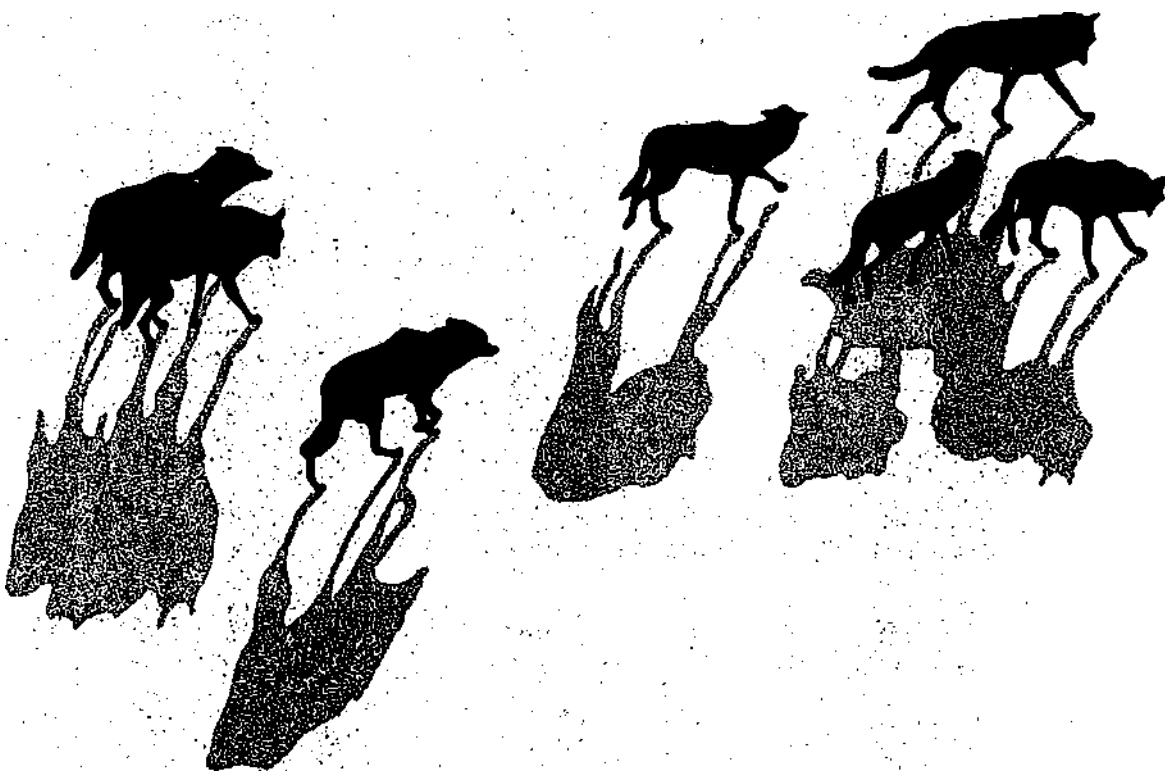


Ecological Studies of Wolves on Isle Royale

Annual Report
1992-1993



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Annual Report—1992-1993*

by

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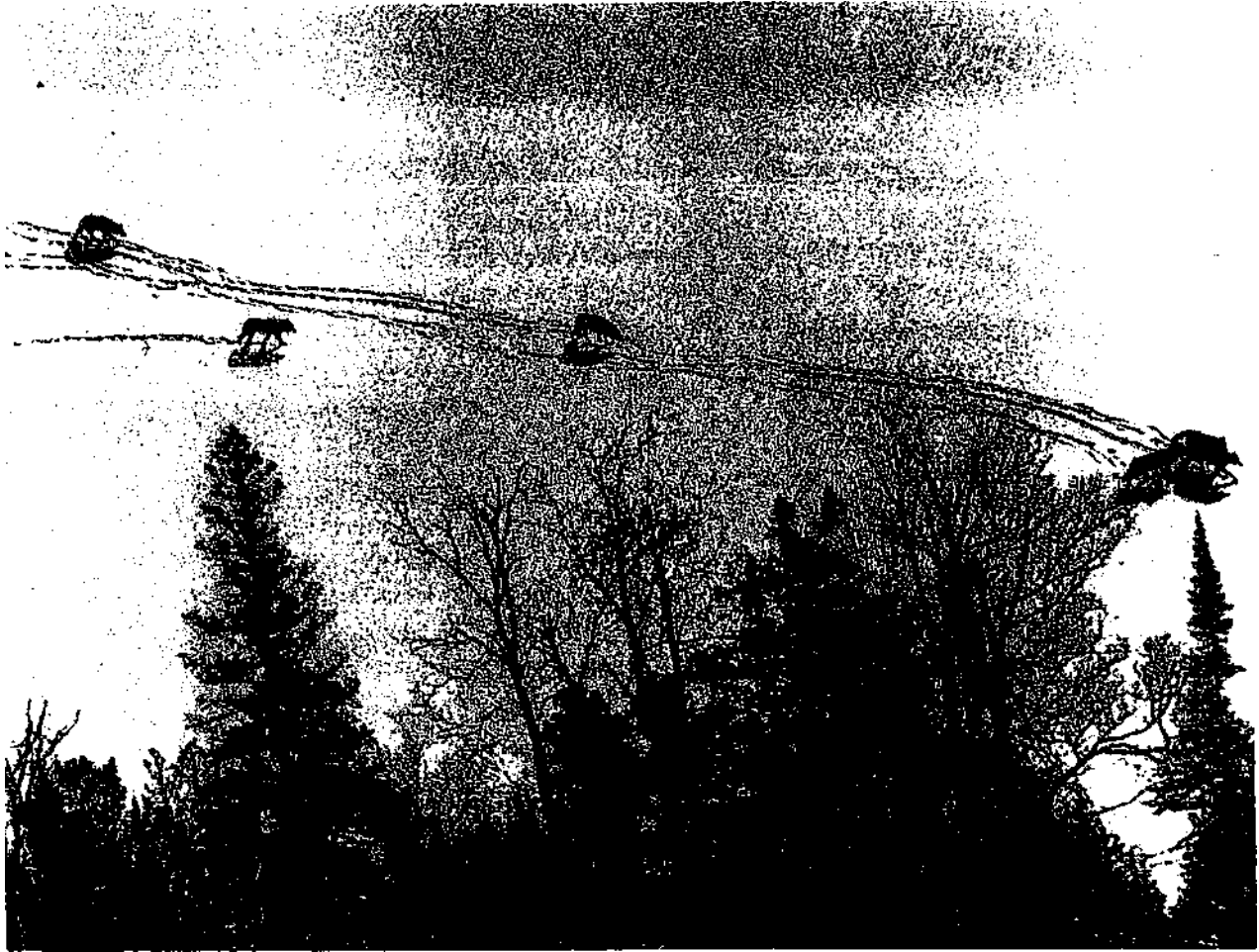
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(Results reported here are preliminary, and in some cases represent findings of collaborators; please do not cite without consulting the author.)

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"All over the planet we must decide, deliberately or casually, whether to kill the things that formed us and that, I believe, still keep us alive. We are not gods by a long shot, but, by chance, we live at a time when we can make godlike mistakes" ... Charles Bowden

Personnel and Logistics

In summer 1992 Rolf Peterson directed ground-based field work, aided by Julita K. Bakiera, Daniel J. Fehringer, Christian L. J. Fink, Mary L. Hindelang, Timothy G. Laske, Brian E. McLaren, Carolyn C. Peterson, Jeremy D. Peterson, and John A. Vucetich. Radio-collared wolves were tracked with air support from Isle Royale Seaplane Service.

In 1993 the annual winter study extended from January 14 until March 2. Peterson and pilot Don Glaser participated in the entire study, assisted by graduate students Brian E. McLaren and Mary L. Hindelang, and the following personnel from Isle Royale National Park: Robert K. Whaley, David C. Soleim, Elizabeth J. Amberg, Stuart L. Croll, Larry A. Kangas, Norman T. Lindsay, Theodore J. Hillmer, Jr., and Jack G. Oelfke.

Summary

In 1992-1993 moose continued to increase and the wolf population remained almost unchanged (Fig. 1). Only 13 wolves were present early in 1993, including two pups in one pack. As only one wolf died in the past year, reproduction was sufficient to maintain wolf numbers. The single reproducing pack increased to seven members, whereas the other two packs remained at two wolves each. Only one lone wolf survived the recent winter. Between the 1992 and 1993 counts, one lone wolf died of unknown causes, and after the 1993 count another lone wolf was killed by the two-member West Pack II. Three females, one in each pack, were in breeding condition and courted by males in 1993. Only one of these pairs has successfully raised young since 1988, however, and population growth is limited by poor reproduction.

In the past 5 years wolf exposure to canine parvovirus appears to have diminished; there is no evidence that disease is contributing to low reproductive success on Isle Royale. Wolf food supply is now expanding rapidly, as large cohorts of moose born in the early 1980's reach a vulnerable age. Reduced genetic variability and a high degree of relatedness among the wolves suggest that inbreeding depression has led to an unusually low reproductive rate. New outbreaks of disease and total loss of females are now the greatest immediate risks facing the wolf population.

The moose population continued to grow in the past year and is now at its highest level in almost 60 years. Coincident with a late spring in 1992 was notable mortality from malnutrition, primarily among old adults and calves born in 1991. Continued expansion of the moose population appears likely.

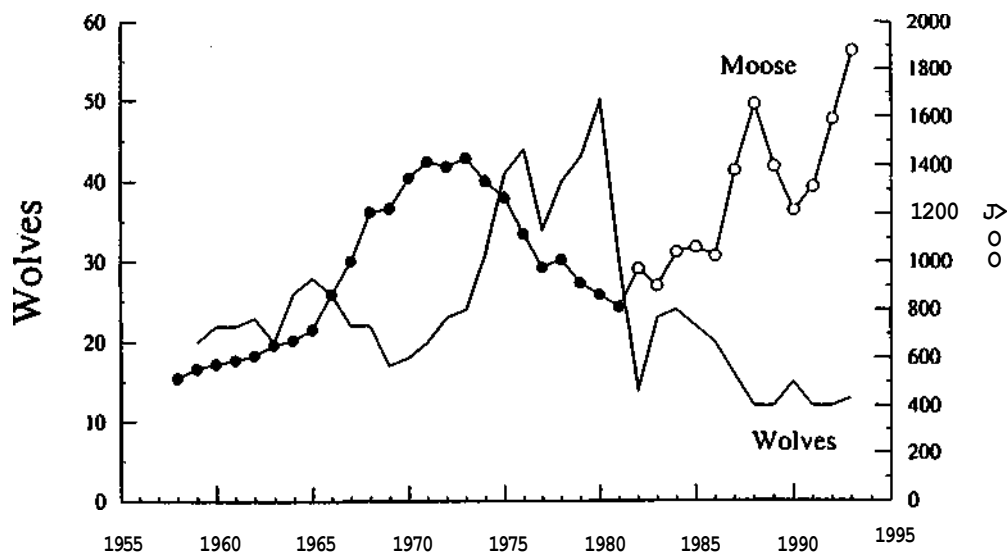


Figure 1. Wolf and moose fluctuations, Isle Royale National Park, 1959-1993. Moose population estimates during 1959-1981 are based on population reconstruction from recoveries of dead moose, whereas estimates from 1982-1993 are based on aerial surveys.

The Wolf Population

In 1993 the wolf population was organized as follows:

450 Pack - 7
550 Pack - 2
West Pack II - 2
Loners - 2
1993 total-13

In 1993 five radio-collared wolves remained.

Female 450, alpha female of the 450 Pack, probably at least nine years old; *Male 430*, born in 1989 in the 450 Pack, now the beta male in this pack; *Male 550*, born in 1988 in the West Pack II, now alpha male of the 550 Pair; *Male 420*, at least nine years old, since 1987 the alpha male of the West Pack II; *Male 470*, probably at least nine years old, remained a lone wolf in 1993 after the death of female 590, his last companion (Fig. 2).

Five of six wolves that have recently died were believed to have been females, leaving only three known females among 10 wolves of known sex. One pup and one yearling are of unknown sex. During the 1993 winter study the West Pack II killed one lone wolf, probably a female born in 1989 at the east end of the island. In the past year a lone wolf with expired radio-collar, female 590, died of unknown causes.

The only reproducing female wolf (450) is estimated to be 9-13 years old. The future of the wolf population will eventually hinge on the reproductive performance of the six "young" wolves—those less than 5 years old. Five of these wolves originated in the 450 Pack, and at least four of the six are males. In 1993 an attempt will be made to live-capture and radio-collar additional young wolves for subsequent monitoring (Fig. 3).

Wolf numbers were maintained through low reproduction matched by equally low mortality (Fig. 4). With the addition of 2



Figure 2. Aged male 470, who has outlived all the eligible and available females on Isle Royale. Even as a loner, he associated with females during each breeding season until 1993, when he was the only lone wolf remaining.



Figure 3. The future of Isle Royale wolves will depend on these young wolves in the 450 Pack, 2 pups (rear) and a yearling (foreground).

Wolf Retribution?

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The behavior of wolves, compared to many other species, is rather well understood, yet the unpredictability of wolves in the wild remains fascinating. At the end of the 1993 winter study, we were again reminded of the limits of our ability to understand these complex animals. On Feb. 26, in our last week of observations, the 550 Pair discovered in their territory fresh tracks of the 450 Pack, which had trespassed 2 km into the Pair's territory and then quickly returned to their own area. Such minor trespassing is fairly common, and we considered it a minor matter. Two days later, however, we watched the Pair returning from their own foray into the 450 Pack's territory. The Pair was traveling as fast as possible, which was difficult for two reasons—the snow was chest deep, and the wolves' sides were distended from a recent gorging. Frequent scent-marking and quick over-the-shoulder glances indicated their agitation. Finally, 10 km into their own territory, they flopped onto their sides and slept, motionless, for the rest of the day. Backtracking these wolves, we were surprised to find that they had not only trespassed a distance of 15 km but had also killed a moose in the center of the 450 Pack's territory. This was the most significant trespass we had seen in more than a decade on Isle Royale. The behavior was unusual for the Pair, which had appeared almost lethargic during the previous six weeks. (They had had no trouble killing moose and had remained for two weeks at each carcass.) Why, all of a sudden, were they so quick to respond to the actions of their neighbors, if indeed that is a correct interpretation? This was the last flight of our winter study, and the 450 Pack would not become aware of their neighbors' trespass until after our departure. We could only guess whether both parties in this territorial contest would now consider the matter "a draw".

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pups, the 450 Pack increased to seven members, while the other two territorial packs each contained only a pair of wolves. West Pack II alpha male 420 was quite sedentary at one site in June, and last September a visitor observed a pup-sized canid nearby, but if a pup was born it did not survive to winter.

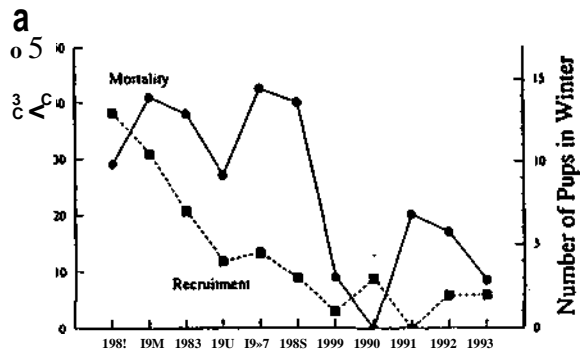


Figure 4. Wolf annual mortality and reproductive success on Isle Royale, 1983-1993.

Mortality between the 1992 and 1993 counts was limited to female 590, a lone wolf whose radio-collar expired early in 1992. No

trace of this aged wolf was found during the 1993 winter study, and her frequent companion, male 470, remained alone throughout the 1993 breeding season.

One of the 13 wolves counted in 1993 was killed by the West Pack II in February. The victim, a three-year-old lone wolf, had dispersed from the 450 Pack at the east end of Isle Royale two years ago. Bone marrow of this wolf was partially fat-depleted (34% fat) (Fig. 5). Just after we discovered the dead wolf, the West Pack II alpha female embarked on an unusually extensive solo patrol of her territory, and from this we surmised that she had killed the lone wolf, presumably another female.

In 1993 the wolf population was organized into three territorial packs (Fig. 6). Following a minor trespass by the 450 Pack, the 550 Pair traveled far into 450 Pack territory and killed a moose (see page 5); there was little reason to attribute this spatial overlap to food shortage.



Figure 5. Only a few bones remained from a wolf killed by the West Pack II in February 1993. Foxes were probably responsible for the complete scavenging.

Predation rates for all three packs were similar to those of previous years (Fig. 7), and wolf utilization of their kills was moderate (most kills were abandoned with skeleton disarticulated but lower legs intact).

Alpha females in all three packs were in synchronous estrous during the third week of February, indicated by vaginal bleeding and close tending by alpha males. Mating was thus likely in three pairs, although none was observed. At the east end of the island, subordinate male 430 and the uncollared alpha male both courted alpha female 450, but 430 was rebuffed by the alpha female and strongly discouraged by the alpha male (Fig. 8).

In the 1980's a chronic decline threatened the wolf population with extinction, prompting more intensive research. The population comprised 19 different wolves since 1988, and 12 of these remained alive in March 1993. Ten of the 19 wolves have been live-captured, blood-sampled for disease and genetic studies, and radio-collared. High mortality prior to 1988 clearly endangered the population, but since 1988 mortality has been very

low. Reproduction must improve, however, if the wolf population is to recover. Current assessment of three possible explanations for the wolf decline follows.

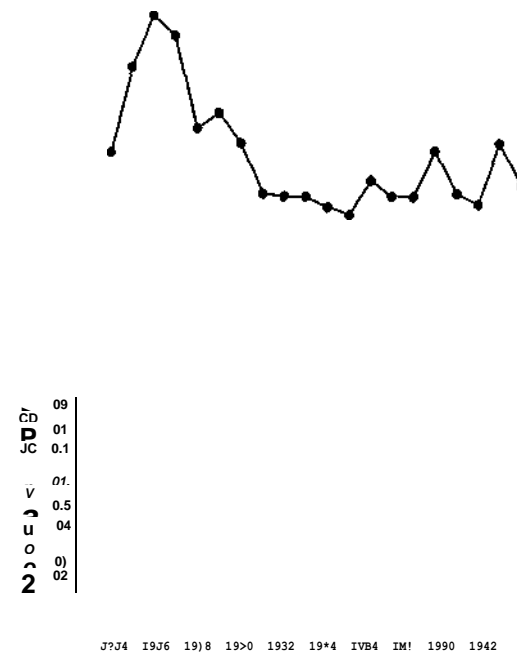


Figure 7. Moose mortality rate in 1993 was similar to that seen in the 1980's.

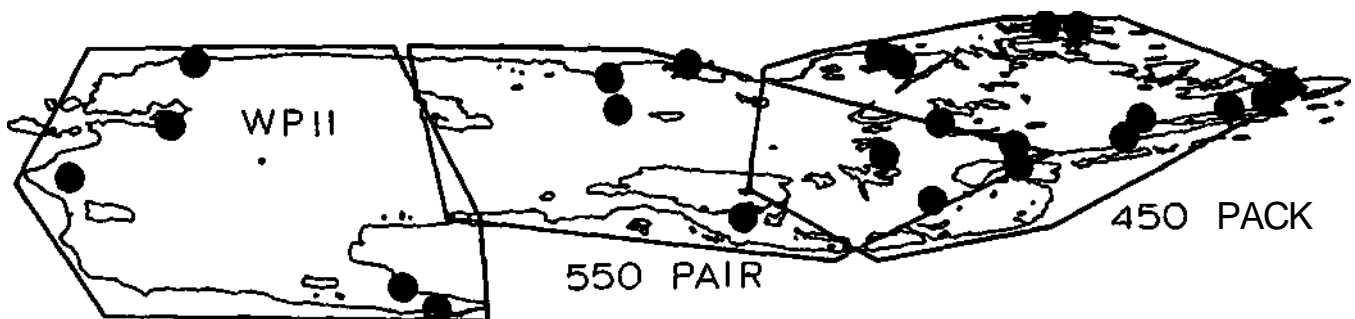


Figure 6. Wolf pack territories and moose carcasses during the 1993 winter study. WP II (West Pack II) and 550 Pack were just alpha pairs (male and females), while the 450 Pack contained seven wolves.

The Moose Population

An upward trend in the moose population continued in 1993 and exceeded levels observed in the past 60 years. Although calf production was low (Fig. 10), probably because of poor nutrition (Fig. 11), it was sufficient to compensate for mortality. Continued growth in moose numbers can be expected.

An aerial census of moose was conducted in February, 1993, by means of intensive counts of small plots totaling 20% of the island area (Fig. 12). On these plots 342 moose were counted, and we estimated 75% of the moose on the plots were seen. The resulting estimate was 1,880, with a 95% confidence interval of ± 320 . This is the highest census-based estimate for Isle Royale moose ever obtained (Fig. 13); moose were probably more numerous in the late 1920's and early 1930's, but population size then could only be crudely estimated from ground-based fieldwork. Spring temperatures in 1992 were unusually cold, and snowmelt was correspondingly late. In the course of spring and summer fieldwork, including 607 km off-trail hiking, we found 17 carcasses of moose that died of malnutrition, the largest single cause of death. This was the largest such die-off we have seen since the early 1970's. Considering our level of sampling and the high moose population, the pro-

portion that died from malnutrition was probably less than 5% of the total population.

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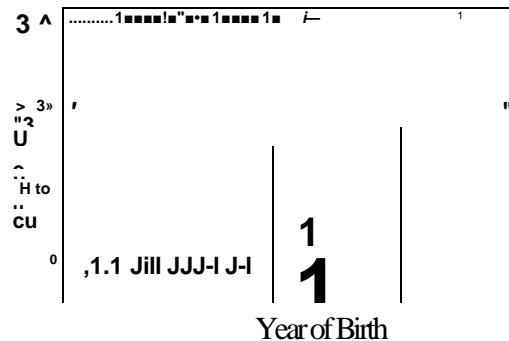


Figure 10. Moose calf abundance (at approximately six months of age) on Isle Royale, as a proportion of the total population. These are single best estimates, the mean of all available counts for each cohort (summer ground observations and aerial counts in autumn and winter).

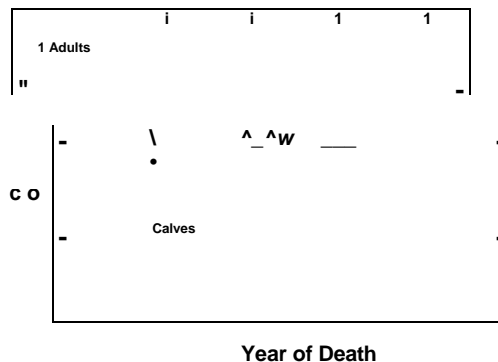


Figure 11. Long-term trends in moose bone marrow fat. Data for calves (which best reflect current conditions) represent mean levels, whereas adult data is the proportion with <70% marrow fat.

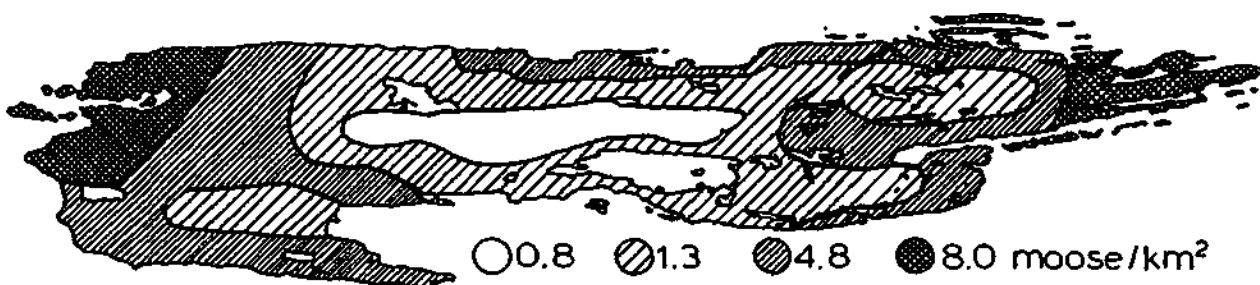


Figure 12. Moose distribution on Isle Royale during the aerial census in February, 1993.

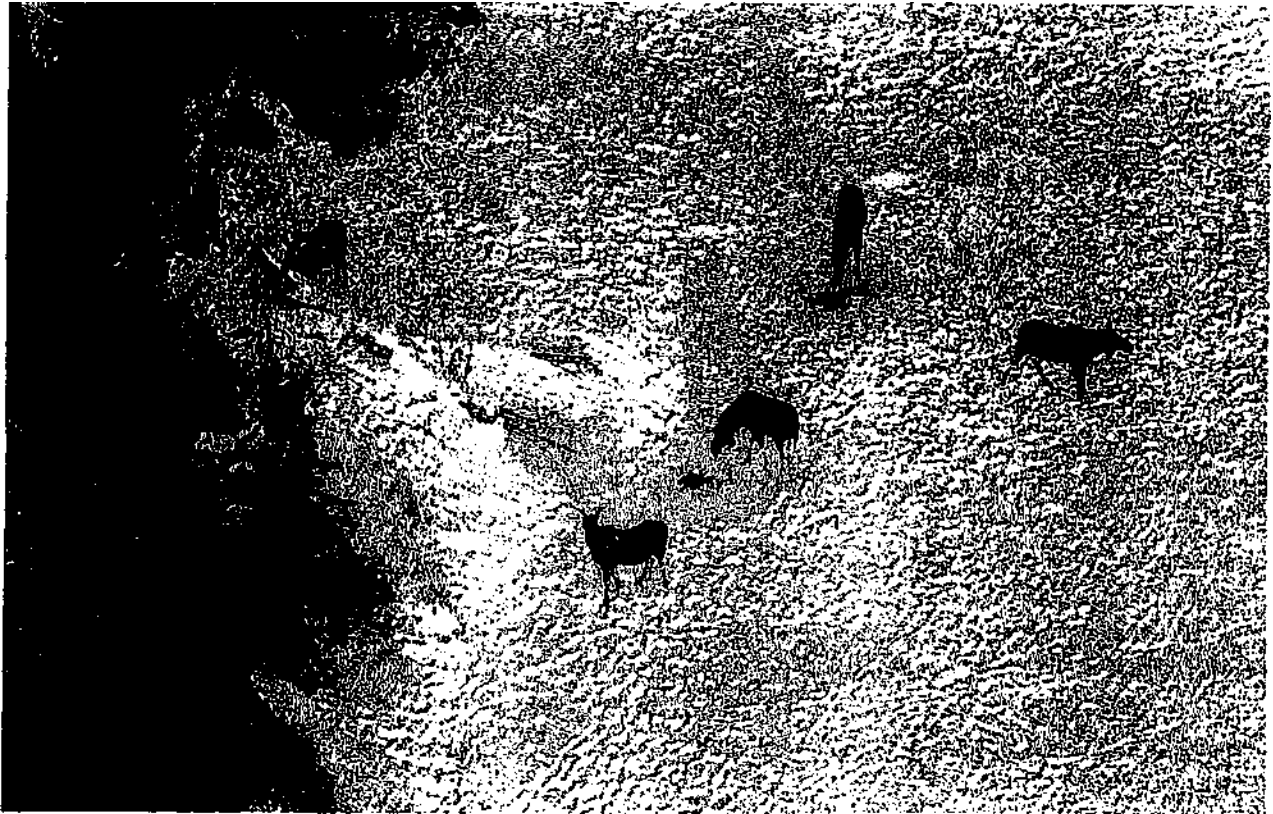


Figure 13. Moose density on Isle Royale has now reached its highest level in almost 60 years. These moose congregated at a sodium spring at Hidden Lake in February.

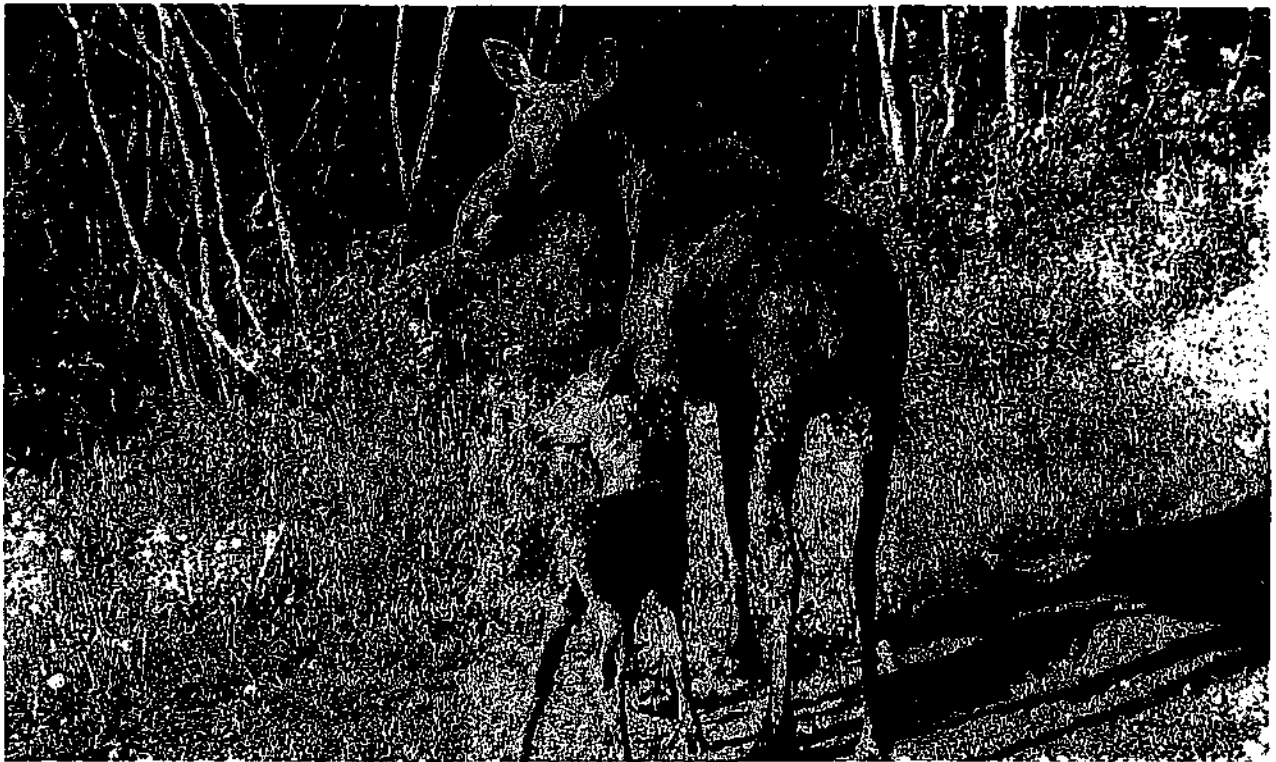


Figure 14. Calf production in 1992 was very low, probably a response to resource shortage resulting from high population density.



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Figure 15. In recent years most Isle Royale moose in spring have lost much of their hair to the ravages of the winter tick.

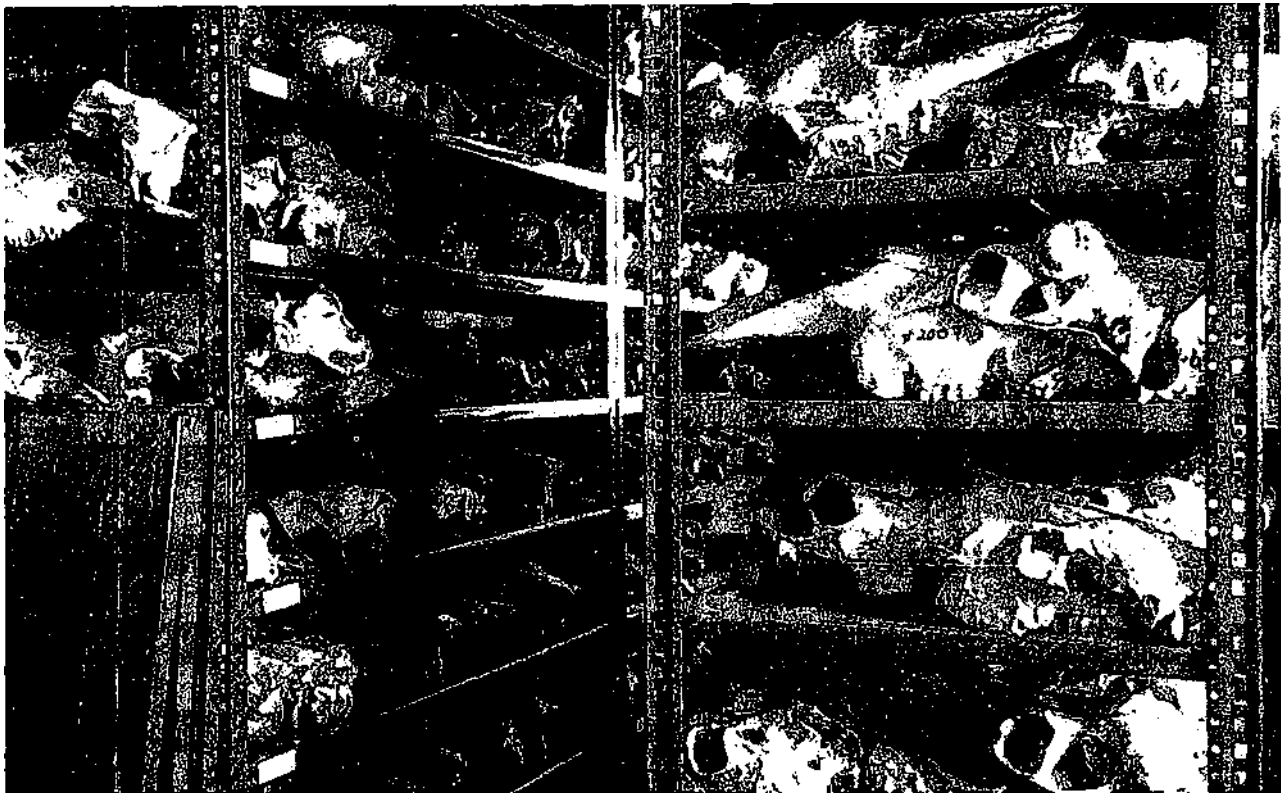


Figure 16. Final resting place for about 40% of Isle Royale moose is a "moose-oleum" maintained by Michigan Technological University at the Ford Forestry Center, probably the world's largest collection of moose skeletal material.

Only 11 calves were observed during 1992 fieldwork, out of a total of 227 moose observations (Fig. 14). Correcting for uneven sex ratio in this sample, summer calf proportion was estimated to be only 6%. Calves constituted 14% of the moose counted on plots in winter, 1993, but census coverage was highest in shoreline areas where cows with calves are concentrated. The weighted average of both counts, 11 % calves, is relatively low compared to earlier years.

A year ago, calves were highly vulnerable to wolf predation, and we thought that the moose population might be stabilized. However, moose estimates have continued to rise. The moose population is growing increasingly older and, as moose density continues to rise, the likelihood of a die-off from malnutrition or effects of winter ticks will increase. Future weather patterns will be important, as winter severity will dictate the extent of malnutrition losses, and springtime temperature may influence tick populations (Figs. 15 and 16).

Anticipating future increase in the already high moose population of Isle Royale,

ongoing studies of moose condition and moose-vegetation interaction take on special significance. It has become evident that moose populations on the two ends of Isle Royale, separated by vacant habitat in the 1936 burn, may be fundamentally different. End-to-end differences in moose-vegetation interaction are suggested by the appearance of balsam fir, a major source of winter forage for moose (Figs. 17 and 18). At the two ends of Isle Royale

40 cm		1	1	1
West	;	East		
30 cm		1		
20 cm	1			
10cm		1		

Figure 18. End-to-end differences in balsam fir are readily evident in the height distribution of trees in the forest overstory.



Figure 17. Balsam fir trees at the eastern end (right) of the western end (left) are heavily suppressed.



Royale grow almost unaffected by moose, while trees at

there also appear to be differences in moose urea excretion in winter, determined from snow-urine sampling. There are also differences in stable nitrogen isotopes determined from both snow-urine samples and moose teeth. Results of recent aerial censuses suggest that moose population trends are different on the east and west portions of the island (Fig. 19). We can no longer consider Isle Royale moose to be a single, homogeneous population.

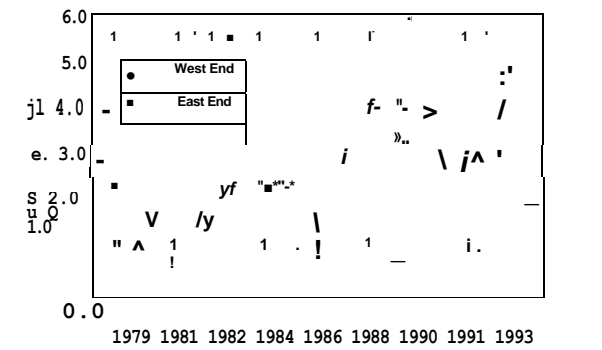


Figure 19. Census data suggest that in the last decade moose density on the east end of Isle Royale has increased more rapidly than on the west end.

Other Wildlife

Beaver colonies were censused by Douglas W. Smith in 1992, continuing a monitoring program begun by Philip C. Shelton in 1962. Results of the complete count of colonies revealed that beaver numbers have continued to slowly decline, although they remain higher today than in 1980, when high wolf predation probably suppressed beaver numbers (Fig. 20). The current slow decline can be attributed to habitat exhaustion, although wolf predation is probably important. For the first time since surveys began, no beaver colonies were recorded on Lake Superior shorelines.

Indices of red fox and snowshoe hare abundance again declined in 1992, following a hare peak in 1988 (Figs. 21 and 22). Foxes rely heavily on hares for food, and they were relatively abundant throughout the period of high hare numbers (Fig. 23).

Sign of river otters has continued to become more abundant in winter. Observations of otters during summer months are no

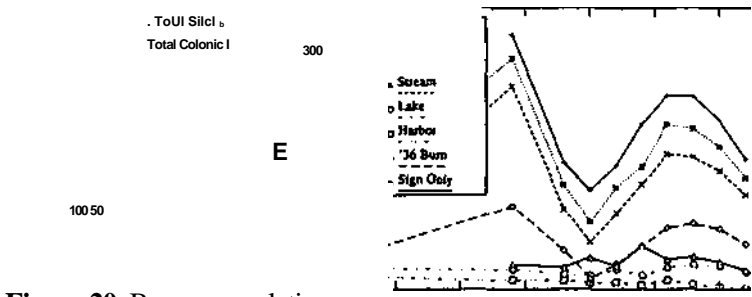


Figure 20. Beaver population trends on Isle Royale, by specific habitat.

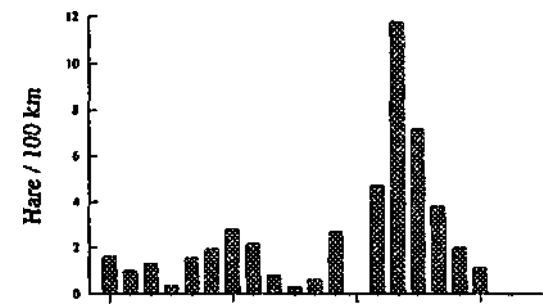


Figure 21. Snowshoe hares on Isle Royale have continued to decline from a historic high level in 1988. Index is the number seen per 100 km hiked in summer.

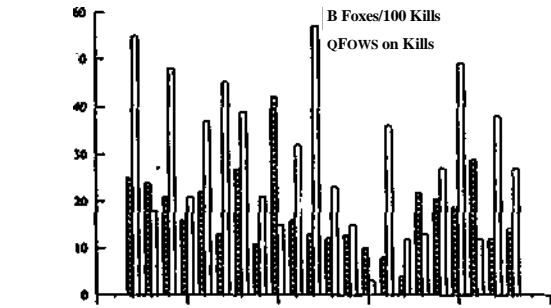


Figure 22. Relative abundance of red foxes from aircraft observations, 1972-1993. Hatched bar is the number of foxes seen away from moose carcasses/100 hours, while the open bar is the number of foxes seen on carcass

longer rare (a family spent several days under our research cabin), and track records from winter surveys indicate that otters are well distributed throughout the island. Most winter sign is along the Lake Superior shoreline, especially where open water persists through the winter.

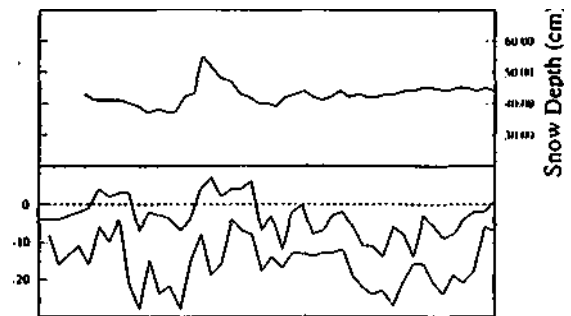
Recovery of bald eagle and osprey populations on Isle Royale has continued, although breeding populations of both species are still very low. In 1992 National Park Service staff recorded 4 active eagle nests, probably fledging a total of 3 young, along with 2 successful osprey nests in which 4 young were produced. During the past winter several bald eagles remained around the Isle Royale shorelines.

Weather, Snow, and Ice Conditions

After a relatively cold summer in 1992 Lake Superior water temperature was low at the beginning of winter. High winds early in winter prevented ice cover, however, and there was little shoreline ice early in the 1993 winter study period. A cold, calm period in mid-Feb-

ruary allowed a flimsy ice connection to the Ontario mainland, but it was lost in high winds 3 days later and never again developed.

Snow depth was lower than average through the 1993 winter period and never interfered with moose movement. Crusting conditions, which restrict moose mobility, were rarely persistent (Fig. 24). Spring weather was very cold, however, and a delayed snowmelt and "greenup" in 1993 might lead to additional moose mortality from malnutrition.



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January February

Figure 24. Snow depth (top) and temperature extremes during the 1993 winter study on Isle Royale.

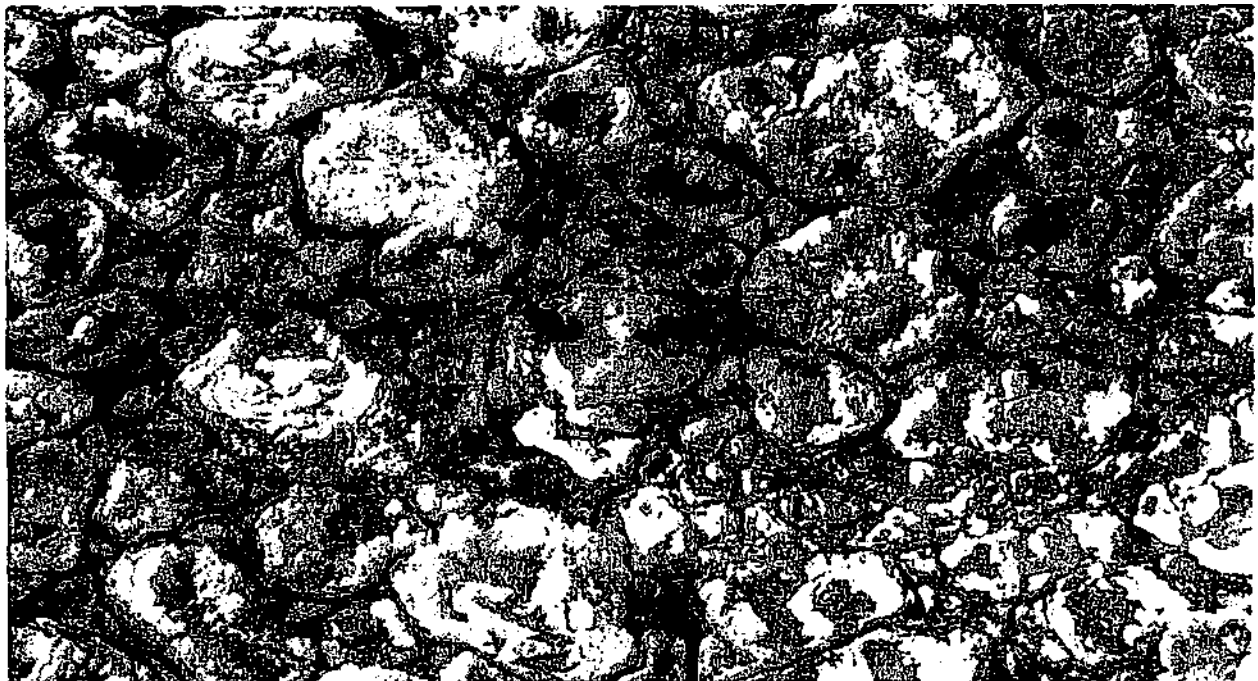


Figure 23. Look carefully in the middle of the photo for 2 foxes on a "pancake" of floating ice. Foxes rarely choose to be in such close proximity to each other, and both soon scampered across the ice pack to shore.

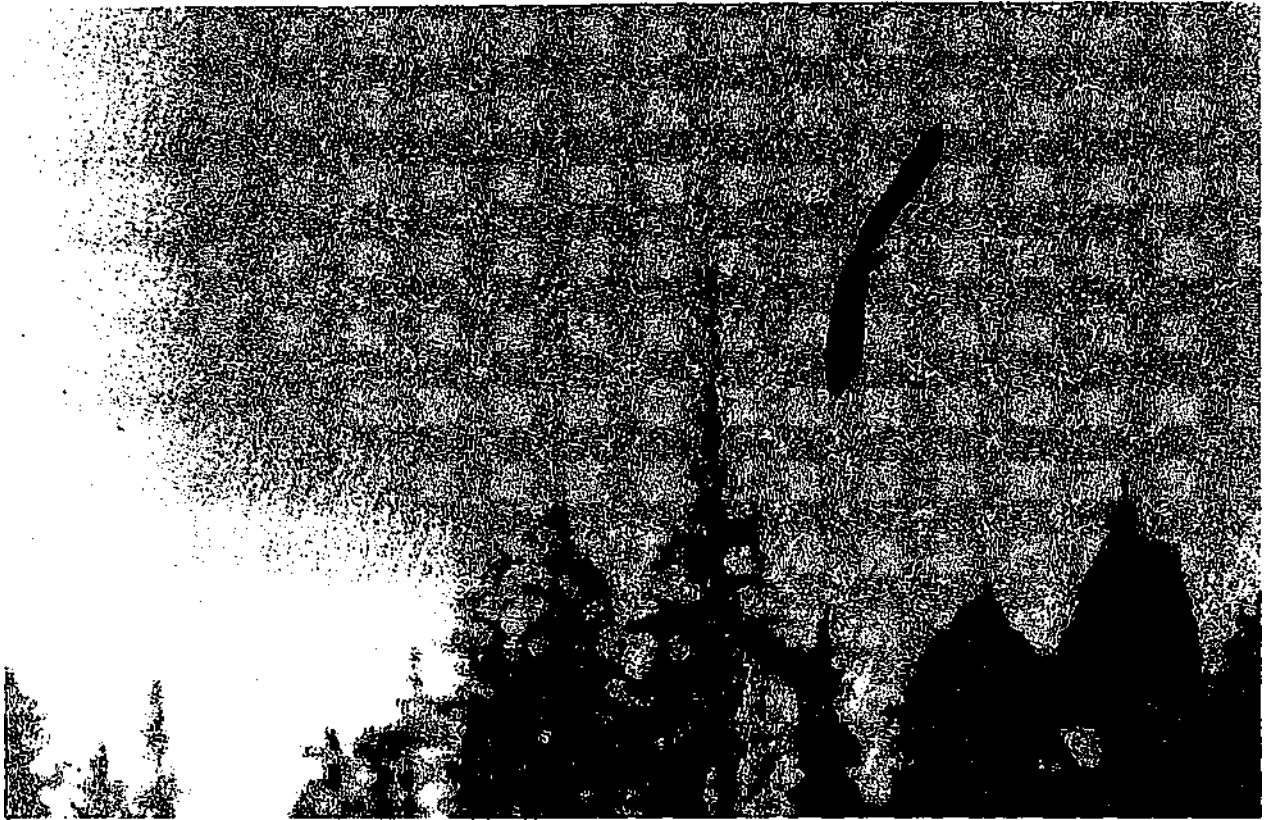


Figure 25. When open water persists around Isle Royale in winter, bald eagles become year-round residents.

The Sanguine Credulity of Youth (—Bible)

On March 1, our last day in the field, we made a point to check a particular moose calf on Houghton Point near the Lake Superior shore. We found the young bull bedded in the snow right next to his mother, as was his habit. No doubt the surroundings were familiar, as cows with calves are commonly quite sedentary in late winter in thick, protective cover. We noted nothing unusual in the demeanor of the calf. He flicked his ears in the morning's light breeze, and stared placidly over his mother toward the lake shore, showing no awareness whatsoever of the bizarre circumstances that were so clear to us. For the calf's mother, who had diligently shepherded her offspring for the first 9 months of its life, had herself fallen victim to the West Pack, now fed and bedded nearby.

Our chronicle had begun two days earlier, following a mid-night wolf attack on the cow-calf pair. Undoubtedly, the calf had been the wolves' initial target, but one of the wolves had somehow gained hold of one of the cow moose's rear legs. Judging from the patterns of wounds, the wolves probably each clamped onto a rear leg in the initial attack, successfully immobilizing the cow.

When we arrived the next morning, the furious action was over; the wolves had been bedded for hours. After arousal, they stretched and walked expectantly toward the bedded cow and calf. With great labor the wounded cow rose and moved under tall spruce cover nearby, where she stood on three legs. But the wolves postponed further interaction, content to lick at a large area of blood-stained snow.

To the wolves, whose work was over, the outcome was certain, and the wounded cow, standing motionless, seemed resigned to her imminent death. But the calf, whose fate was as certain as the cow's, seemed oblivious to its dire straits. Even after its mother had died and wolves had fed extensively, the small bull returned to her hollowed-out carcass for security. This called to mind a distinction, drawn years ago by Durward Allen, between humans and other animals—the capacity to worry about the future seems to be peculiar to the human brain.

HI: *Food shortage.*

Relative abundance of food, in the form of old moose, adequately explained fluctuations in wolf population size during 1959-1980. In the 1980's wolf numbers fell somewhat below the expected number, but a wolf decline was explained by the scarcity of old moose. The predicted wolf "low" was in 1988-1990 and, indeed, wolves fell to their lowest level in those years. Failure to recover in the 1990's, however, suggests that something other than food shortage is now limiting population growth (Fig. 9).

H2: *Disease.*

Canine parvovirus (CPV), a new virus that rapidly spread across many continents in the 1970's, may have played a role in the spectacular wolf crash of 1980-1982, when over 52 wolves died at Isle Royale. No wolves were handled during this period and the presence of the disease was not confirmed until 1988. Positive blood titers for this disease, however, were found only in two wolves captured in 1988,

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Figure 8. Intense courtship behavior preoccupied the leaders of the 450 Pack in late February. Female 450 is shown with the alpha male hovering over her, accompanied closely by beta male 430.

and since then antibodies to CPV have steadily declined. Red foxes on Isle Royale are not a reservoir for this disease and, because wolves are so rare, the virus may have failed to maintain itself in the past 5 years. CPV may have been an important cause of wolf mortality earlier in the 1980's, but it cannot explain low wolf numbers since 1988.

H3: *Genetic losses.*

Molecular geneticist Robert Wayne has confirmed that Isle Royale wolves are all descendants of a single female, and that all the wolves sampled are as closely related as sib-

lings or parents and offspring. Substantial genetic variability has been lost because of the small number of breeding wolves. The predicted outcome of this condition is inbreeding depression, or reduced reproductive success. This phenomenon, by itself, was not responsible for the population decline prior to 1988, but it could explain the lack of recovery since that time. The rather sudden emergence of genetic "problems" can be explained by high mortality during 1980-1988—genetic variability is lost with the passage of each generation.



Figure 9. Headnetted Earthwatch volunteers and R. Peterson (foreground) examine a young bull thair that died of malnutrition in spring, 1992.