

Ecological Studies of

Wolves

on

Isle Royale



2000–2001



**"Ethics are
nothing else
than reverence
for life."**

Albert Schweitzer, 1936

Ecological Studies of Wolves on Isle Royale

Annual Report 2000–2001*

by

Rolf O. Peterson

and

John A. Vucetich

School of Forestry and Wood Products

Michigan Technological University

Houghton, Michigan USA 49931-1295

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Results reported here are preliminary and, in some cases, represent findings of collaborators; please do not cite without consulting the authors.

Cover photo: Middle Pack breeding female is watched by pup, while breeding male walks behind the pup, in February 1999.

Opposite photos: Top, cow moose and growth-retarded yearling in July 1995; center, two young foxes in a ritualized autumn spat; bottom, Middle Pack coursing the Isle Royale shoreline in 1999.

Inside back cover photos: Clockwise, from top left, three wolves in unsuccessful chase of cow-calf pair, Carolyn and Trevor Peterson negotiate a beaver dam crossing, hiker in hawkweed, swallow-tail butterflies at a sodium lick, and cow moose in spring.

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Ecological Studies of Wolves on Isle Royale



“... while (moose and wolves) are considered by some to be in a state of imbalance, such situations have a habit of balancing themselves as time goes on—such is the phenomenon of dynamic equilibrium.”

—Robert M. Linn, Naturalist, Isle Royale National Park
(July 1956 memo to the superintendent of the park, in response to public concern about the future of moose on Isle Royale)

Personnel and Logistics

In summer 2000, Rolf Peterson directed ground-based fieldwork, aided by Greg Burkhart, Cynthia D. Carter, Philip DeWitt, Justin Gude, Patty Hernandez, Carolyn Peterson, Jeremy Peterson, and Greg Wright. Fieldwork continued from May 12 through the end of August. In 2001 the annual winter study extended from January 16 to February 27. Peterson and pilot Don E. Glaser

participated in the entire study, assisted in the field by volunteers Cynthia D. Carter, Anne M. Chouinard, Jennifer Fox, and Greg Wright, and the following personnel from Isle Royale National Park: Alex Egan, Bill Munsey, Larry A. Kangas, Jack G. Oelfke, Mark C. Romanski.

Summary

After many years of slow recovery, the wolf population in 2000–01 abruptly dropped by a third, from 29 to 19 animals (fig. 1). Although five pups were raised in 2000–01 in three packs, mortality during the past year (15 died from the 29 present in 2000) was unusually high. Last year's mild winter coupled with a simultaneous scarcity of moose calves may explain the high mortality. Exposure to diseases will be determined when wolf live-capture efforts are resumed in spring 2001.

Reorganization of wolf pack territorial boundaries continued during the past year. In 2001 the Middle Pack with six wolves controlled about three-quarters of the island, while the East Pack (also six) and a new territorial Trio divided the remaining quarter. Wolf density on the east quarter of Isle Royale was over four times higher than in the western three-quarters, explained by a three-fold difference in moose density.

The moose population changed little in size from 2000 to 2001. Recruitment of calves from the 1999 cohort was low, but adult survival in the past year was relatively high. Calf abundance in winter 2001 (14 percent) approximated the long-term average, and the

population was estimated at 900 moose (1.7 moose/km²). The winter of 2000–01 brought above-average snow depths, leading to above-average kill rate for wolves. Calf moose were particularly vulnerable, constituting two-thirds of the wolf-kills that were ground-checked. Assuming there are no new diseases, we expect wolf numbers to recover, based on abundant food (winter-weakened moose plus an ample cohort of calves born in 2000). The moose population should continue to slowly climb for many years. On the island's western half, a general decline continued for balsam fir, an important winter forage for moose. Besides fir, arboreal lichens and cedar seemed to provide most of the food for moose in winter 2001.

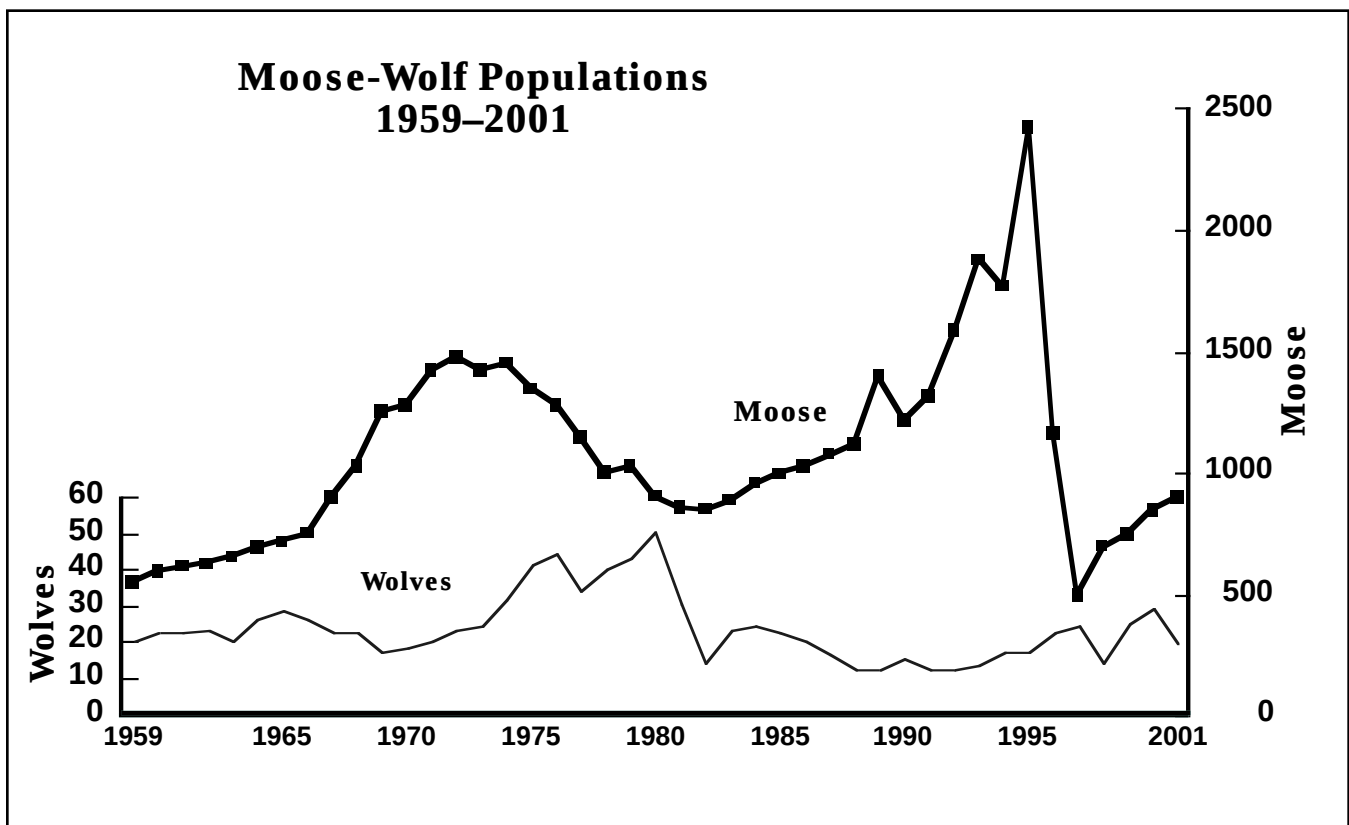


Figure 1. Wolf and moose fluctuations, Isle Royale National Park, 1959–2001. Moose population estimates during 1959–88 were based on population reconstruction from recoveries of dead moose, whereas estimates from 1989–2001 were based on aerial surveys.

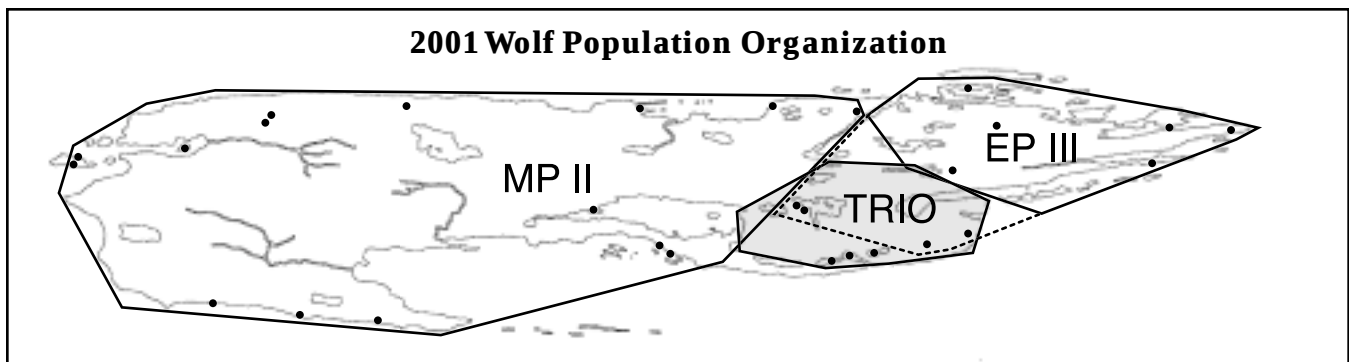


Figure 2. Wolf pack territories and moose carcasses (wolf kills and otherwise) during the winter study in 2001. Scent-marking was observed by all three of the packs. The dotted line indicates occasional movements by EP 111.

The Wolf Population

In 2001 we were surprised to find that the wolf population had declined substantially from the previous year. Wolf numbers climbed from 25 in 1999 to 29 in 2000. But in 2001, only 19 wolves were present (fig. 2):

East Pack III.....	6
Middle Pack II.....	6
Trio, east end	3
Duos.....	2
Singles	2
Total 2001	19

The wolf decline was attributed to high mortality, which claimed 15 of the 29 wolves (51 percent) present in 2000 (fig. 3). Offsetting the mortality was modest reproduction—in winter 2001 East and Middle packs each had two pups and a single pup survived in the newly formed Trio (fig. 4). Although we did not locate summer dens or homesites for the Middle Pack or Trio, we know there were just two pups in the East Pack in June 2000.

The only wolf still wearing a radio collar in the past year was female 1072, the breeding female in the East Pack, collared in May 1997. She died last autumn or early winter, but we recovered only her radio collar and a lower jaw from under the snow in January. Her teeth showed signs of heavy wear (fig. 5).

Both East and Middle packs declined, yet a new territorial group became established in the moose-rich east end of the island. The new group, a breeding pair and one pup born in 2000, was probably spawned by one of the wolf pairs identified during the previous winter. Usually such groups do not successfully reproduce, but the east-end Trio in 2001 actively scent-marked an area that was avoided by both East and Middle packs. Early in the 2001 winter study, the East Pack overlapped movements with the Trio, but in February the East Pack avoided the small area claimed by the Trio. Both the larger packs were observed

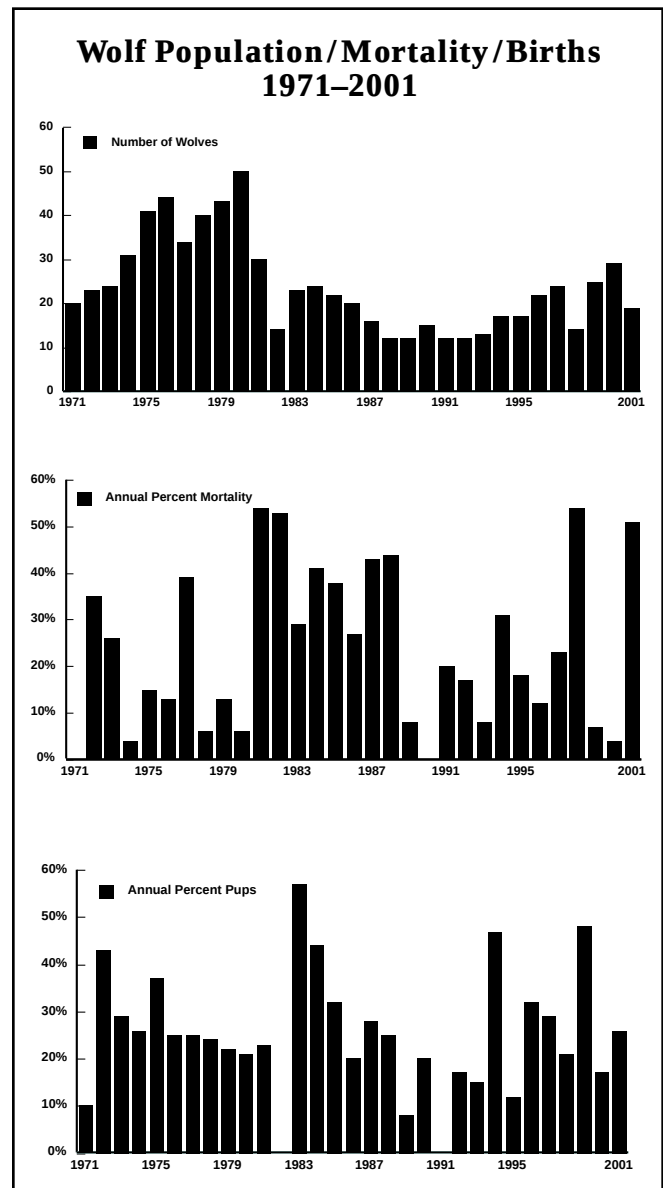


Figure 3. Wolf population size (top) is explained by patterns of mortality (middle) and reproduction (bottom). The decline in 2001 can be attributed primarily to high mortality in the previous year.



Figure 4. All three territorial packs on Isle Royale contained one or two pups in winter 2001.

changing their direction of travel after encountering scent-marks from the Trio. After two previous winters of territory expansion, the takeover by the Middle Pack of the entire western three-quarters of the island was completed (fig. 6). Only occasional movements of lone wolves occurred through Middle Pack territory.

We did not anticipate the major wolf decline in 2001, but it is likely that a combination of factors lined up against the wolves. For example, the winter of 1999–2000 was quite mild, and most of the snow melted before the end of February, providing great mobility for moose and difficult hunting for wolves. Also in the winter of 2000, moose calves (primary wolf prey) were exceptionally scarce, probably a result of the drought and hot summer of 1998, which produced low fertility in cow moose in 1999 and a failed cohort of calves. Exposure to new disease has not yet been explored, but efforts to live-capture wolves will resume in spring 2001 and may give us the opportunity to screen for new pathogens.

The winter of 2000–01 brought a season of plenty for those wolves still alive on Isle Royale. Calves were abundant and highly vulnerable to wolves because of deep snow (fig. 7). Calves made up two-thirds of the kills we examined on the ground during the 2001 winter study, and wolves appeared to have little difficulty

locating suitable prey (fig. 8). We confirmed wolf-kills involving a cow-calf pair in two cases and suspected a double-kill in a third case (fig. 9). If the decline in wolves in the past year was food-caused, then we predict a quick



Figure 5. Only a lower jaw (and radio-collar) was collected from female wolf 1072, breeding female from the East Pack since the mid-1990s. At least eight years old, she died late in 2000.



Figure 6. The Middle Pack, though cut in half in the past year from 12 to 6 wolves, continued to claim the western three-quarters of Isle Royale.

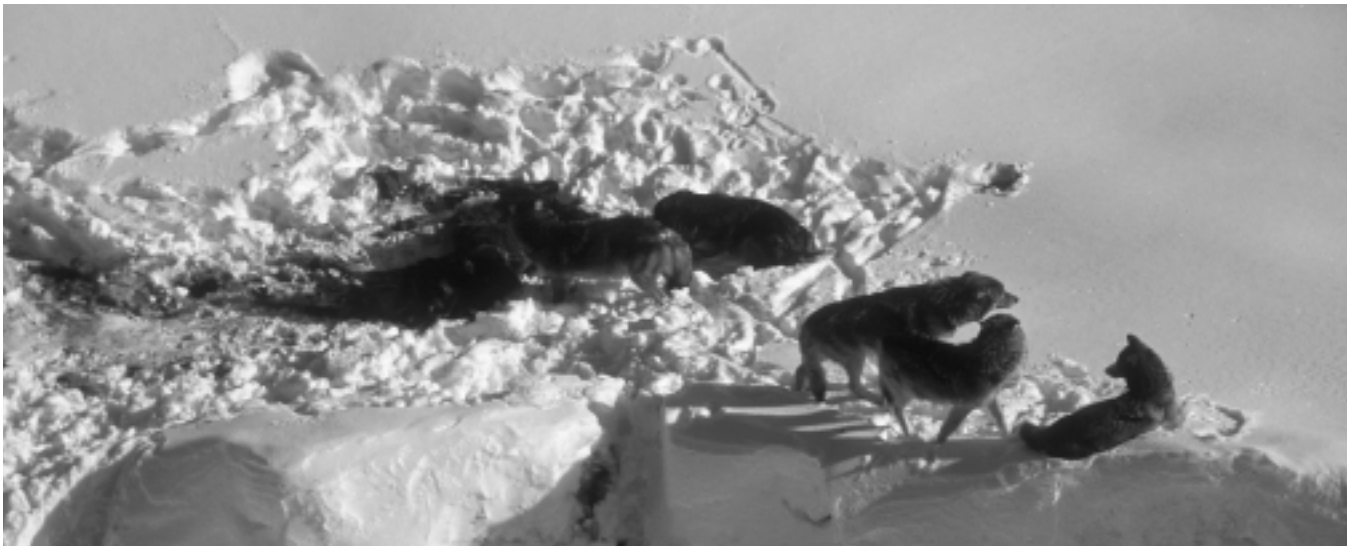


Figure 7. With deep snow in the interior, the shorelines of Isle Royale were primary travel routes and kill sites for wolves in winter 2001.

resurgence in wolf numbers in 2001–02 (fig. 10). It will be particularly interesting to see if the East Pack allows the newly established Trio to remain in territory that has traditionally belonged to the East Pack. Probably one of the breeding wolves in the Trio originated in the East Pack, but tolerance is not guaranteed if food becomes scarce and the parent pack expands its territory.

Wolf density in winter 2001 was about four times higher on the island's east end (about 170 wolves/1,000 km²) than on the area occupied by the Middle Pack (about 40 wolves/1,000 km²). This is attributed to the stark differences in moose density that emerged after the moose die-off of 1996, which was more severe at the west and middle parts of the island than at the east end.

In 2000 parasitologist Philip S. Craig from the



Figure 8. Among the few adult moose killed by wolves in winter 2001 was this aged bull with broken and partially healed femur (above) and severe arthritis in both hip joints.

Another Day, Another Struggle

The physical struggles between wolves and moose carry potential for great danger for both sides. The hunting strategy of wolves must emphasize self-preservation, and they often wait patiently for a moose already in trouble to make a move that further imperils it. For scientists at Isle Royale, years may pass between opportunities to observe wolves actually killing a moose, but for most wolves on the island these are weekly events through the winter.

A nonterritorial pair of wolves often traveled the central south shore of Isle Royale during the 2001 study, and, at about noon on February 2, we found them curled up just inside the trees along the shore of Malone Bay. We saw a maze of tracks and suspected the wolves had killed a moose in the thick spruce cover, yet we could not see a moose anywhere, dead or alive. When we checked again, just before sunset, there was indeed a moose present, a live cow moose standing three meters out in Lake Superior, up to its knees in ice water. The two wolves remained curled up in the trees, 20 meters from the moose. Two weeks earlier, a calf moose had been killed only a kilometer down the shore, and we wondered if this was the mother, perhaps wounded in an earlier confrontation.

By the next morning, the moose was standing on the snow-covered shoreline, unable to move, its head hung low. Its watery refuge had filled with floating ice chunks brought in by the wind. It was simply a matter of time before the waiting wolves would feed.

At 4:00 PM that afternoon, almost 29 hours after we were first on the scene, we returned to find the matter quickly draw to a close. The moose still had no visible

wounds and there was no blood on the snow, but one wolf stood 10 meters away, facing the moose, and the moose simply stood and returned the stare. Then the moose abruptly folded its front legs and lowered its forequarters to the ground, as if it was bedding normally. Both wolves leaped on the moose and it collapsed on its side, holding its head up and kicking weakly with its hind legs.

One wolf immediately began to work at the rear end of the moose while the other tugged and shook the back of the moose's neck. This wolf periodically grabbed an ear and pulled hard, without any obvious useful result, but it concentrated its biting maneuvers on the side of the neck and throat area. When the wolf had a firm grip and pulled hard, the entire head and neck of the moose jerked back, and the wolf periodically spat out a mouthful of hair.

An adult moose is some 10 times larger than a wolf, with extremely thick hide. It is difficult for a wolf to inflict a fatal wound on such prey. Fully 12 minutes of constant wolf attack passed before spots of blood began to appear in the snow at the rear of the moose. As one wolf continued to bite in the throat area, the moose's head slowly sank lower. With an air of finality and a firm grip on the moose's neck, the anterior wolf jumped sideways across the moose's chest, pulling the moose's head straight up and then suddenly forcing it down to the snow surface (see fig. 9). After this maneuver the moose never moved, and the contest was over. Only then, after 15 minutes of furious activity, did the wolves stop to rest for a few seconds.



Figure 9. This cow moose was finally killed by two wolves after spending a night standing in Lake Superior. Two weeks previously, a calf was killed nearby, and it is possible this cow had been wounded at that time.

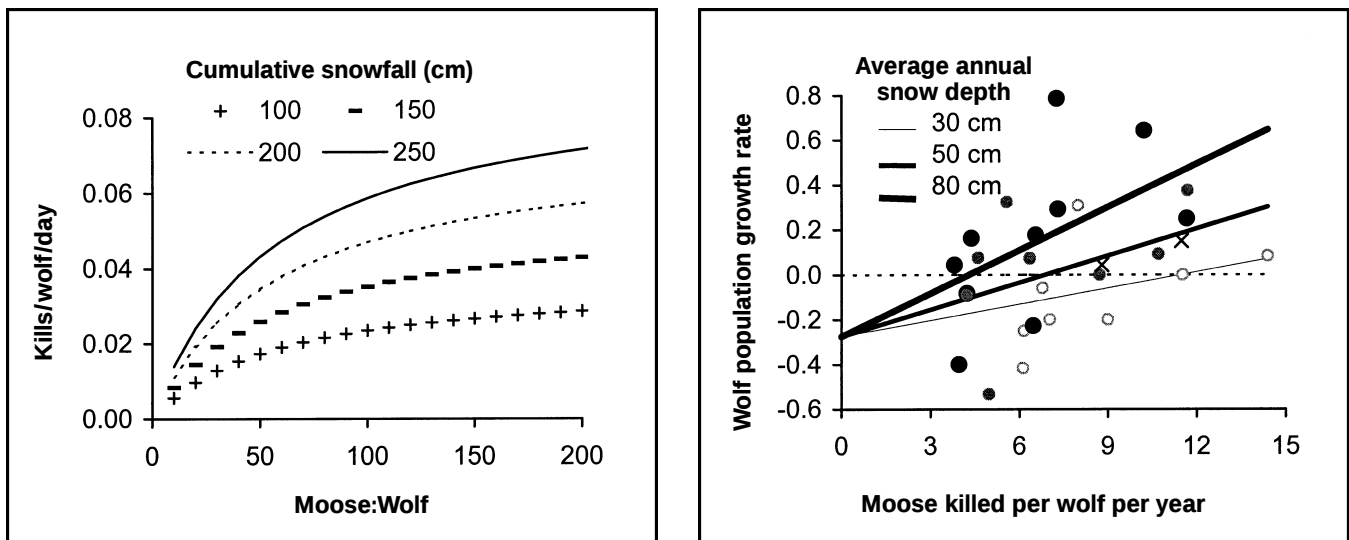


Figure 10. (Left) Wolves kill more moose (y-axis) during years when there are more moose per wolf (x-axis). These relationships, called functional response and numerical response, together determine the nature of predator-prey dynamics. Winter climate has an important impact on both relationships. In years with more snow, wolves not only kill more moose (left), they are also more efficient at converting moose killed into wolf population growth (right), possibly because moose are less fit.

University of Salford in the UK tested wolf scats from Isle Royale for antibodies to *Echinococcus granulosus*, the hydatid tapeworm. This tapeworm requires both wolves and an ungulate species to complete its life cycle, and we have often found the diminutive tapeworms in dead wolves recovered at Isle Royale. Prevalence of cysts is

high in moose, the alternate host, and all moose examined from Isle Royale that are at least three years old harbor hydatid cysts in their lungs. Craig found antibodies for *Echinococcus* in all but three of the 88 scats collected from Isle Royale wolves in winter 2000.

The Moose Population

During February 2001, the moose population was estimated at 900 animals (+/- 95 percent confidence interval of 193) or 1.7 moose/km². This compares to an estimated 850 moose in 2000 and 750 in 1999. Calves constituted 14 percent of the 191 moose counted on census plots, almost the same as the long-term average of 13 percent for Isle Royale moose (fig. 11). Five sets of twin calves were observed during winter 2001, a high number consistent with the high overall calf numbers from the cohort of 2000 (fig. 12). Low (< 10 percent) calf abundance in three of the last six years was attributed to poor nutritional condition caused by high moose density (cohorts from 1995 and 1996) or summer heat (1999 cohort).

In the warm spring of 2000, conditions were favorable for winter tick development, and in winter 2001 it was not uncommon to observe moose with hair loss from ticks. Most of the major hair loss for moose occurs in March after the annual winter study ends.

With average to above-average snow during winter 2001, moose were found primarily in shoreline coniferous forests that afford maximum cover (fig. 13). This confinement concentrated moose in closer proximity to wolf packs, leading to above-average

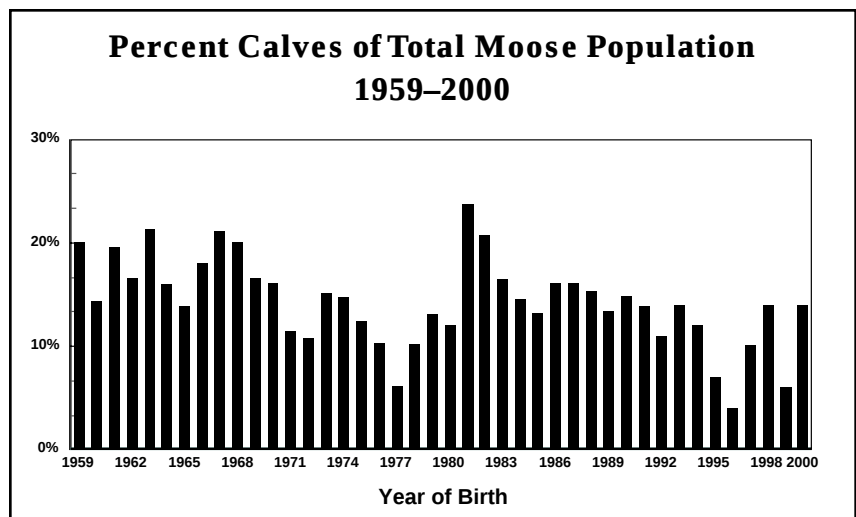


Figure 11. Moose calf abundance (at approximately six months of age) on Isle Royale, as a proportion of the total population. These are best estimates, a weighted mean of aerial counts in fall and/or winter.



Figure 12. This cow moose and her twins were found on Washington Island in January, before the Middle Pack made its initial visit and killed a cow and calf. After that kill, this moose trio disappeared, so perhaps they abandoned their small island refuge.



Figure 13. Rolf Peterson examining remains of cow moose several days after it was killed by two wolves (same kill shown in fig. 9).

mortality in winter (fig. 14). About half the island, primarily the middle and western interior areas, had very few moose (fig. 15). In this area, moose were often seen feeding on arboreal lichens from tree trunks or fallen trees, as traditional winter forage for moose from buds and twigs was very sparse (fig. 16).

In spite of a chronic shortage of winter forage, moose were in relatively good condition during winter 2001, based on bone marrow fat levels in dead animals. Mean marrow fat in calves was as high in 2000 and 2001 as at any time in the past 30 years (fig. 17).

The extent of moose nutritional stress in midwinter has been monitored at Isle Royale since 1988, through chemical analysis of snow-urine, in collaboration with Dr. Glenn DelGiudice of the Minnesota Department of Natural Resources. In recent years, this index has indicated relatively favorable forage intake patterns

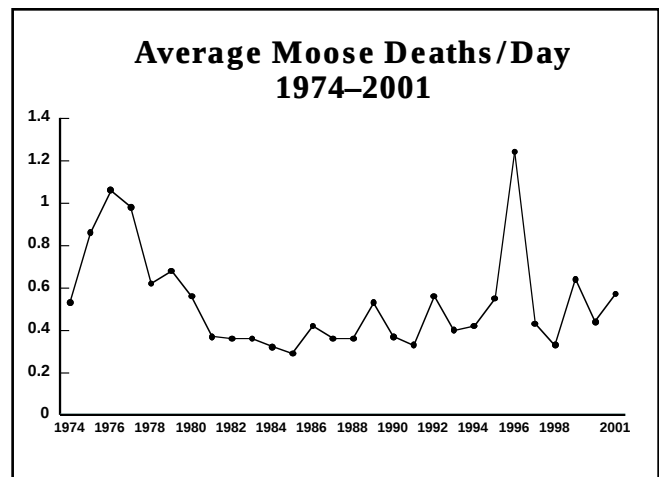


Figure 14. Moose mortality rate in midwinter was above average in 2001, probably because deep snow favored hunting wolves and hampered moose calves.

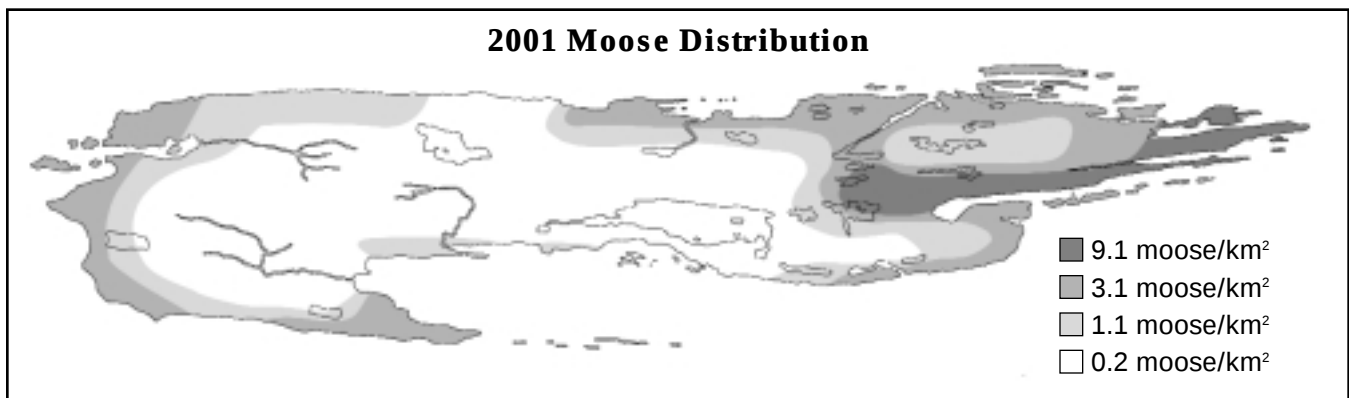
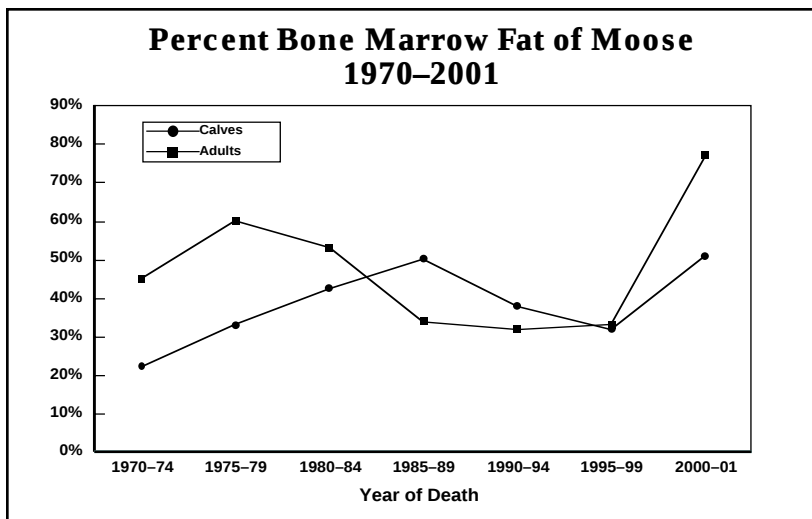


Figure 15. Moose distribution on Isle Royale during the aerial census in February 2001.



Figure 16. This cow moose and her calf spent a couple of days in the vicinity of a fallen spruce tree, gleaning arboreal lichens from the trunk and upper branches.



◀ **Figure 17.** 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 greater than 70 percent marrow fat.

Figure 18. Mean levels of urea:creatinine (U:C) ratio for snow-urine samples from Isle Royale moose (for individual moose, a U:C ratio > 4.0 indicates severe nutritional restriction, according to studies by G. DelGiudice). The consistent differences between the east end (abundant balsam fir) and the west end (little fir) are not fully understood, but may reflect differences in forage species. ▼

(fig. 18), especially after the moose die-off in 1996.

We have now collected bones from 366 moose that died in 1996, when we estimated that as many as 1,500 moose may have starved. About half of these skeletons were discovered by Earthwatch volunteers in spring and summer expeditions. In summer 2000, depending on site conditions, we still found maggot casings present among the bones after five years of weathering. Of those moose for whom we could determine sex (N=336), 58 percent were male and 42 percent were female, underscoring the greater vulnerability of males to winter malnutrition.

In a recent paper in *Science*, Joel Berger and other authors highlighted the loss of calf protective behavior in cow moose in areas where large carnivores have been eliminated. Conceivably, this could lead to ungulate populations that would be unusually vulnerable to predation should large carnivores recover or be restored. Berger et al found that within a generation after large carnivores became reestablished, cow moose changed their behavior to provide better protection for offspring by being more alert and more aggressive. Moose behavior on Isle Royale has been shaped by wolf predation for 50 years, and cow moose with calves are very alert to potential dangers. This is shown by the close proximity of cows and calves in winter (fig. 19); in about half of the cases, we estimated that calves were no more than one body length away from their mothers.

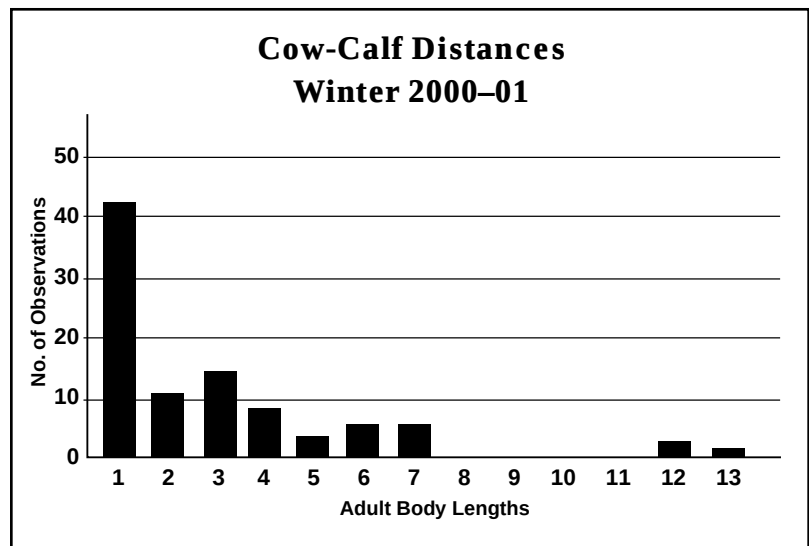
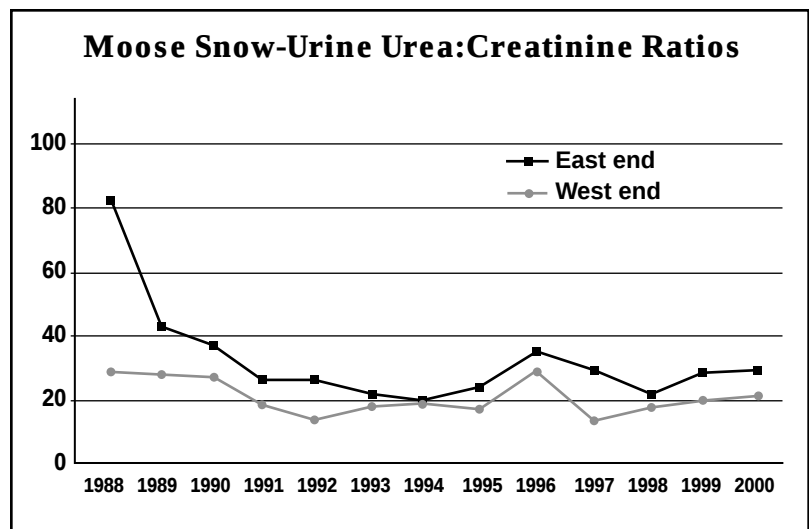


Figure 19. Distances observed between cow moose and their calves in winter at Isle Royale. Selection pressure from wolf predation has led to this very prominent cow-calf bond, the only long-term association that exists between individual moose.



Figure 20. At the island's west end, it can be clearly seen that moose browsing leads to differences in growth rates of white spruce (not eaten, tree at left) and balsam fir (heavily eaten in winter, stems on right and in background).

Forest Vegetation

The simple food chain at Isle Royale—wolves, moose, and vegetation—has long provided a valuable real-world test for theories about trophic relationships in a three-link system. Because of the variety of plant species used by moose and the complications introduced by variable plant chemistry and large ruminant physiology, understanding moose-vegetation interaction is a difficult scientific task. Through the 1990s, we concentrated on understanding the influence of moose herbivory on balsam fir growth and survival (fig. 20). This single species appears to be the most important component of winter browse for moose. We could almost say, “as fir goes, so goes the moose population” (fig. 21).

In 2001, in cooperation with the National Park Service and and USDA Forest Service, we began to establish permanent vegetation plots throughout Isle Royale, a process that will take many years. Spatial arrangement of plots and most measurements will follow the protocols of the Forest Service's nationwide Forest Inventory and Analysis program. We are also collaborating with Ron Moen, of the University of Minnesota's Natural Resources Research Institute, who is modeling future forest-fire potential and subsequent forest change relative to intensive moose herbivory.

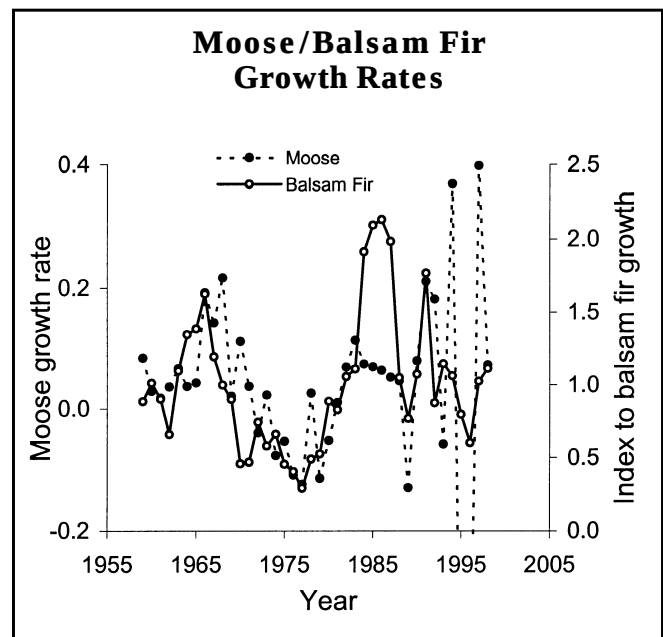


Figure 21. Annual growth in the moose population appears to be linked to tree-ring growth in balsam fir (shown here are island-wide averages, which obscures some important differences between east and west ends).

Genetic Studies

Increased interest in the plight of Isle Royale wolves in the late 1980s coincided with rapid development of new tools for molecular biologists interested in studying the genetics of individuals and populations. Wolves and other species inhabiting Isle Royale provide interesting case histories of genetic change through time on this island, influenced by the characteristics of the founding population, population size, breeding behavior, and natural selection pressures.

DNA can be isolated and amplified from animal droppings, and we have begun work (in collaboration with Robert Wayne at UCLA) on the feasibility of long-term tracking of genetic change in Isle Royale wolves using fecal DNA. Work on this study should begin in earnest in 2001.

Paul Wilson at Trent University (Ontario) has studied genetic variation in moose from Isle Royale and other locations in North America. For several moose populations extending from Manitoba to Newfoundland, including Isle Royale, genetic variation was estimated using neutral DNA markers, assessed by multi-locus DNA fingerprinting and five microsatellite loci, and a specific portion of the *DRB* gene in the Major Histocompatibility Complex (*Mhc*). Genes in the *Mhc* locus have major influence on the immune system. Surprisingly, the degree of genetic variation differed markedly between the neutral markers and the *Mhc DRB* gene. Isle Royale moose showed the lowest genetic variability in neutral markers, consistent with the notion that there was a single founding event, but they also had relatively high variability at the *Mhc* gene. Ontario moose showed the opposite pattern—high genetic variation at the neutral loci and low variability at the *Mhc* gene. Wilson and his colleagues believe that selection pressures such as sport hunting and the deer brainworm (*Paraelaphostrongylus tenuis*) may lead to selection for specific *Mhc* alleles, a hypothesis that can be tested with additional DNA profiling. Without

exposure to hunting or to deer and their host of parasites, Isle Royale moose may have different selection pressures, reflected in genetic diversity at the *Mhc* site.

Using randomly amplified polymorphic (RAPD)

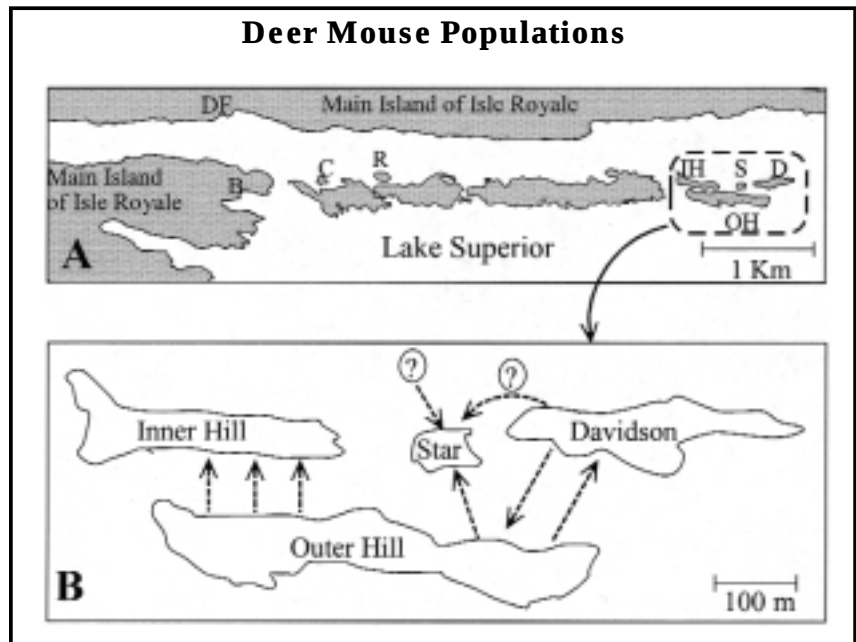


Figure 22. Small islands at the east end of Isle Royale provided sites for field studies of deer mouse genetics and demography, 1995–2000. The islets in panel A are located on the south shore of the northeast end of Isle Royale. Demographic and genetic data were collected from labeled islets (C = Cemetery, R = Rabbit, IH = Inner Hill, D = Davidson, OH = Outer Hill, S = Star) and main island sites (B = Bangsund, DF = Daisy Farm). The arrows in panel B illustrate documented movements of individual mice among islets, which occurred primarily in summer (based on fish stomach contents, lake trout predation is one of the challenges that swimming mice face).

**Minimum Genetic Distances
Between Deer Mouse Populations**

	B	DF	OH	D	IH	C
DF	0.04					
OH	0.11*	0.06*				
D	0.06*	0.03*	0.02			
IH	0.12*	0.06*	0.00	0.02*		
C	0.04	0.04	0.10*	0.07*	0.11*	
R	0.02	0.02	0.07*	0.04*	0.08*	0.01

* $P < 0.03$, Monte Carlo approximation of Fisher's exact test for population differentiation

Table 1. Genetic similarity as defined by Nei, M., 1972, *American Naturalist* 106: 283–92, between populations of deer mouse populations at Isle Royale. (See figure 22 for deer mouse population labels.)

DNA markers, during 1995–2000, MTU PhD student Leah Vucetich has studied the genetics and demographics of unmanipulated, wild populations of deer mice (*Peromyscus maniculatus*) that live on the small islands surrounding Isle Royale's main island, as well as the Ontario and Michigan mainland areas closest to Isle Royale. Because movement of mice between islands is greatly restricted (fig. 22), this study provided insight into the effects of habitat fragmentation on genetic deterioration and population viability. Populations separated by large distances of contiguous habitat were genetically similar, but populations separated by small distances of water were genetically distinct (Table 1).

Other Wildlife

The National Park Service conducts aerial and ground surveys of osprey and bald eagle nests each summer. These species have been increasing for the past 15 years both at Isle Royale and in the Lake Superior region (fig. 23). In 2000 a total of 12 eagle nests fledged 14 young, while 7 osprey young were fledged in 7 nests.

Long-time beaver researcher Philip C. Shelton returned in October 2000 to conduct an aerial count of food caches at Isle Royale. This count has been completed every two years since 1978 (and as far back as 1962). The long-term decline in beaver abundance that began in the late 1980s has continued to the present (fig. 24) and is attributed to the gradual decline in habitat quality as young deciduous forests continue to be replaced by late-successional forests dominated by coniferous species. Currently beaver abundance is lower than at any time in the last 40 years.

Snowshoe hares are reaching peak levels in boreal

Also, genetic diversity was lower in islet populations than in main island populations. Average population growth rate, variance in growth rate, and population size variability were positively related with genetic diversity. Genetic diversity helped explain survival patterns of individual mice. A small but significant amount of genetic variation was detected between mice that survived their first winter and those that did not. Inbreeding depression appeared to reduce population viability in this set of wild and unmanipulated populations.

forests of Michigan and Minnesota, and Isle Royale mirrors this regional trend (fig. 25). Spring and summer indices based on hare observations by ground personnel declined from 1999 to 2000, both at Isle Royale and in northern Minnesota. Yet track abundance in winter remained relatively high in most boreal forest areas of Isle Royale. Goshawks, an important predator of snowshoe hares, were observed from aircraft four times during the 2001 winter study. Observations of red foxes in winter continued to be relatively low in 2001 (fig. 26).

For most of the 1990s, evidence of marten presence in winter has been found in the Windigo area near the winter base camp. Windigo District Ranger Larry Kangas has been especially diligent in searching for marten tracks. On February 16, 2001, Kangas recorded the first wintertime observation of a marten (since the early 1900s), north of Washington Harbor.

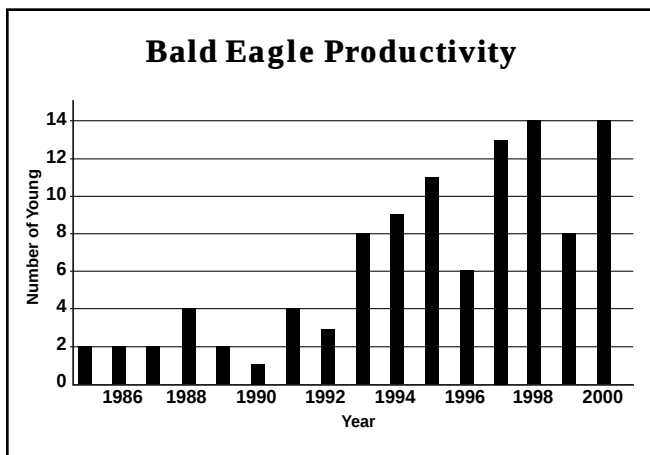


Figure 23. The number of young bald eagles produced at Isle Royale, 1985–2000 (surveys by Natural Resources Division, Isle Royale National Park). Poor reproductive success was attributed in 1996 to an exceptionally late spring and in 1999 to a regional windstorm on July 4 (which flattened forests in the Minnesota-Ontario border region).

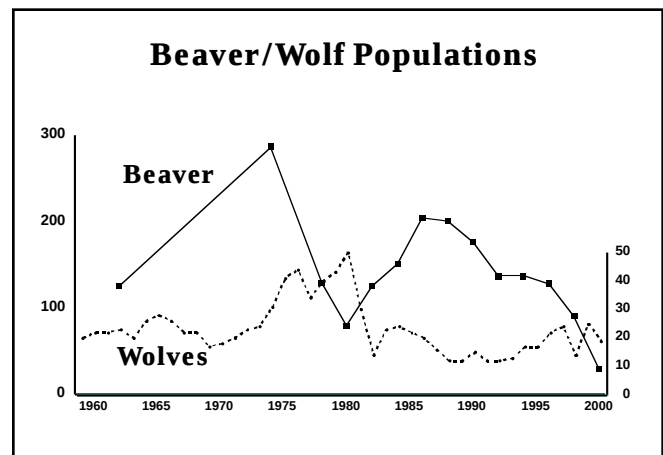


Figure 24. Beaver abundance dropped in 1980 when wolves reached a peak, but the recent decline is linked to an aging forest that is increasingly composed of coniferous tree species.

Playing the Odds

In summer, water provides the best escape habitat against wolf attack, and cow moose with calves often prefer small islands. Some 20 offshore islands at Isle Royale are large enough for moose to survive through winter. In mild winters, as in 1999 and 2000 at Isle Royale, moose inhabiting some offshore islets never had to face wolves because ice did not form. Even though ice bridges to small islands usually do develop, giving wolves temporary access, evidently some moose prefer to face wolves in familiar surroundings where they have intimate knowledge of escape routes and thick cover so they can successfully fend off wolves. Islets are preferred even when they provide little food, and calves are chronically undernourished, often growing at a slow rate.

Wolves seem to know that small islands are excellent areas to search for moose. Often they seem almost reckless in their desire to cross thin ice bridges to reach these islands. Shoreline ice provides the wolves with new and easy travel routes. As bays of Lake Superior freeze over, wolves quickly explore and scent-mark these areas.

This was the situation in February 2001, when calm, below-zero nights quickly produced shoreline ice and opened up most offshore islands to wolf access. On February 22, the Middle Pack of six left a kill about midway along the north shore of Isle Royale and traveled through the night 20 miles along craggy ice floes and shoreline rocks to Washington Island, off the southwest end of Isle Royale. We had previously counted seven moose there, including a cow moose with twins and another cow with a single calf.

On February 23, we found the Middle

Pack stretched out and asleep in the midday sun in an open swamp on Washington Island, possibly the first time these wolves had ever been on this island. They awoke and rose slowly, greeted each other with wolves' typical enthusiasm, then filed through deep snow into the wind, directly toward a cow and calf bedded high on an open ridge, about a half-kilometer away.

Often moose are able to detect approaching wolves even when standing upwind, and this cow and calf were soon on the alert with huge funnel-shaped ears pointed toward the pack. When the wolves were still a couple hundred meters away, the cow turned and trotted, her calf close behind, along the ridge and then down into the same lowland valley that the wolves were crossing. Unexpectedly, the cow then turned in the direction of the wolves and began walking carefully toward them.

In a few seconds, the wolves sighted the moose and broke into their fastest run toward the cow and calf. The cow had now moved to protect the vulnerable rear-end of her small calf, and the calf had to break trail through deep snow as they tried to escape. The moose were quickly overtaken by the wolves who immediately leaped up and grabbed the rear end of the cow. The cow slowed and made a faltering run for another 20 meters. The calf paused briefly and looked back at its mother, now beset with wolves pulling on its rear legs and front shoulder, then trotted away, quickly disappearing into the thick spruce forest.

When several wolves are able to get hold of a moose, it rarely escapes, and this cow was pulled down after a few seconds of furious but unsuccessful

kicking and whirling. The moose's head was pulled back onto the snow and blood began to stain the snow as six wolves tugged in all directions on the legs and tough hide of the cow. In less than a minute it was clear that the cow would never move again.

We wondered how long the lone calf would elude the wolves, or how soon the wolves would bother to search for it. One wolf almost immediately left the cow's carcass and followed the calf's tracks for 20 meters, then lay down and remained watchful in the direction the calf had fled. Three other wolves joined the first, and they seemed to prod each other a few meters at a time along the calf's path before bedding down again. They seemed to be in no hurry to search for the vulnerable calf, so we left the area until late in the day.

We returned at sunset and followed the wolves' furrowed trail through the forest toward the outer shore of the island, about 300 meters to the north. On the icy shore, we found the engorged wolves, appearing almost uncomfortably full. And out on the open ice-pack lay the dead calf, with one wolf still feeding. It had apparently been chased by the wolves 75 meters out onto "pancake-ice," ice polygons frozen together with slippery surfaces and very rough edges. On this surface, with its sharp-edged hooves, the calf would have had impossible footing, so the wolves probably had only to leap on the calf after it slipped and fell. It is hard to imagine a more naive attempt to escape from wolves, but without its mother, the calf reverted to its instinctive habit of running to water. The carcass of the calf's mother lay largely intact, and the wolves now had over a half-ton of moose available.



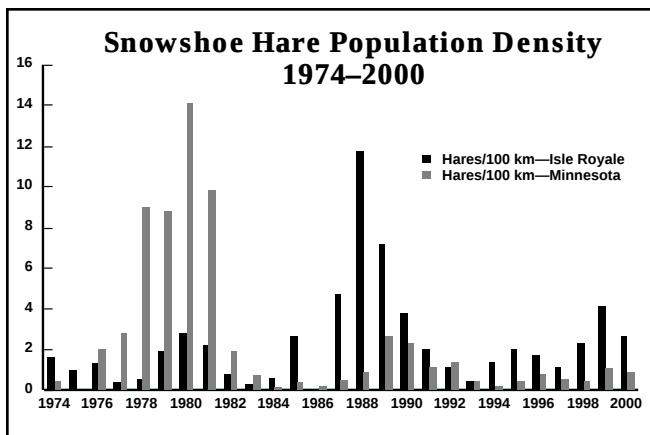


Figure 25. Relative snowshoe hare density reaches a peak about every 10 years, both at Isle Royale and on the mainland in Minnesota. Counts were made at Isle Royale during all hikes in May–August, while hares were counted in Minnesota on routes used to count drumming ruffed grouse in spring (Minnesota Department of Natural Resources, with thanks to William E. Berg).

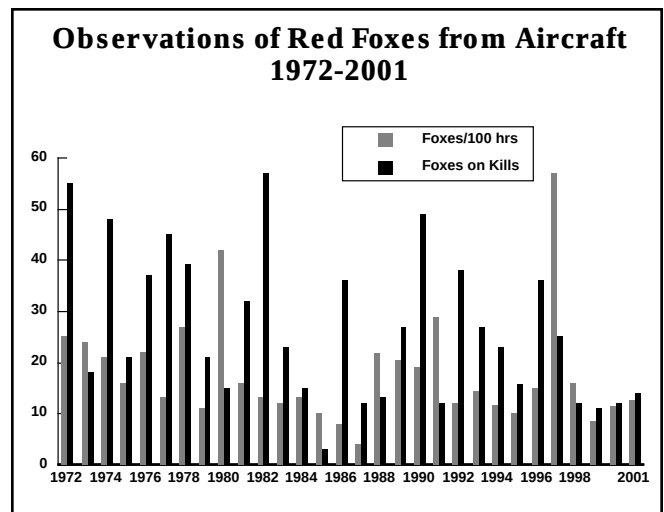


Figure 26. Relative abundance of red foxes from aircraft observations in winter, 1972–2001. Gray bar is the number of foxes seen away from moose carcasses/100 hours, while the black bar is the number of foxes seen on carcasses.

Weather, Snow, and Ice Conditions

The winter of 2000–01 began with snow and cold weather in November. When we arrived at Isle Royale in mid-January, snow depth was about average, at 50–60 cm. Two major snowstorms in February brought snow depth to 75 cm or more for most of the month. That amount is considered deep for moose as it approaches the belly height of calves (fig. 27).

While we were spared thawing conditions during the winter study, also missing were periods of very cold temperatures that make ice in open portions of Lake Superior. Thus another year passed without any ice bridge connection between Isle Royale and the Ontario mainland. Over the past three decades, less snowy winters have been the general trend (fig. 28).

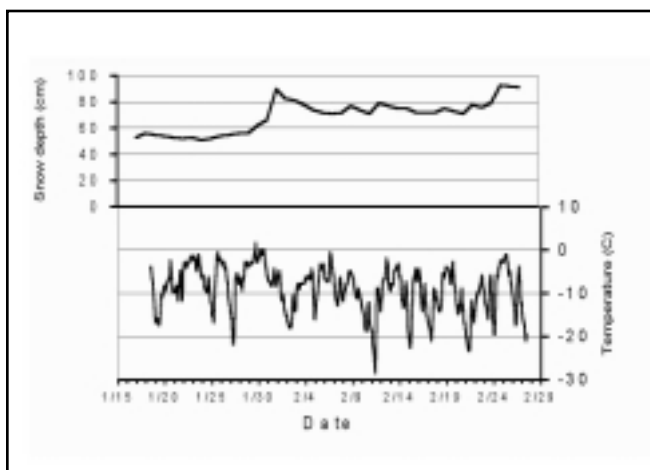


Figure 27. Snow depth (daily) and ambient temperature (hourly) during the 2001 winter study on Isle Royale.

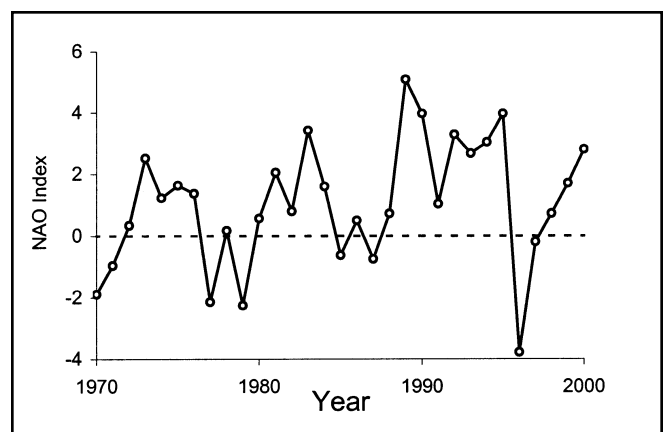
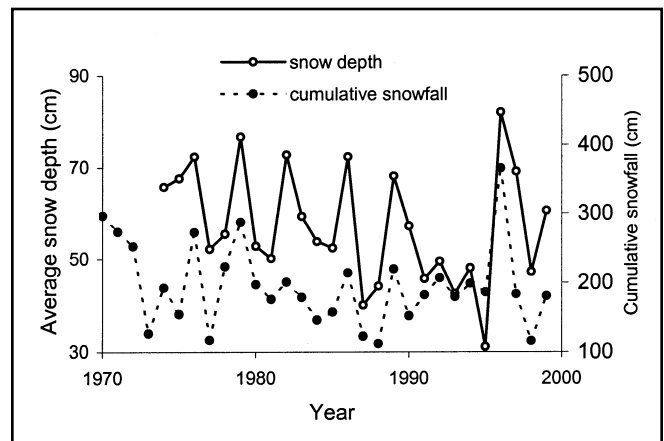


Figure 28. Average midwinter snow depth at Isle Royale and cumulative snowfall in nearby Thunder Bay, Ontario (upper panel) with North Atlantic Oscillation (NAO) Index (lower panel). The NAO is one of the most important large-scale weather patterns in the world, second only to the Earth's seasonality and El Niño. A low NAO Index is associated with snowy winters in the boreal forest of North America.



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