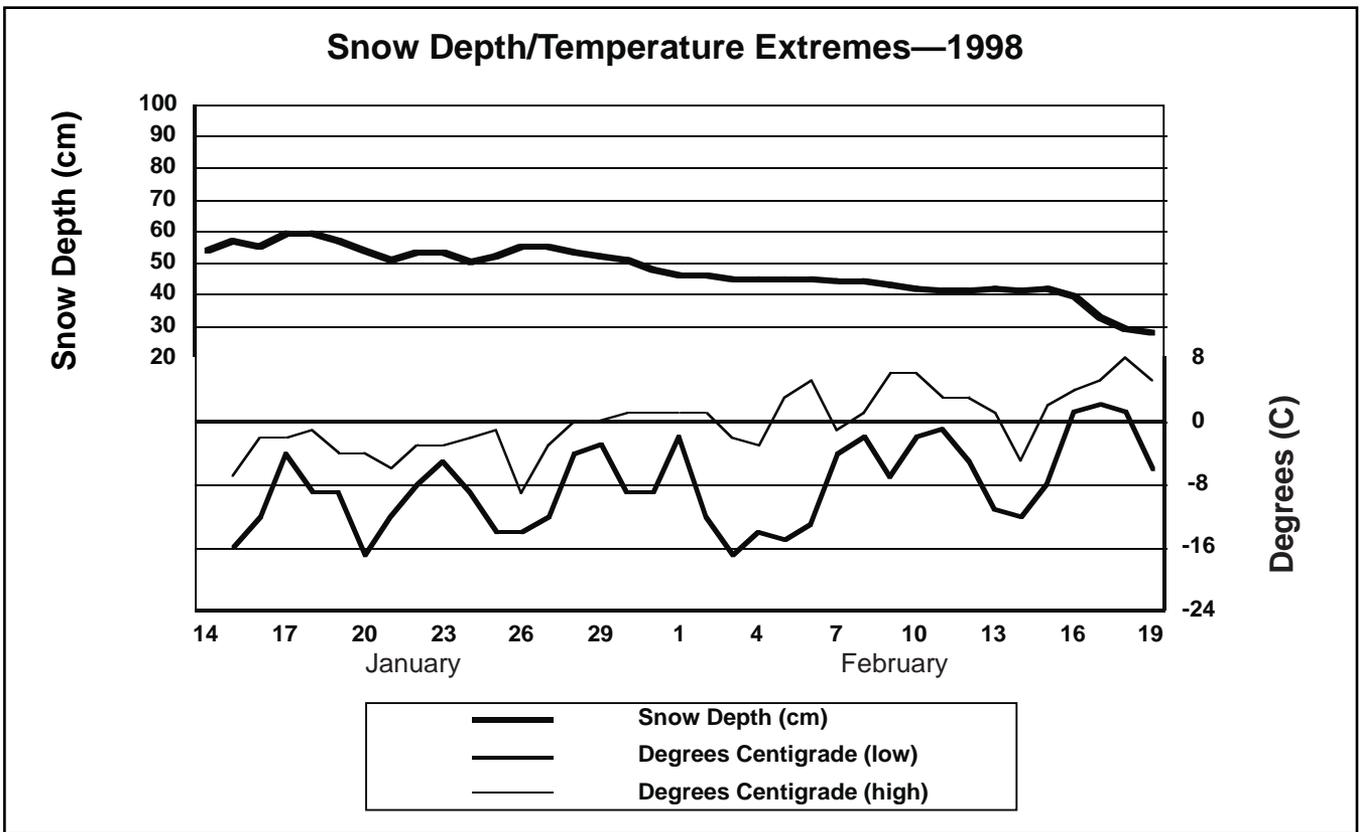


Figure 23. Snow depth (top) and temperature extremes (bottom) during the 1998 winter study on Isle Royale.





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THANK YOU to all who help!