Ecological Studies of Wolves on Isle Royale
1999–2000
... what remains of our natural out-of-doors, of our wilderness and what belongs in it, is worth keeping. I shall not say that keeping it will be cheap or easy or without opposition or without the confusion of differing objectives.

Paul L. Errington
Of Man and Maturity published posthumously, 1968
Ecological Studies of Wolves on Isle Royale

Annual Report 1999–00*

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Results reported here are preliminary and, in some cases, represent findings of collaborators; please do not cite without consulting the author.

Cover photo: East Pack female wolf with full stomach heads "home" toward the pack den in June 1999; photographed by automatic Trailmaster® camera, triggered by breaking of infrared beam.

Opposite photos: Top, Middle Pack traveling in new territory along the shoreline of Siskiwit Bay in February 1999; center, male 420 of the West Pack in 1992, the last male breeder in this pack; bottom, cow moose foraging in Washington Creek near Windigo.

Inside back cover photos: Top left, aerial view of Isle Royale; right, red fox scavenging near wolf-killed moose; center, moose skull awaits discovery in thick cedar forest; bottom, river otter grooming its waterproof coat of fur.

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Ecological Studies
of
Wolves on Isle Royale

“Phenomena intersect; to see but one is to see nothing.”
—Victor Hugo, The Toilers of the Sea

Personnel and Logistics

In summer 1999, Rolf Peterson directed ground-based fieldwork, aided by Anne Chouinard, Justin Gude, Carolyn C. Peterson, Trevor S. Peterson, Marcel Potvin, John A. Vucetich, and Leah M. Vucetich. Fieldwork continued from May 15 through the end of August. In 2000, the annual winter study extended from January 11 to February 28. Peterson and pilot Don Glaser participated in the entire study, assisted in the field by volunteers Cynthia D. Carter, Anne M. Chouinard, Amy K. Jacobs, and Tracy A.D. Mott, and the following personnel from Isle Royale National Park—Larry A. Kangas, Jack G. Oelfke, Mark C. Romanski, and William I. Munsey.
**Summary**

The wolf population continued to increase during the past year, from 25 to 29 wolves, and in 2000 it was higher than at any point since 1980 (fig. 1). Mortality during the past year (4 percent) was exceptionally low, and a total of five pups were raised in two packs.

The wolf population is apparently being restructured, from three territorial packs to just two; the Middle Pack began to take over West Pack terrain in 1999, and the takeover appeared complete in 2000, with Middle Pack claiming 75 percent of the island area (and about half the moose). This pack killed a radiocollared wolf that originated in the East Pack and was observed attacking another single female in its range, but several "foreign" singles or pairs of wolves persisted within Middle Pack territory in 2000. The Middle Pack (with up to 12 wolves) and the East Pack (now 10 wolves) together claim the entirety of the island. Wolves formerly known as West Pack were still probably present in 2000, but they could not be identified with certainty.

Moose on Isle Royale were little affected by winter conditions in 1999–2000, but winter ticks prompted by warm spring and summer weather in 1998 appeared responsible for malnutrition deaths recorded in late winter and spring 1999. Calf abundance in winter 2000 was exceptionally low (6 percent), and the population was estimated at 850 moose (1.6 moose/km²), up slightly from the 1999 estimate. Hot weather, in addition to severe winters, may prompt moose population change.

Plant species consumed by moose have enjoyed more favorable growth conditions since 1996, when over three-quarters of the moose population died of starvation, yet some woody plants may not recover normal vigor because of previous overbrowsing. For balsam fir, growth and survival studies indicate that the species continues to decline toward extinction on the island’s west half, while fir on the east half recovered quickly from heavy browsing in 1996.

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**Figure 1.** Wolf and moose fluctuations, Isle Royale National Park, 1959–2000. Moose population estimates during 1959–1988 were based on population reconstruction from recoveries of dead moose, whereas estimates from 1989–2000 were based on aerial surveys.
The Wolf Population

Continuing the slow but steady recovery begun in the mid-1990s, the wolf population increased from 25 in 1999 to 29 in 2000, the highest density in the past two decades (equivalent to 53 wolves/1,000 km²). The wolves were organized in 2000 as follows (fig. 2):

- East Pack III .................. 10
- Middle Pack II .................. 12
- Duos ............................. 6
- Singles ........................... 1
- Total 2000 ..................... 29

East and Middle packs were relatively large, at 10 and 12 wolves. The East Pack had two surviving pups in winter, while the Middle Pack had three. Mortality during the past year was exceptionally low (only one death occurred among the 25 wolves present in 1999, or 4 percent annual mortality), allowing the population to increase (fig. 3). Wolf mortality in the future is difficult to predict because it is inherently more variable than reproduction, but it is likely that wolf numbers will cease to increase as soon as mortality increases to its usual level.

There were no efforts to live-capture and radio-collar wolves in 1999, as this practice was under review by the National Park Service at Isle Royale. Live-capture efforts for wolves will resume in 2001. Two radio-collared wolves in the East Pack were monitored during 1999–2000. Female 1070 continued as the breeding female, while male 670 dispersed from the East Pack before summer 1999. Male 670 had been frequently suppressed by the dominant breeding male in the East Pack in 1999. In winter male 670 was paired with a female in a small area along the boundaries of East and Middle packs, but he was killed by the Middle Pack in February 2000.

The territory claimed by the Middle Pack in the 1990s contained relatively few moose, with the forest having been burned in 1936 and now grown out of reach of browsing moose (fig. 4). The pack had 200–300 moose in its territory in 1991–95, but moose were steadily declining even before the moose die-off of 1996, probably because of intensive predation by wolves. In 1996–1998 there were only about 100 moose left in the Middle Pack’s usual range, and it was anticipated that the Middle Pack might itself be vulnerable to food shortage. However, in 1999 the pack enlarged its territory to the west, effectively moving aside the two-member West Pack. The Middle Pack takeover was complete in 2000, with Middle Pack claiming 75 percent of the island—anything not already claimed by the East Pack. With this territory enlargement, the Middle Pack now has access to over 400 moose, about half of the island’s population (fig. 5). The other half of the moose population was found on the 25 percent of the island controlled by the East Pack (figs. 6 and 7).

There were a few minor matters left to be taken care of as the Middle Pack ousted the West Pack, namely the fate of several wolf pairs and singles that continued to roam the vast territory now claimed by the Middle Pack. Two days after killing male 670, the Middle Pack tracked down and attacked another wolf that had formed a potential breeding pair (see

![Figure 2. Wolf pack movements and moose carcasses (wolf kills and otherwise) during the 2000 winter study. Both Middle and East Packs scent-marked their territories. Dotted line is area of male 670 and partner.](image-url)
Snow depth was low during the winter study of 2000, but cold temperatures kept the snow soft and fluffy in January and most of February. Wolves were much impeded by the soft snow, so moose found it easy to outrun wolves. Warm temperatures in late February quickly melted most of the snow, and the wolves were left without the usual favorable late-winter hunting conditions on crusted snow. The mild winter of 1999–2000, on balance, probably aided moose at the expense of wolves. An analysis in 1999 by Eric Post et al. in *Nature* (28 October) revealed the significance of the North Atlantic Oscillation (NAO) in wolf predation patterns at Isle Royale; a low NAO index means increased winter severity in northern North America, and at Isle Royale severe winters have historically led to moose declines because of increased predation.

**Figure 3.** Wolf population size (top) is explained by patterns of mortality (middle) and reproduction (bottom). The increase in 2000 can be attributed primarily to low mortality in the previous year.

**Figure 4.** Surveying their new domain in old forests at the west end of the island, the Middle Pack rests while traveling through deep snow on the Minong Ridge near Windigo.
Figure 5. As the Middle Pack increased in size in 1999–2000, it was able to maintain access to adequate prey (indicated by moose/wolf ratio in inset graph) only by enlarging its territory (see maps).

Figure 6. With Isle Royale closed to human visitors in winter, traveling wolves make full use of some of the amenities constructed for backpackers, such as trails and footbridges. Shown here is the East Pack near Moskey Basin.

Figure 7. East Pack begins its nighttime activity with a group greeting as the sun sets.
The Moose Population

During February 2000, the moose population was estimated at 850 animals (1.6 moose/km²) from an aerial census of moose on 17 percent of the island area (91 plots measuring 1 km² in area, see fig. 8). The 95 percent confidence interval for this estimate was +/- 206. The 1999 estimate was 750 +/- 141 moose.

Given relatively high mortality and low reproduction during 1999–2000, it is unlikely that the moose population grew in size during this interval. The proportion of calves in the population (6 percent) in February 2000 was one of the lowest on record (fig. 9). Also, in spring 1999, we discovered several carcasses of moose that died of malnutrition, probably caused by heavy infestations of winter ticks the previous winter (fig. 10).

The low calf proportion in winter 2000 was surprising, as wolf numbers and kill rates were not high and winter weather was mild. The exceptional drought and warm temperatures in summer 1998, however, may have had a long-term influence persisting into 2000. Moose appeared to be in poor condition in winter 1998–1999, probably because hot weather during the previous summer led to lower net energy intake. Also, heavy tick loads that winter followed the early spring of 1998, another negative impact of warm weather on moose (fig. 11). Fertility levels and pregnancy success in cow moose in 1998–1999 may have been low because of heat-induced problems.

During winter 2000, moose were not heavily concentrated in coniferous forests near shorelines, their usual pattern, but lack of fresh snow precluded mapping new distribution patterns before the census. In the interior highlands, moose density in 2000 was twice as high as in 1999, while, in the conifer habitats near the lakeshore, moose density in 2000 was only half the 1999 level.

Moose mortality during the winter study in 2000 was near average levels, even though wolf packs were large (fig. 12). Moose were in good condition, judging from high marrow fat levels in wolf-killed moose (fig. 13). At no time during the winter was snow an impediment for moose, and the ground was 50 percent snow-free at the end of February. It can be anticipated that early spring in 2000 will allow winter tick populations to develop further; they are one of the most significant parasites for Isle Royale moose.

Moose nutritional status in midwinter has been monitored since 1988 through chemical analysis of snow-urine, in collaboration with Dr. Glenn DelGiudice of the Minnesota Department of Natural Resources. The urea/creatinine ratio in snow-urine reflects the extent of muscle catabolism in over-wintering moose (fig. 14). Body condition of moose has improved markedly since the moose die-off in 1996.

In 2000, a collaborative effort was initiated with Dr. Steven Monfort of the Conservation and Research Center (Smithsonian Institution) to determine moose pregnancy rate in winter from pregnancy hormones detected in moose feces. It has been suspected that moose fertility is relatively low at Isle Royale because of poor nutrition induced by high moose population density, and, in radio-telemetry studies in the 1980s, it was found that most radio-collared cows at Isle Royale did not have calves in successive years. Additional years of data will be required to obtain enough samples, but early results from 2000 suggest a pregnancy rate of 53–71 percent, quite low for this species. Two cow moose accompanied by calves were judged by fecal hormones to be nonpregnant.
Figure 9. 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 10. In June 1999, Earthwatch volunteers Jeff Storm (with saw) and Dean Varian collect bones from a dead moose calf that probably died from the effects of winter ticks. This parasite (which shuns people) grows on moose in winter and leads to premature loss of the winter coat of hair along with other costly physiological effects.

Figure 11. A large bull moose was photographed in August 1999 (left) while taking refuge from summer heat in Lake Superior. It was breathing at a very fast rate, trying to cool its massive body. The moose was killed by wolves in October 1999, and its skull and antlers were discovered by an Earthwatch crew in August 1999 (right). Its antlers had the largest maximum spread (51 inches, or 129 cm) of all moose collected in the last 30 years at Isle Royale.

Figure 12. Moose mortality rate in midwinter 2000 was near long-term average levels, in spite of larger pack size than anytime in the past two decades.

Figure 13. 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.
**Forest Vegetation**

Selective browsing by moose is a vital influence on forest structure and species composition throughout Isle Royale. For over a decade, balsam fir (*Abies balsamea*) populations have been monitored because this browse species grows rather slowly and its physical structure is determined by the intensity of moose browsing (see published studies by B.E. McLaren).

On the western half of Isle Royale, there has been virtually no regeneration of mature fir trees since the arrival of moose on the island almost a century ago (fig. 15). The mature fir trees in the canopy, established before 1915 when moose initially reached high density, are now steadily dying of "old age." Thus, the seed source for this species is rapidly disappearing (figs. 16 and 17), while all regenerating trees have been suppressed at heights <1.5 meters by intensive moose browsing (fig. 18). Based on survival of tagged trees, virtually all mature fir trees are predicted to disappear by 2008–2011.

Balsam fir on the eastern end of Isle Royale grows under more favorable light conditions, and, as a consequence, the species is better able to withstand removal of foliage by moose. During a period of rela-

*Figure 14.* Proportion of snow-urine samples from Isle Royale moose which indicated exhaustion of body fat reserves in midwinter (urea/creatinine ratio > 3.5, from G. DelGiudice). High U/C ratios in the late 1980s reflected years with high winter tick populations, while in the mid-1990s moose density reached historic highs, resulting in malnutrition.

*Figure 15.* The author examines a decades-old balsam fir tree, suppressed by annual browsing by moose, at the west end of Isle Royale.
Figure 16. Survival studies of tagged balsam fir trees at the west end of Isle Royale reveal that mature trees are quickly dying out, without replacement by younger trees. Shown here is Trevor Peterson checking tags on a mature tree snapped off near the base, a common form of mortality.

Figure 17. Semiannual tallies of 473 mature balsam fir trees permanently tagged in 1988 have revealed a steady loss due to senescence. As these trees die, the seed source for this species is steadily disappearing.

Figure 18. Tree-ring width in this balsam fir tree from the west end of Isle Royale reveals many years of growth suppression following the severe winter of 1971–1972, when moose damage to fir was extensive (photo by A. Chouinard).

Figure 19. An enclosure to exclude browsing moose was constructed at Windigo in 1979. Twenty years later the regrowth of the forest inside the enclosure demonstrates the influence of moose browsing on the ecology of forests.
with trees virtually stopping growth when moose density was high. Following the moose die-off in 1996, most fir trees in the understory have not recovered from previous years of overutilization, and, in fact, there is substantial annual mortality in these stunted individuals (fig. 20A).

In contrast, on the east end of Isle Royale, growth of fir trees was not as strongly influenced by moose density (fig. 20B). In particular, fir trees recovered quickly from the single year of high browsing damage in 1996, when severe winter conditions created a desperate situation for moose.

Spruce budworm, a major insect defoliator of balsam fir, emerged on Isle Royale in 1988 after an absence of about 50 years. Budworm damage was locally severe, but extensive mortality of fir has not occurred. Since that time, this forest insect has diminished somewhat in abundance, and damage was relatively light in the late 1990s.

Even after a century, the forests of Isle Royale are still reacting to the arrival of moose, but responses vary across the island because of different soil depth, forest type and disturbance, and densities of moose and plants. New measurements of forest composition and structure will be initiated in 2000 in order to better describe and understand the dynamics of forest change.

Figure 20. Stem growth patterns of a representative fir tree at the west end (Windigo) and east end (Lane Cove) of Isle Royale. The black-to-grey patterns correspond to mean ring width along the height of the tree. Each column corresponds to ring widths along the stem for a particular year.
Figure 21. Tree-ring width for individual balsam fir in the forest understory on the west half of Isle Royale (A) reveals growth patterns largely determined by browsing by moose in winter, while moose effects were not as pronounced at the east end of the island (B). Shown here are ring-width measurements in cross sections from the base of the stem (Anne Chouinard, unpubl. data).
Endurance and Opportunity

The Middle Pack was intent on expanding its territory in 2000. After spending five weeks at the west end of the island, on 16 February the Pack moved twenty miles east, to country that in 1999 was used by both Middle and East packs. There the Middle Pack found a kill made by collared male 670 (originally from the East Pack) and a female. The Middle Pack followed the duo’s tracks, and when they caught the pair at another kill, they chased male 670 for a mile and killed him. After consuming the moose killed by the duo, the Middle Pack returned to the first kill they had discovered.

Two days later, near this kill, tracks showed that the Middle Pack had encountered another wolf pair and had given chase. By aircraft we followed these tracks for six miles, to, and then along, the south shore of the island near Chippewa Harbor. We caught up to the 11-member pack at water’s edge just before noon, vigorously shaking themselves dry, while twenty feet out in Lake Superior, standing on a submerged rock in ten inches of water, stood a bedraggled wolf, cowering, its hindquarters almost underwater.

During the next hour we circled overhead. After several minutes of rolling in the snow to dry off, Middle Pack wolves either lay in the snow, watching the victim in the lake, or strutted stiffly back and forth along the shore in front of the hapless wolf. Suddenly, in quick succession, three wolves jumped into shallow water and leaped for the rock where their quarry stood quivering. Confronted by this snarling trio, it fought for its life, snapping furiously toward the lunging pack members. The lone wolf was forced backward into neck-deep water, but it retained its footing and held the attackers at bay; they retreated to shore to shake and roll again in the snow.

While we watched, the pack led a series of attacks on the wolf on the rock, a dozen in all. The desperate defense of the lone wolf was effective, but the ordeal, including standing neck-deep in ice water, took its toll. During the last few encounters the loner adopted a new strategy—when attacked on its rock, it retreated into the lake and swam along the shore about thirty feet to another submerged rock, buying a few moments before the pack members jumped back to shore and ran down to the new location, where they renewed their attack.

We became aware of a new element when the breeding male of the Middle Pack jumped to the rock to confront the lone wolf. Instead of pressing the attack, however, he slowly wagged his raised tail. Then he circled around to the wolf’s side and regarded its hindquarters; the male was interested in courting the stranger, a newly-arrived female in heat. His arousal prompted the alpha female to jump to the rock, along with a helper. A severe attack then followed, and Middle Pack wolves firmly grabbed the female and threw her on her back in the water. In less than a minute, however, the pack retreated and the lone female rose to her feet.

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After forty-five minutes, the lone female, once again facing a violent attack, swam out into Lake Superior, heading for a rocky point about fifty yards down the shore. Her “dog-paddle” strokes seemed vigorous, and I thought she might be able to reach shore and get away with an all-out run. But she could...
only crawl out of the water and stiffly walk a few steps before starting to shake her drenched fur.

Within seconds, the Middle Pack arrived and knocked her over. The whole pack crowded around and bit her, shaking their heads as they held on. When the pack pulled back briefly, the female snapped at the wolves that surrounded her. The last wolf pressing the attack held the female’s throat for several seconds, then left her lying motionless on the shoreline rocks. The Middle Pack retreated toward the forest edge, huddled excitedly, and then lay down in the bright afternoon sun, keeping an occasional eye on their victim. We thought the female was dead, but she raised her head briefly, which brought the pack running. They crowded around, vigorously biting her legs and throat.

Five minutes later, at one o’clock, the female appeared to be dead at last. We flew to a nearby frozen lake and landed to conserve our fuel supply. A half-hour later, we checked the scene and found no change—the pack was sleeping and the carcass of the lone female had not been moved. We headed back to our base camp to refuel.

At half past three, we found the pack heading into the island’s interior. We planned to land to collect the carcass, but as we circled we saw a wolf approaching the attack scene in the tracks of the Middle Pack. This was the trailing member of the Middle Pack. As it drew near the attack scene, this new wolf became very uneasy, looking all around with tail tucked between its legs. Eventually, it followed tracks to the water’s edge and saw the dead wolf. Without hesitation, the newcomer approached and, when only two feet away, the lone female raised her head! The oncoming wolf kept its distance but moved near the female’s hindquarters, revealing himself to be a potential suitor. Perhaps the female mustered a low growl from her torn throat; for some reason the male retreated a few feet, climbed up on a nearby rock, and lay down to watch. The female laid her head back on the bedrock shore.

Periodically, the male approached the female, and his attention seemed to breathe life into her. Almost an hour after his arrival, she managed to hold her head up. We left the pair alone for two hours, returning for our final check of the day at six o’clock. The male and female were both gone, and we marveled at her resilience.

The next day, the Middle Pack was miles away, busy with other matters, and from the aircraft we could find no sign of the wounded female and her new friend. We then landed on a nearby lake and snowshoed to the attack scene. Not surprisingly, about fifty yards into the woods, we found a succession of three bloody beds of the female. The snowy imprints of her throat and hindquarters were saturated with blood. We followed parallel tracks of both wolves, with occasional drops of blood marking the female’s path, as far as we could.

Five days later, we were rewarded with a clear view of the wounded female and her suitor standing on a rocky knoll, about a half-mile from the site of the attack. The female was standing while the male faced her and attentively licked her wounded neck for several minutes. The pair had occupied the site for a day or two, judging from the number of icy beds nearby, and there were just a few drops of blood in the area. Obviously the female was getting better. Her companion provided much-needed attention to her neck wound and may have saved her life, but now he became quite a pest, displaying an array of courtship behavior. The female had no evident interest, and she had to expend valuable energy to whirl and snap at his unwelcome advances. She tried to curl up and lie down but was forced to stay on her feet to fend him off. Standing tall and wagging his tail nearly vertically in the air, the male moved constantly round and round the female, and she reluctantly moved in circles.

For almost an hour, we circled overhead and watched the female ward off all physical contact with the male except his attention to her wounded neck. Twice she grabbed a mouthful of snow; it seemed she had not been able to get to the lake for water, about a hundred yards distant. Prevented from displaying common courtship behavior, such as pawing the female’s back, inspecting or mounting her rear, and playfully chasing in mutual excitement, the male tried a new approach, something I’d never seen before in wolf courtship—he stood in front of the female and quickly dug a deep hole in the snow, as though caching food. This was similar to some of the hunting-related courtship behavior of red foxes.

Two hours later, when we checked the pair for the last time, the male was still making a nuisance of himself and the female continued to snap at him. Two individuals, one focused on mere survival and the other on reproductive imperatives, neither with much chance of success outside the existing territorial packs. We felt fortunate to observe the pair again, but this was our last flight of the winter season. In this case, a final outcome would be known only to the wolves.
\textbf{Whatever Happened to Inbreeding?}

A decade ago, the wolf population was at its lowest level and unresponsive as the moose population grew and grew. It was discovered that the wolves were probably all descendants of a single maternal ancestor and were heavily inbred. The passing of each generation brought another 15–percent reduction in genetic variability, because so few individuals were typically involved in reproduction. The scientific literature contains much theoretical discussion and a few cautionary case histories of how loss of genetic variation might spell doom for a small population. The expected outcome for the wolves of Isle Royale was bleak, according to prevailing scientific opinion.

Loss of genetic variability can be manifested in poor reproduction, and certainly Isle Royale wolves were reproducing poorly in the early 1990s. The West Pack seemed to epitomize the dilemma, as it declined from eight wolves in 1987 to just two by 1990. From 1988–1999, the pack had only one surviving offspring, a male born in 1995, and the pack numbered only two to three wolves during these eleven years. Nevertheless, during this time the West Pack managed to defend half of Isle Royale as its traditional territory; perhaps it was more tradition than actual defense. Over the span of two years the Middle Pack gradually moved farther onto West Pack turf, until the takeover was complete by January 2000.

Did the West Pack ultimately fail because of poor reproduction driven by genetic losses? If so, then the ousting of this pack from its territory represented natural selection for more successful genetic combinations, although there may be much more to the story. Such is the nature of genetic “purging”—this may explain why, for now, deleterious effects of inbreeding seem forestalled for Isle Royale wolves.

During 2000–2001 we will embark on a new study of genetic variation revealed by DNA in wolf scats, in the hope that this provides an adequate method to monitor the "genetic decay" of this population.

\textbf{Other Wildlife}

The National Park Service conducts aerial surveys of osprey and bald eagle nests each summer. Both species have been increasing for the past 15 years both at Isle Royale and in the Lake Superior region. In 1999 a total of 6 eagle nests fledged 8 young, while 7 ospreys were fledged in 11 nests.

With the passage of each decade, snowshoe hares in the region have reached cyclic highs in population density (fig. 22). Hare populations on Isle Royale follow roughly the same pattern as hares in Minnesota, suggesting a common link to weather patterns, while local conditions undoubtedly contribute to differences in peak populations. In Minnesota, the 1980 hare peak may have been the highest of the 20th century, while, at Isle Royale, the 1988 peak was unprecedented in the memory of long-time residents.

Fluctuations in the red fox at Isle Royale are more difficult to document and explain than its principle prey, the snowshoe hare. Two indices of fox observations in winter provide a rough idea of changes over the past 25 years (fig. 23). These data suggest that foxes were relatively scarce just before snowshoe hares reached a peak in 1988, but foxes then increased for several years as hares became scarce.

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{snowshoe_hare_population_density.png}
\caption{Relative snowshoe hare density reaches a peak about every ten years, both at Isle Royale and on the mainland in Minnesota. Counts were made at Isle Royale during all hiking routes 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).}
\end{figure}

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{foxes_pop.png}
\caption{Relative abundance of red foxes from aircraft observations in winter, 1972–2000. Grey 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.}
\end{figure}
Weather, Snow, and Ice Conditions

As the year before, the winter of 1999–2000 started late, with almost no snow before the middle of December. Snow depths were very shallow when we began the winter study, and little new snow was received in January and February (fig. 24). Fortunately the snow cover was maintained by below-freezing temperatures until the third week of February, when a major thaw occurred and most snow quickly melted. Overall, winter temperatures were not far from winter norms for Isle Royale (fig. 25). As in the previous three winters, little ice formed on Lake Superior during the winter of 1999–2000, and at no time was there an ice connection between Isle Royale and mainland Ontario.

![2000 Snow Depth/Temperature Extremes](image)

**Figure 24.** Snow depth (top) and temperature extremes (bottom) during the 2000 winter study on Isle Royale.

![Range of Temperature Extremes](image)

**Figure 25.** Range of average daily maximum and minimum temperatures during annual winter studies at Isle Royale, 1972–2000.
$3.95
Available from
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1396 Highway 169
Ely, MN 55731-8129
218-365-4695
http://www.wolf.org

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800 East Lakeshore Drive
Houghton, MI 49931-1869
800-678-6925
http://www.portup.com/imha/home.htm

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Michigan Tech Fund
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THANK YOU to all who help!