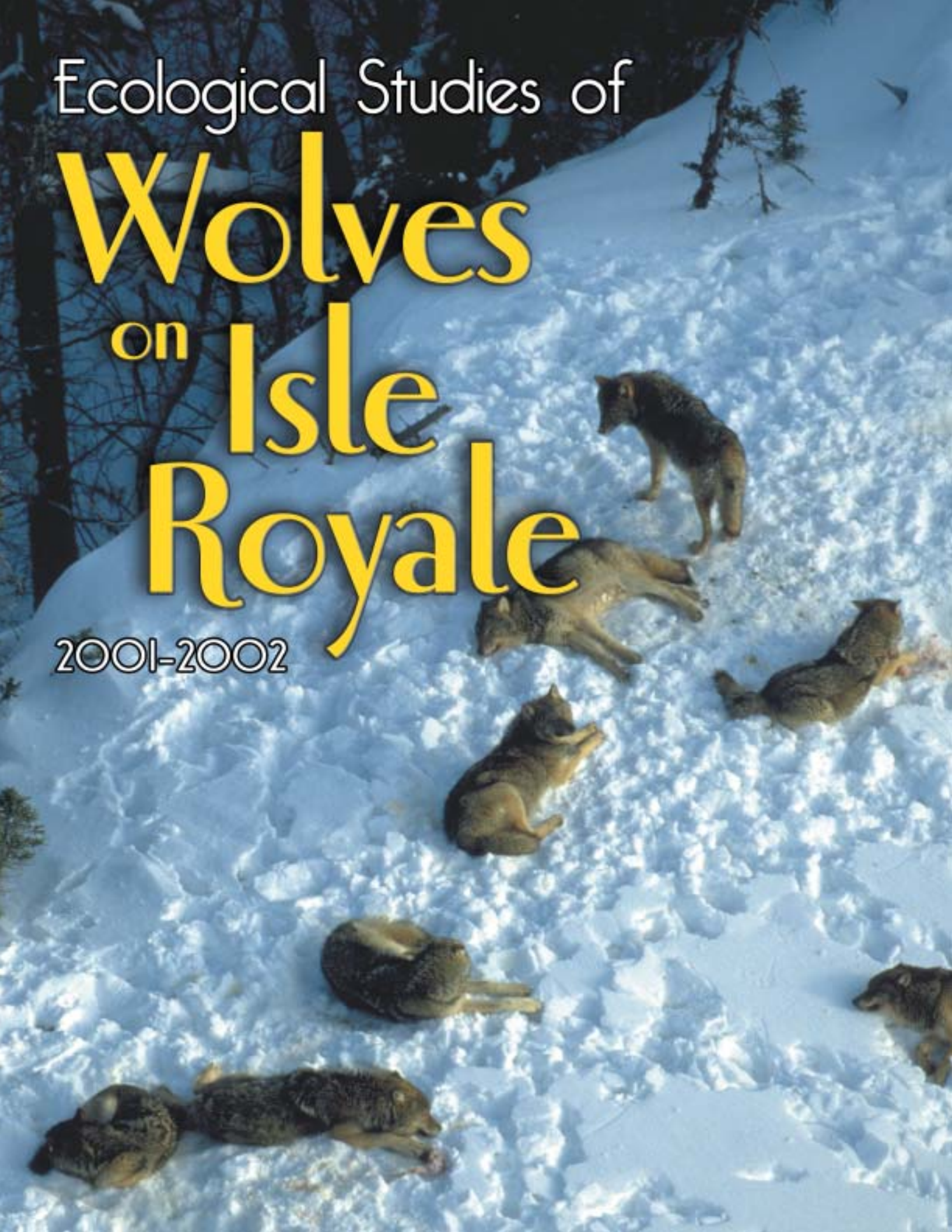
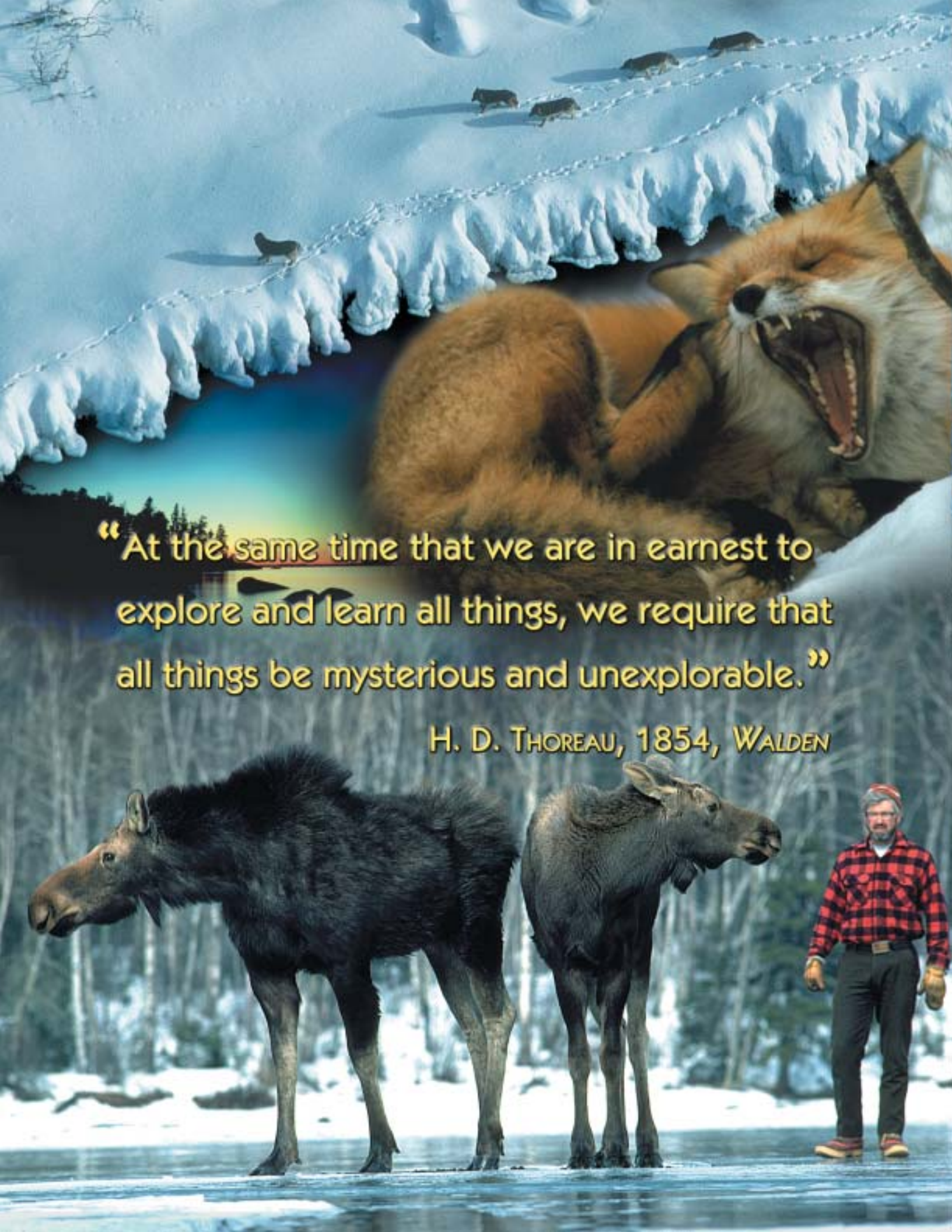
Ecological Studies of Wolves on Isle Royale

2001-2002




"At the same time that we are in earnest to explore and learn all things, we require that all things be mysterious and unexplorable."
H. D. Thoreau, 1854, Walden

Ecological Studies of Wolves on Isle Royale

Annual Report 2001–2002*

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Results reported here are preliminary and, in some cases, represent findings of collaborators; please do not cite without consulting the authors.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: Engorged wolves in the East Pack lie sprawled on a ridge after a recent kill, February 1999.

Opposite photos: Top, Middle Pack on the Isle Royale shoreline in 1999; center, a red fox yawns and scratches while awakening; bottom, pilot Don Glaser watches two moose stranded on glare ice in 1984.

Inside back cover photos: Clockwise, from top left, setting sun, wild rose, cow moose and calf in June, Middle Pack on a kill in 1994, and hiking on the Minong Ridge.

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Ecological Studies of Wolves on Isle Royale

"There is not a thing that moves on the earth, no bird that flies on its wing, but has a community of its own like yours."

—Qu'ran 6:38

Personnel and Logistics

In summer 2001, Rolf Peterson directed ground-based field work, aided by Greg Burkhart, Madeline Campbell, Philip DeWitt, Alex Egan, Mark Johnson, Tim Laske, Ken J. Mills, Tim Pacey, Erin Parker, Carolyn Peterson, Trevor Peterson, Marcel Potvin, Mark C. Romanski, John A. Vucetich, Leah M. Vucetich, and Greg Wright. Fieldwork continued from April 24 through August. In 2002 the annual winter study extended from January 10 to February 27. Peterson and pilot Don E. Glaser participated in the entire study, assisted in the field by Layne Adams, Keren Tischler, John A.Vucetich, and Leah M.Vucetich, and the following personnel from Isle Royale National Park and/or the National Park Service — Phyllis Green, Gary Vehquist, Elizabeth Valencia, Jack G. Oelfke, and Mark C. Romanski. Isle Royale staff Larry Kangas, Dave Laban and John Lines assisted further with logistics. U.S. Forest Service pilots Wayne Erickson, Dean Lee, and Pat Lowe safely flew several supply flights to Isle Royale from Minnesota.

Summary

During 2001-2002, the wolf population declined again, from 19 to 17 individuals, after dropping from 29 to 19 in the previous year (fig. 1). Pups were born in all three packs in 2001, but only two packs contained pups in winter 2002. The East Pack (six wolves) contained four pups, the Chippewa Harbor Pack (five wolves) had three pups, and the Middle Pack had none. Mortality during the past year (47 percent) was very high for the second consecutive year, possibly related to a shortage of old moose. Four wolves live-trapped and radio-collared in May 2001 were found to be disease-free and in good physical condition.

Wolf pack territorial boundaries shifted as the Chippewa Harbor Pack took over East Pack area, apparently killing the East Pack alpha male and at least one other wolf during inter-pack fighting. Wolf density continued to be highest at the east end of the island, where moose are usually concentrated in winter. During the mild winter of 2001-2002, however, moose were more evenly distributed between the two ends of the island, possibly increasing potential for inter-pack strife at the east end.

Following a catastrophic dieoff in 1996, the moose population has been slowly increasing. Calves made up 11 percent of the moose counted during the 2002 census (slightly below average), and moose population size increased to an estimated 1,100 (2.0 moose/km^2). Winter weather during the 2002 study was extremely mild, with less snowfall than in any of the previous 43 years. In spite of low snow, wolves killed moose, especially old adults, at a relatively high rate. Moose fed on abundant fallen trees resulting from a windstorm in December, and mild winter conditions should reduce the chronic nutritional stress that Isle Royale moose usually face in winter. Continued increase of the moose population in the near future is anticipated, with annual variation related to weather patterns.

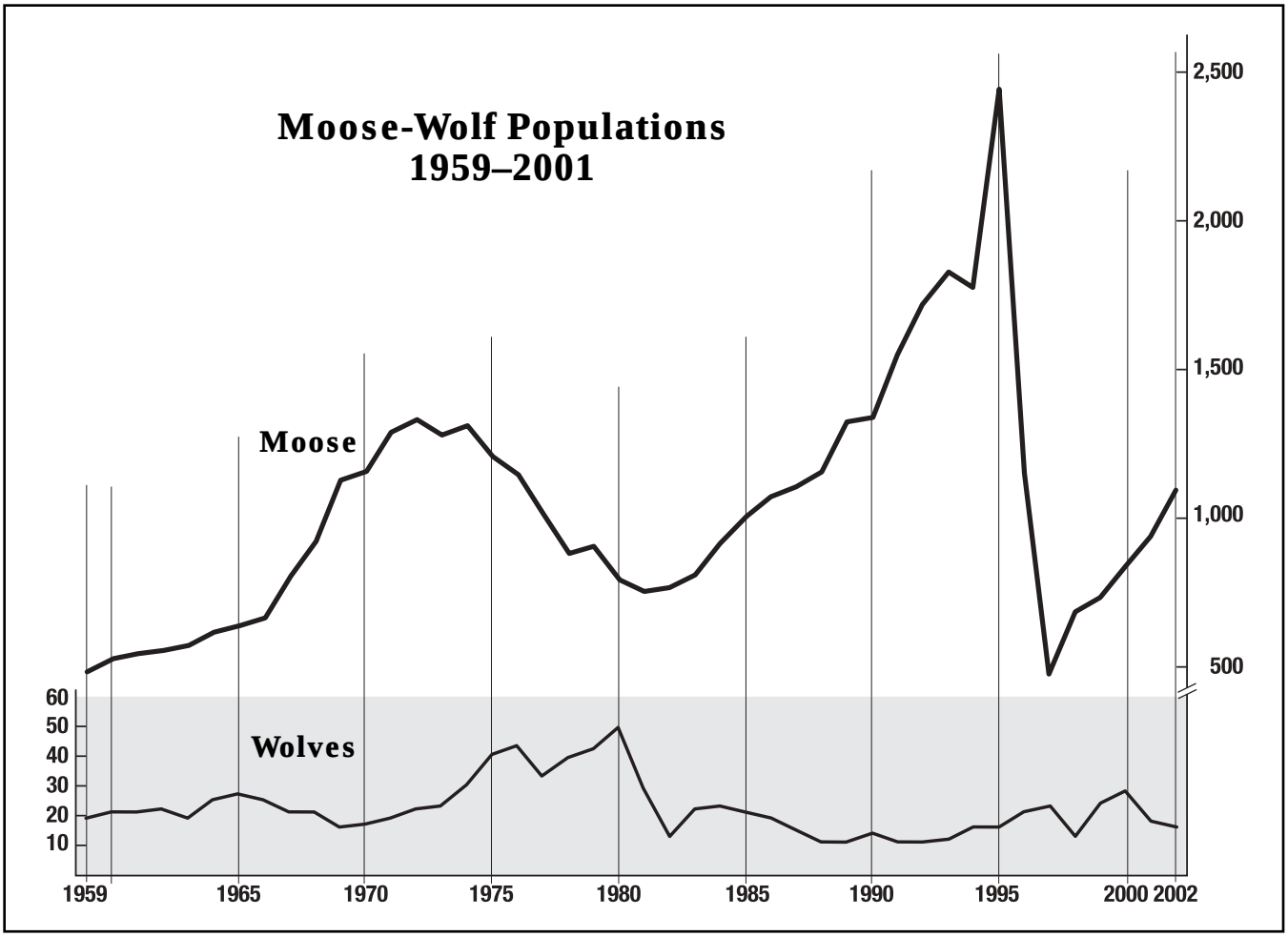

Figure 1. Wolf and moose fluctuations, Isle Royale National Park, 1959-2002. Moose population estimates during 1959-1993 were based on population reconstruction from recoveries of dead moose, whereas estimates from 1994-2002 were based on aerial surveys.

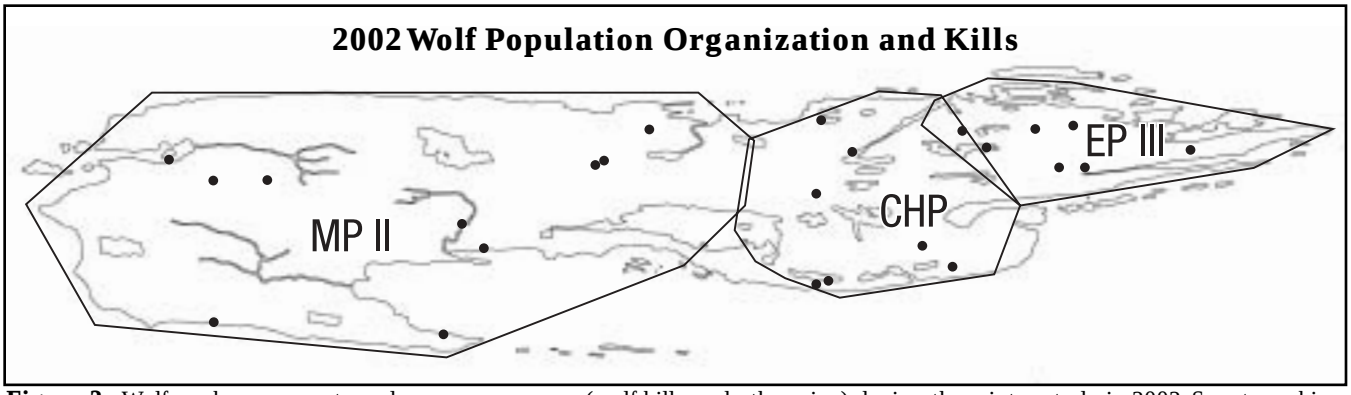

Figure 2. Wolf pack movements and moose carcasses (wolf kills and otherwise) during the winter study in 2002. Scent-marking was observed by all three of the packs.

The Wolf Population

During the 2002 winter study, we found three wolf packs and 17 wolves on Isle Royale, two fewer wolves than in 2001 (fig. 2). A dramatic decline the previous year was attributed to aftershocks from the hot drought year in 1998, but perhaps a more chronic shortage of prey (old moose) is limiting wolf population growth. The composition of the wolf population changed little:

East Pack III	6
Middle Pack II	4
Chippewa Harbor (formerly east end Trio)	5
Singles	2
Total 2002	17

For the second consecutive year, the wolf population declined as a result of high mortality (fig. 3). Nine of the 19 wolves present in 2001 had died by the 2002 study, an annual mortality rate of 47 percent. All three territorial packs produced pups in 2001, but they survived the winter only in the East Pack (four pups) and the Chippewa Harbor Pack (three pups). Six pups were known to be present in the East Pack in summer 2001.

Four wolves were live-captured and radio-collared in May, 2001, two each in the East and Middle packs:

Male 410—alpha male, East Pack
Female 200—non-breeding female, East Pack
Male 670—subordinate male, Middle Pack
Female 1071—alpha female, Middle Pack

All four captured wolves were found to be in good health and free of diseases, notably canine parvovirus (see sidebar) and distemper (fig. 4). Male 670 had underdeveloped guard hairs, especially noticeable on the tail, and was missing most of the hair on the lower neck area (fig. 5). His "ropetail" appearance was similar to that of a subordinate male packmate in the Middle Pack and the alpha male in the Chippewa Harbor Pack. Such wolves were

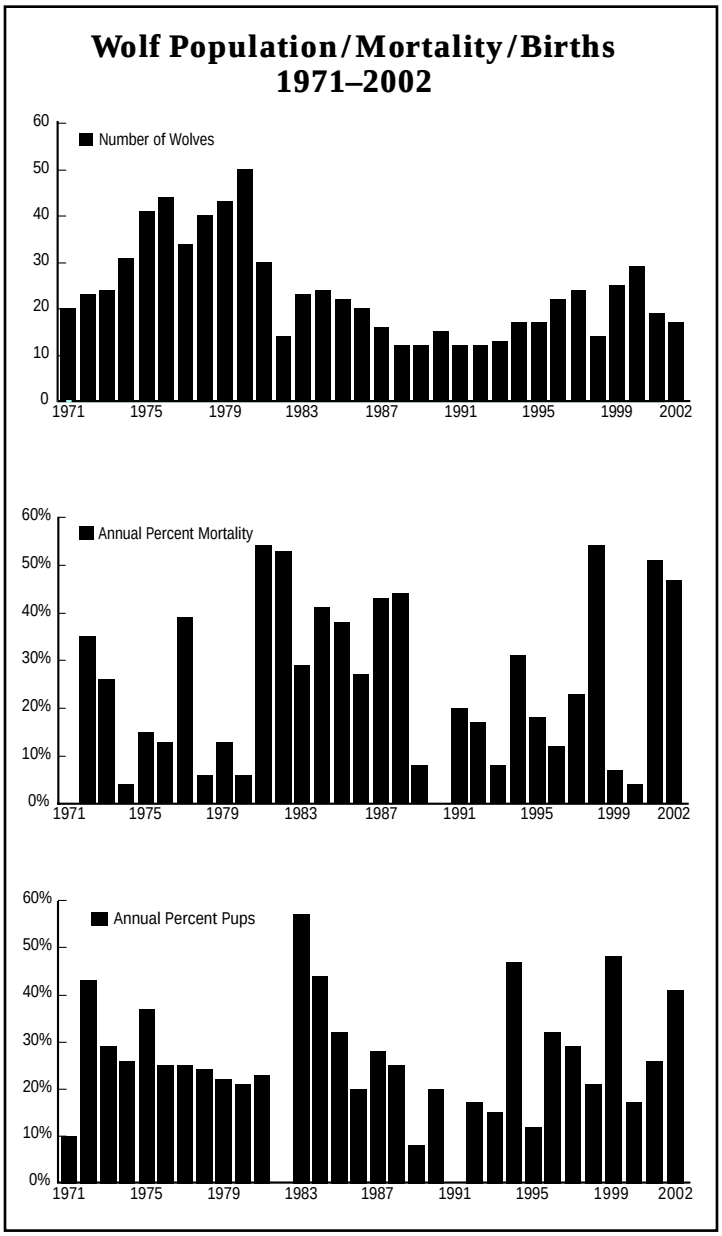

Figure 3. Wolf population size (top) is explained by patterns of mortality (middle) and reproduction (bottom). The decline in 2002 resulted from high mortality in the previous year.

Figure 4. In his prime, alpha male 410 walked a beaver dam in July, 2001 (photographed by remote camera). A few months later he was killed by the neighboring pack in a territorial skirmish.

observed rarely during the 1980s and 1990s, but they were common in the East Pack in the 1970s, dominated by a single breeding female for the entire decade. The cause of this unusual pelage remains unknown.

Female 200 from the East Pack could not be located during the 2002 winter study. Her radio-signal was never detected, and only three collared wolves were observed; her disappearance is unexplained. It is possible that she could have fallen through ice and sunk in deep water, the fate of another collared wolf in the 1990s.

The signal transmitting from Male 410 was in mortality mode when the 2002 study began, but the location of his carcass was not pinpointed for several weeks, when it was found under the ice of Moskey Basin (fig 6). Meanwhile, the Chippewa Harbor Pack repeatedly visited and scent-marked the site of 410's demise, suggesting a violent confrontation between the Chippewa Harbor and East packs. After excavating 410's carcass from Lake Superior ice, we found a broken back and trauma to the throat, confirming death from inter-pack strife (fig. 7). The fox-scavenged skull of a second wolf was found a few hundred meters away. The site of 410's death continued to be visited and scent-marked by the Chippewa Harbor Pack throughout the entire 2002 study, while they simultaneously enlarged their territory at the expense of the East Pack.

The East Pack alpha male (410) was probably killed in late December, and the East Pack contained only a female and four pups until a new breeding male was recruited by 29 January 2002. The Chippewa Harbor Pack also gained a sixth wolf on February 24 2002, after an incoming female in estrous was courted by the alpha male and tolerated by the alpha female. By that time both non-breeding members of the Middle Pack had left their pack and traveled widely, after they were consistently suppressed by the alpha male and also after they scent-

Figure 5. Male 670 in the Middle Pack sported an unusually bare neck when live-captured in May, 2001. The skin area was unblemished and new hair was growing. No ectoparasites were detected, and the cause of this condition is unknown (photo by Mark Johnson).

Figure 6. Alaska biologist Layne Adams begins to excavate the carcass of male 410 from the ice of Moskey Basin in February, 2002. This site was visited and scent-marked repeatedly by the neighboring pack, which was probably responsible for 410's death.

Figure 7. Rolf Peterson conducts a necropsy on male 410. His back was broken and his throat had been grabbed tightly by other wolves (photo by John Vucetich).

marked with slightly raised legs (a privilege usually reserved by the alpha pair). At the close of the 2002 study the Middle Pack comprised only the alpha pair, yet their territory covered almost three-quarters of the island. In all three packs, females came into estrous in February and were actively courted by alpha males.

In spite of low snow that put them at a disadvantage, wolves killed moose at a high rate during January and February, 2002 (fig. 8). Pack sizes were small, so much was left to scavenging ravens and foxes (figs. 9 and 10).

The skeleton of a wolf that died in the late 1990s was recovered in 2001. It has some interesting anomalies that appear to be congenital deformities, possibly genetic in nature (fig. 11). While wolves on Isle Royale continue to become more inbred with the passage of each generation, we have nevertheless little reason to conclude that this has resulted in consistent reproductive problems. For example, the alpha female in the East Pack had six pups in 2001, and four of these survived through the 2002 winter study.

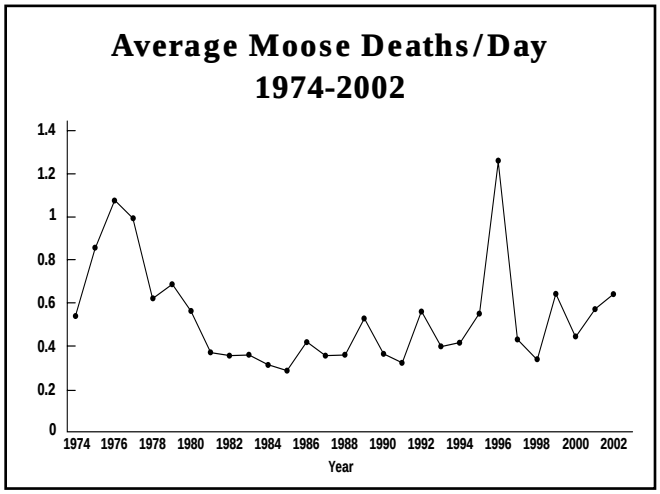

Figure 8. Moose mortality rate in midwinter was above average in 2002, in spite of low snow depth.

Figure 9. Wolf in Chippewa Harbor Pack chases ravens away from a freshly killed moose calf.

Figure 10. Remote camera catches scavenging fox (above) shortly after wolves killed the moose, and an eagle plus ravens several days later (below).

Figure 11. Unusual cervical vertebrae from wolf skeleton recovered in 2001, with congenital developmental anomalies (lacking normal lateral processes) (photo by John Vucetich).

How Canine Parvovirus Got to Isle Royale

For more than a decade it has been suspected that canine parvovirus (CPV-2) arrived at Isle Royale in 1981, causing the population crash that left only fourteen wolves alive in 1982. The question of how the disease got to Isle Royale has lain unanswered, but Dr. Larry Anderson, a retired veterinarian and member of the Board of Directors of the International Wolf Center, recently shed some light on this subject.

Three days after the Fourth of July weekend, in 1981, a dog with symptoms of severe diarrhea and vomiting was brought to Anderson's Northshore Veterinary Hospital in Duluth, Minnesota. By the next day, the dog was dead, the first victim Anderson had seen of the new malady that later became known as canine parvovirus disease.

Over the Fourth of July holiday, the dog had been at Isle Royale, arriving in a private boat with its owners who met friends from Chicago (also with a dog on board) for the holiday. Given the timing of the death of the dog from Duluth, it would have been exposed to the highly contagious virus while at Isle Royale. It is Anderson's recollection that the dog from Chicago also died of parvovirus disease, and indeed this dog probably brought the virus to Isle Royale.

The dog disease quickly spread from Duluth to the North Shore of Lake Superior, to Iron Range communities in northern Minnesota, and to the Twin Cities. At Isle Royale, all eight wolf pups known to exist in three packs in July 1981 died before winter, and the wolf population dropped from thirty to fourteen animals. CPV-2 disease evidently disappeared from Isle Royale by 1989, but the wolf population remained low until the mid-1990s.

Presently, CPV-2 is absent from Isle Royale, and a "no-pets" regulation instituted in 1978 remains in effect. Genetic "variants" of the CPV-2 virus are being recognized, and it should be noted that Isle Royale wolves (and many dogs) do not possess antibody protection against these newly appearing diseases.

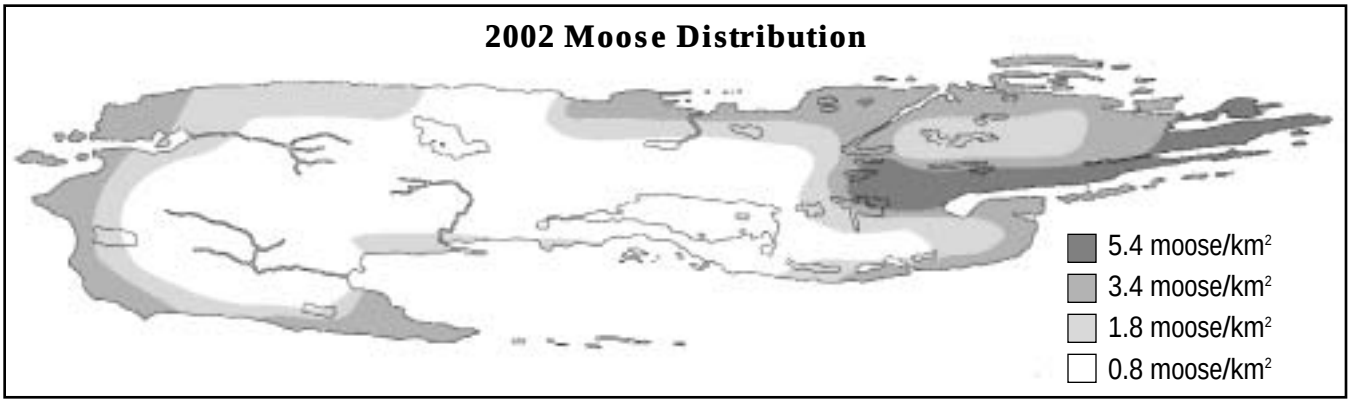

Figure 12. Moose distribution on Isle Royale during the aerial census in February 2002.

The Moose Population

During February 2002 the moose population was estimated at about 1,100 animals (+/- 95 percent confidence interval of 240), or 2.0 moose/km² (fig. 12). This compares to an estimated 900 moose in 2001 and 850 in 2000. Calves constituted 11percent of the 230 moose counted on census plots, slightly below the long-term average of 13 percent for Isle Royale moose (fig. 13). Variable calf abundance since the mid-1990s has been attributed to weather effects (snowy winters and hot summers), which can be pronounced in a high-density population (fig. 14).

Winter weather was very mild during the 2002 study, and snow depth was only 8 cm when the winter study began. Moose often congregated in small groups of up to six animals, and they were found on ridgetops in the island's interior, areas normally vacant of moose in winter. Fearing that moose sightability would deteriorate in the event of a major thaw, the annual moose count was begun about a week early, in late January, and most plots were counted before the usual movement of moose into conifer-dominated lowlands was completed (fig. 15). Under these "early winter" conditions, the number of moose on census plots on the west half of the island doubled, while the number on the east half dropped 25 percent. This raises the intriguing possibility that moose may routinely migrate between ends of the island (indeed, in the mid-1980s two out of 22 radiocollared moose did migrate from the west to the east end in winter).

With such unusual moose-counting conditions, the detection rate for moose (sightability) was assumed to be higher than the 75 percent norm (from tests with radio-collared moose during the 1980s). For the final estimate of 1,100 moose we assumed a detection rate of 85 percent, because the number of moose seen in level transect flights was approximately twice the usual level.

Undergraduate student researcher Kenneth Mills has completed a study of moose antler size and asymmetry on Isle Royale, using more than 100 skulls with antlers recovered during previous years of research (fig. 16). The wealth of comparative data from other populations provided some insight into the nutritional well-being of moose on Isle Royale. Antlers are secondary organs in which bulls can invest energy over and above that required for survival, so large antlers indicate a luxurious nutritional plane. Not surprisingly, antler size for Isle Royale moose was smaller than other North

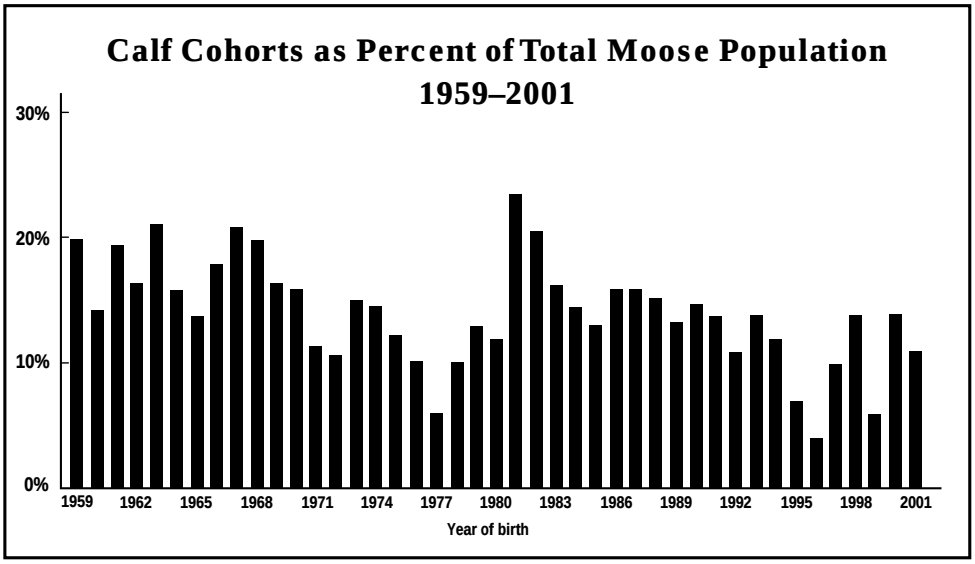

Figure 13. Moose calf abundance (at approximately six months of age) on Isle Royale, as a proportion of the total population. These are best estimates, a weighted mean of aerial counts in fall and/or winter.

Figure 14. Moose congregate at a mineral spring in May, where Isle Royale moose obtain scarce sodium (photo by Tim Laske).

Figure 15. In winter, moose normally abandon deciduous highlands and seek the cover of coniferous lowlands (foreground), where they subsist heavily on balsam fir. In 2002, many moose remained in deciduous cover until snow crusted in late February.

Figure 16. MTU student Ken Mills determines the symmetry of moose antlers by measuring their volume using water displacement (see figures 17 and 18).

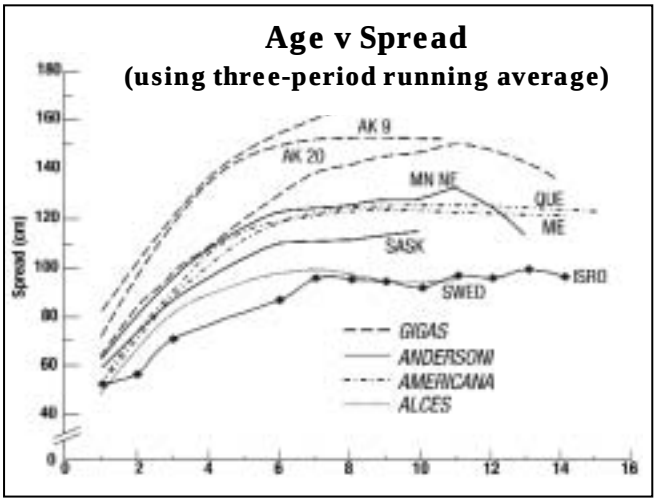

Figure 17. Moose on Isle Royale grow antlers similar in size to moose in Sweden, where moose density is also very high. The Isle Royale data are from moose that died of natural causes, so size of moose aged 1-6 years are not representative of the population. Other populations were sampled by hunters.

American moose populations, which all exist at lower population density (fig. 17). However, Isle Royale moose antler growth was similar to that of moose in Sweden, where moose density is also relatively high (often >1-2 moose/km^2). The maximum observed antler spread for Isle Royale moose was smaller than that measured in any other population around the world (fig. 18).

Low snow depth in 2002 meant that wolves had difficulty attacking their favorite targets, cows with calves (fig. 19). Calves comprised only six of 19 wolf-kills examined in winter 2002, about half the calf proportion observed in kills in 2001, when snow depth was near normal. In observations of six unsuccessful attacks on cows with calves in 2002, the wolves gave up almost immediately after meeting strong defensive behavior from kicking moose. Eight other unsuccessful attacks on adult moose were observed, when moose were little hampered by snow. The final portion of one successful attack on a cow moose was observed after wolves had already killed her calf (fig. 20).

Fat level in moose bone marrow from wolf-kills in 2002 was high for calves and low for adults (fig. 21). Current nutritional conditions for the moose population are probably best reflected by the calf levels, while the low fat levels in adults killed by wolves may indicate that wolves had to hunt hard for vulnerable adult moose—

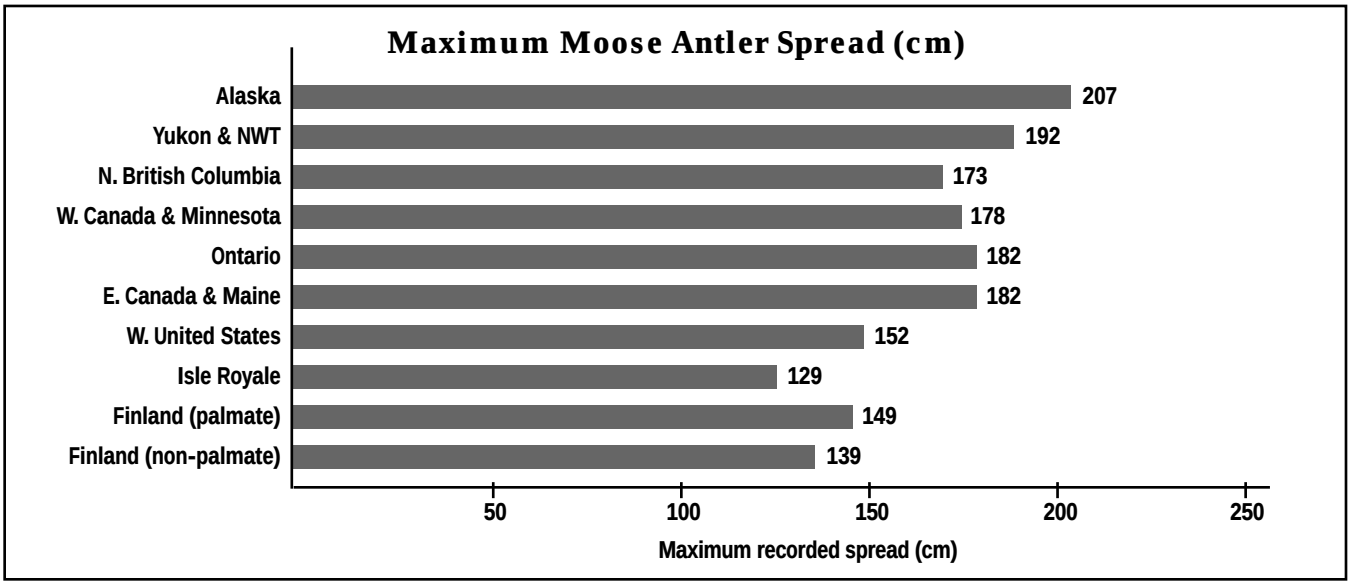

Figure 18. The antlers of Isle Royale moose are among the smallest of any moose population, a result of nutritional limitation. Comparative data from Gasaway et al. 1987, *Swedish Wildlife Supplement.*

Figure 19. Wolf abandons an aggressive cow moose that could kick easily in shallow snow.

Why Can't We Just Be Friends?

It was once common for wolf advocates to claim that wild wolves pose no threat to humans. However, in the past decade wolves have injured people in several places across North America, including Algonquin Provincial Park (Ontario), coastal British Columbia, southern Alaska, and Ellesmere Island.

Although the factors leading to attacks are not fully understood, it seems certain that wolves are likely to harm humans when the two species have lost their fear of each other. In Denali National Park, wolves have repeatedly stolen and damaged articles from camps while people are present, and in Algonquin, children have been seriously injured by "tame" wolves investigating campgrounds. People in sleeping bags on the ground, not in tents, may be particularly vulnerable to curious wolves that aren't overtly afraid of humans. At Isle Royale, wolf sightings by visitors have increased more than three-fold over the past four decades, and an article published in 2001 in a regional outdoor magazine described an Isle Royale kayaker sustaining minor injuries from a wolf bite while camping at a non-designated area along the shoreline. However, the animal involved could have been a fox, and, in any case, the canid retreated quickly. The incident was never reported to Park staff, and some details remain sketchy.

Throughout history, and in many parts of the world today, wolves' fear of humans has resulted from persecution—shooting, trapping, and poisoning. While maintenance of fear is highly desirable, violence toward wolves is not a goal of any park or reserve. Aversive conditioning, such as electric shocks or rubber bullets, is a possibility, though not an ethical or aesthetically pleasing one.

Wolves on Isle Royale have remained fearful of people, even after fifty years of total protection. What can be done to maintain mutual respect between wolves and people, to minimize the risk of wolf-inflicted injury?

At Isle Royale,

- ➤ Park managers should continue to limit visitor access to areas frequented by wolves through existing nighttime closures in parts of the island. No new restrictions are necessary, as the status quo, in place for more than 20 years, appears to provide wolves with enough space to avoid people.
- ➤ Visitors must pack out trash and dispose of fish entrails appropriately, so that wolves do not associate people with food.
- ➤ Upon seeing a wolf, visitors should resist the temptation to get closer and do nothing to entice the wolf to approach.
- ➤ Photographers wanting wolf pictures should visit places where long-distance photography is possible (Yellowstone), or where wolves live in captivity (International Wolf Center, Ely, MN). The dense forest cover at Isle Royale eliminates most opportunities for long-distance wildlife viewing.

Wolves do not need human friendship; they need wild lands. If there is an increase in wolf-human encounters on Isle Royale, the wolves will likely suffer more than the people. Recently, all wolves in North America that have injured humans have been killed.

Figure 20. (above) Alpha male and subordinate male packmate in fatal attack on cow moose that had just lost its calf to the pack, while (below) another cow moose, injured by wolves that killed her calf, eventually walked away to an uncertain fate.

only rare adults in poor condition were available.

Steven Monfort (Conservation Research Center, National Zoological Park) has analyzed winter fecal samples from cow moose at Isle Royale for progesterone hormone, indicating pregnancy status. We suspect moose on the island may have a low pregnancy rate because of chronic nutritional limitation. In 2000 and 2001 samples from 39 moose were analyzed, and only 54 percent were judged pregnant (>5 micrograms/gram of progesterone). We will continue collections in subsequent years to evaluate annual and spatial variation.

In the past five years we have examined skeletons and other remains from 380 moose that starved to death in 1996. Calves were particularly vulnerable during this time of desperate food shortage, but a surprising number of young and middle-aged adult moose also succumbed (fig. 22). For moose less than 13 years of age, more males than females died. Females predominated among moose 14 years and older. We expect that older moose already in physical decline were more vulnerable than younger adults, and heavy mortality of those old moose may be contributing to the current low numbers of wolves. Over the long term, the number of wolves on Isle Royale is best correlated with the number of old moose present.

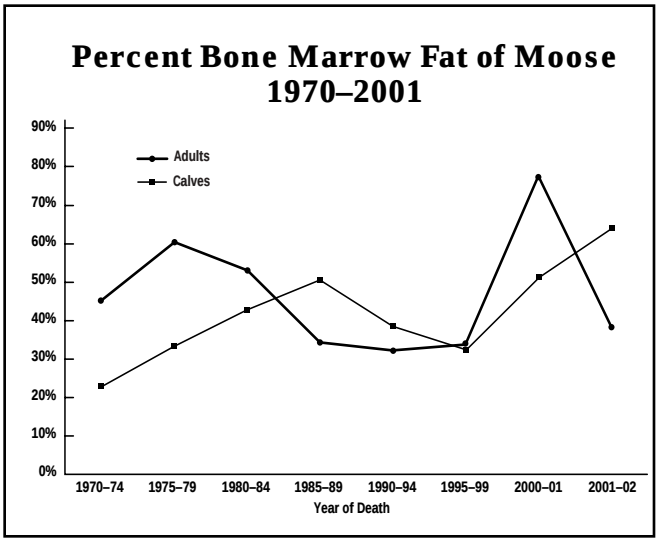

Figure 21. Long-term trends in moose bone-marrow fat. Data for calves (which best reflect current conditions) represent mean levels, whereas data for adults is the proportion with greater than 70 percent marrow fat.

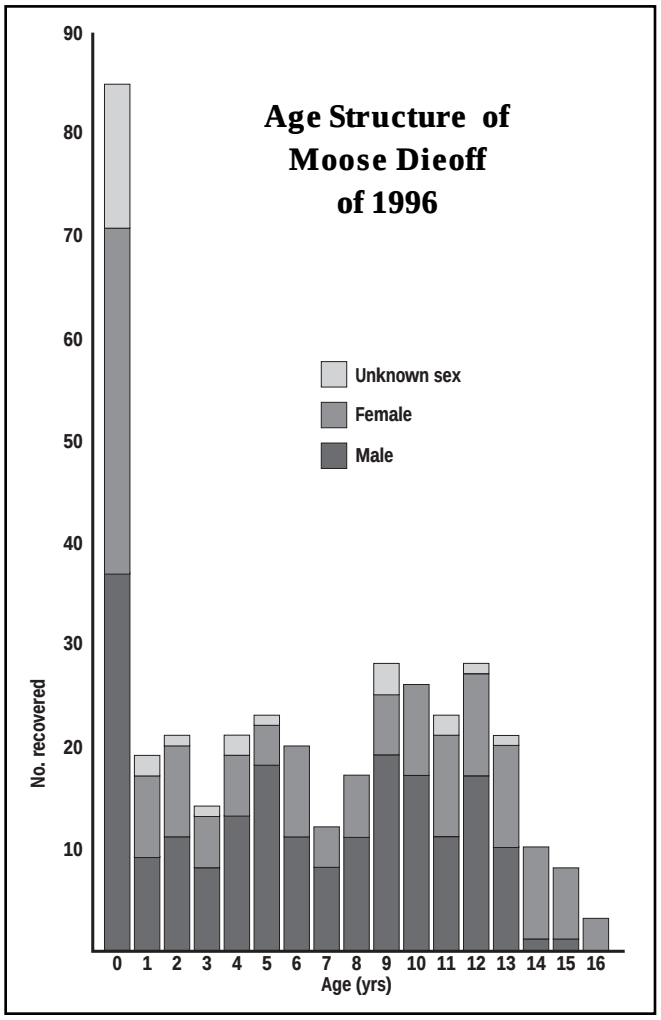

Figure 22. Age structure of 380 moose that succumbed in the catastrophic dieoff of 1996. Calves were very vulnerable, but moose of all ages likewise died.

Forest Vegetation

Foraging moose moved about freely during winter 2002 and were able to avoid the normal shortages in browse. A windstorm in December blew down many trees, and moose made frequent use of tree tops and lichens formerly out of reach. Balsam fir has dramatically declined in old forests at the west end of Isle Royale, where it is unable to regenerate because of heavy moose browsing. A sample of tagged balsam fir trees at the west end showed the highest mortality of the last 13 years (fig. 23). Annual mortality of these trees has averaged around 5 percent since measurements began in 1988, but in the six months prior to the 2002 winter study 16 percent of these trees were lost, primarily to wind.

Because of its singular importance to moose in winter, balsam fir has been a central focus of research in the past decade. In 2002, M.S. student Madeline Campbell will complete an analysis of fir demography. Various plots were established in the 1990s to monitor growth and survival of fir trees, which exhibit very different patterns at opposite ends of Isle Royale. At the east end fir exists at high density and grows normally into adult-sized trees, but at the west end fir is less abundant, more limited by lack of light under dense forest canopy, and almost never escapes from suppression by moose to grow into a reproducing tree (fig. 24). As the current canopy trees die out at the west end, after a century of moose browsing,

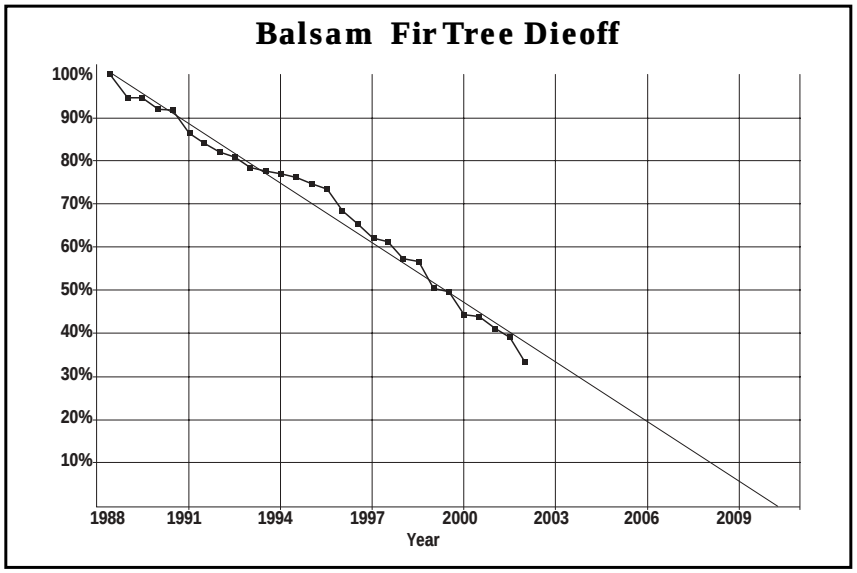

Figure 23. Balsam fir trees in the forest canopy that were tagged in 1988 have died off without replacement at a steady rate. The remainder are expected to die by approximately 2010.

Figure 24. Trees within a moose exclosure (left) erected in 1979 at the west end of Isle Royale (Windigo) have grown to normal stature, while the forest outside remains heavily suppressed by moose browsing (photo by John Vucetich).

the seed source for fir will likewise disappear, and the heavily browsed fir in the understory will slowly die out within a few decades. This tree species provided about 60 percent of winter forage intake for moose in the 1980s, so its gradual disappearance at the west end is certain to impact moose. Already, during the 1996 dieoff, moose at the west end were reduced more than at the east end, where ample fir sustained moose during desperate conditions.

So far, density of seedling fir at the west end has not diminished (fig. 25), so there is still an ample seed rain. Only a small fraction of one percent of all fir seeds successfully germinate, and it is not possible to predict how many seed trees are necessary to maintain the seed supply. There are many factors that will affect annual seeding of fir, such as irregular cone years, squirrel harvest of most cones, secondary dispersal across snow and ice, germination substrate, and availability of light.

Forest fires started by lightning are allowed to burn at Isle Royale, providing fire danger is not extreme. In August 2001, one naturally ignited fire burned about 5 ha in a jack pine stand at the east end of the island. This was the largest natural fire since 1988.

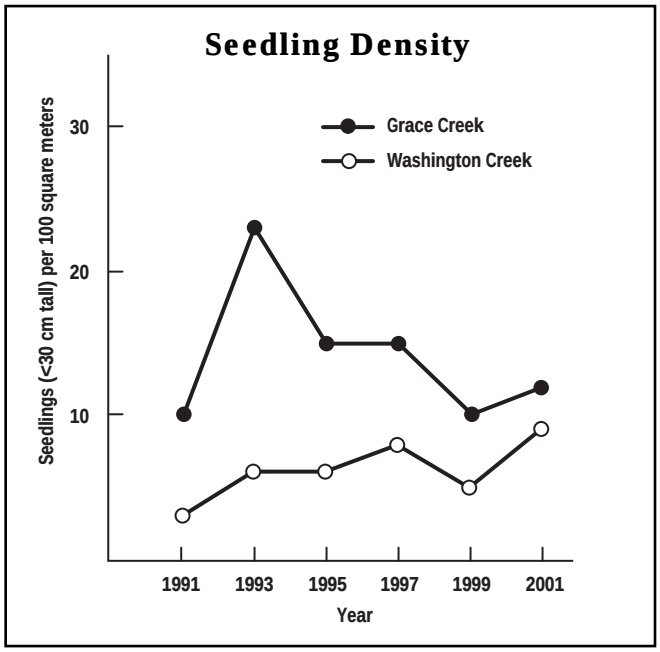

Figure 25. In spite of a disappearing seed source as balsam fir in the canopy die out at the west end of Isle Royale, seedling density has been maintained. That situation should change dramatically within a decade.

Figure 26. Trevor Peterson examines a decades-old eagle nest on Hat Island that crashed to the ground in August, 2001, after the supporting white pine snapped off in a windstorm. The fate of the resident eagles was unknown, but the young eagles had already fledged.

Other Wildlife

The National Park Service conducts aerial and ground surveys of osprey and bald eagle nests each summer. There was little change in the number of nest sites counted in 2001 when compared to the previous year. Eagle nests dropped from 12 to 11, with 11 young fledged (fig. 26). The number of osprey nests was unchanged, at seven, with seven young fledged.

Snowshoe hares were more frequently seen in 2001, but other signs suggested that their numbers may be dropping, consistent with a cyclical decline in the region (fig. 27). Two goshawks (hare predator rarely observed in winter at Isle Royale) were observed in winter, but the number of fox observations declined to very low levels (fig. 28).

Otters became quite common at Isle Royale during the 1990s (fig. 29), apparently gaining ground as lake herring rebounded over a decade ago. Double-crested cormorants also increased at this time. Both cormorants and herring diminished in the late 1990s, but otters have remained at high levels.

Marten tracks were observed in two sites near Windigo in winter, 2002. This carnivore species is a recent arrival to Isle Royale that has remained very rare, probably because prey are scarce. Only one observation of marten and a questionable photo have been recorded in the past decade.

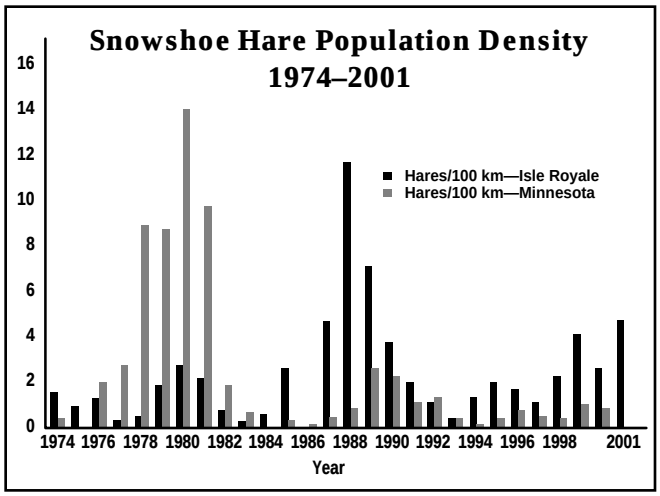

Figure 27. Relative snowshoe hare density reaches a peak about every 10 years, both at Isle Royale and on the mainland in Minnesota. Counts were made at Isle Royale during all hikes in May-August, while hares were counted in Minnesota on routes used to count drumming ruffed grouse in spring (Minnesota Department of Natural Resources, with thanks to William E. Berg).

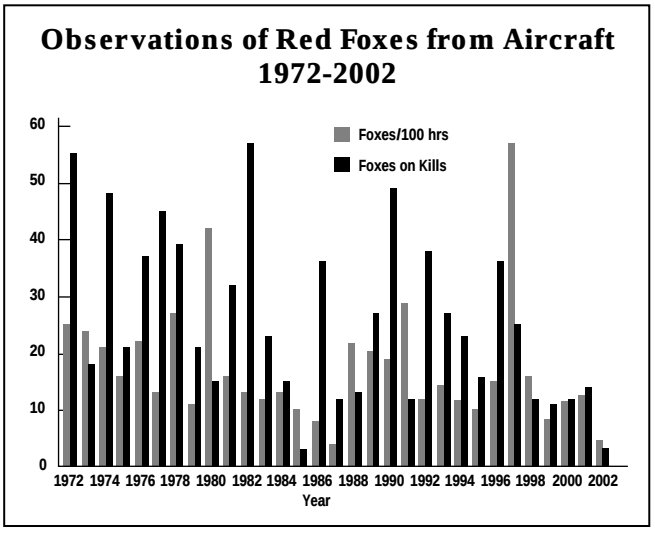

Figure 28. Relative abundance of red foxes from aircraft observations in winter, 1972-2002. Grey bar is the number of foxes seen away from moose carcasses/100 hours, while the black bar is the number of foxes seen on carcasses.

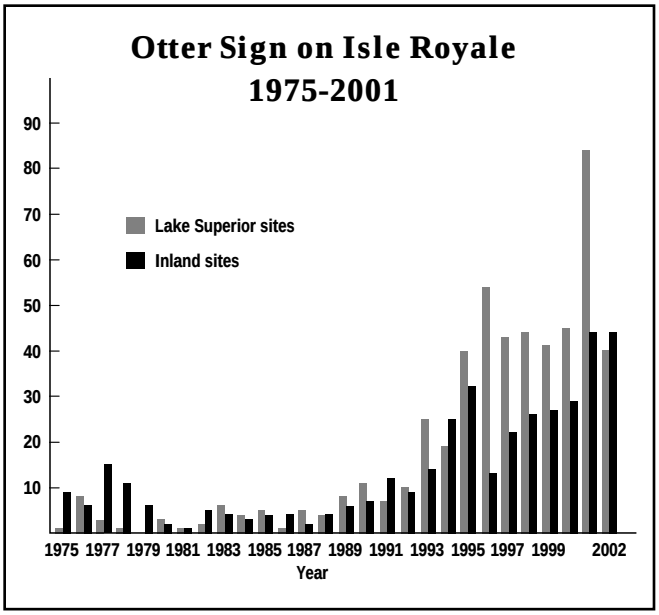

Figure 29. Otters have recently become quite abundant on Isle Royale, especially when lake herring in Lake Superior were briefly abundant in the early 1990s. They have persisted, while cormorants and herring again became scarce in the late 1990s.

Weather, Snow, and Ice Conditions

Shoreline ice on Lake Superior was almost entirely lacking during the winter study, 2002, and only 10 cm of harbor ice was found at Windigo when the study began. The small survey aircraft could land safely on January 12 with Peterson and Glaser aboard, but another week passed before there was sufficient ice (20 cm) to land the heavier U.S. Forest Service Beaver aircraft with additional personnel and supplies. At no time was an ice bridge to the mainland present.

Snow depth was only 13 cm when the winter study began, and for most of the study period only 20-30 cm of snow was recorded (fig. 30). This was the lowest amount of snow observed in 44 years of annual monitoring. Low snow fundamentally altered wolf-moose relationships. Freeze-thaw crusts formed when temperatures rose in February (fig. 30), forcing moose into their usual wintering locales. In March, after the end of the 2002 study, more snow fell than in the previous four months.

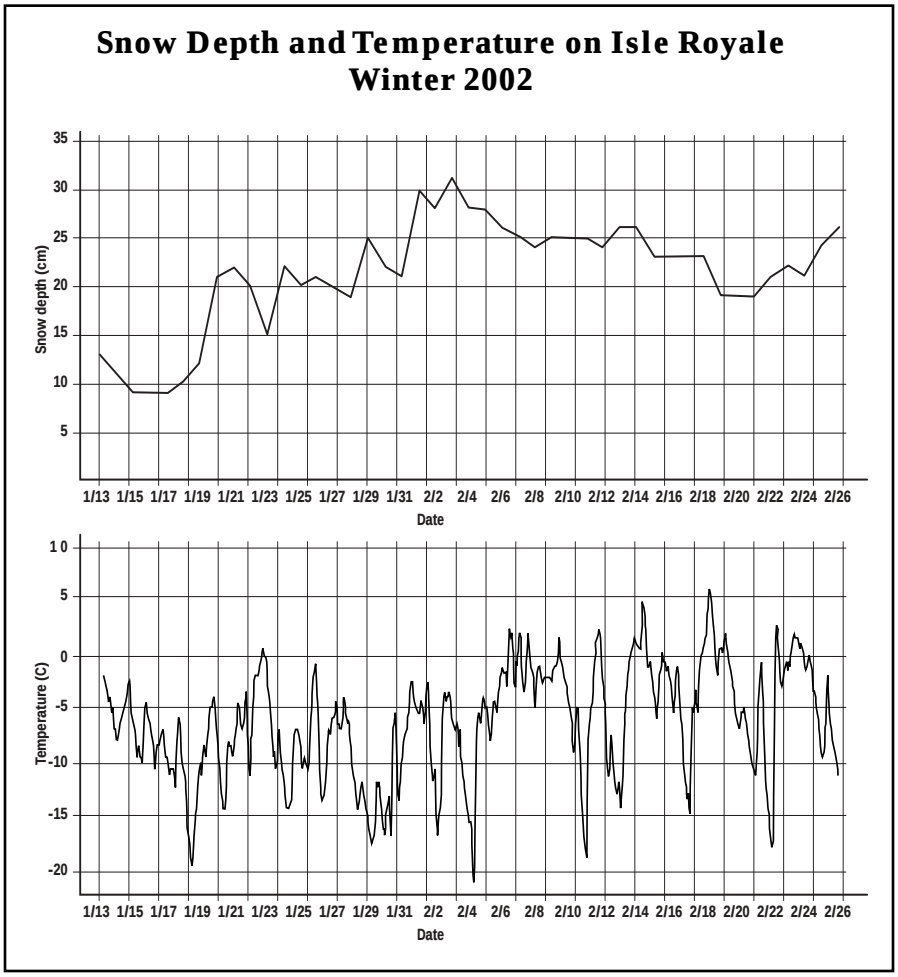

Figure 30. Snow depth (daily) and ambient temperature (hourly) during the 2002 winter study on Isle Royale.

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THANK YOU to all who help!