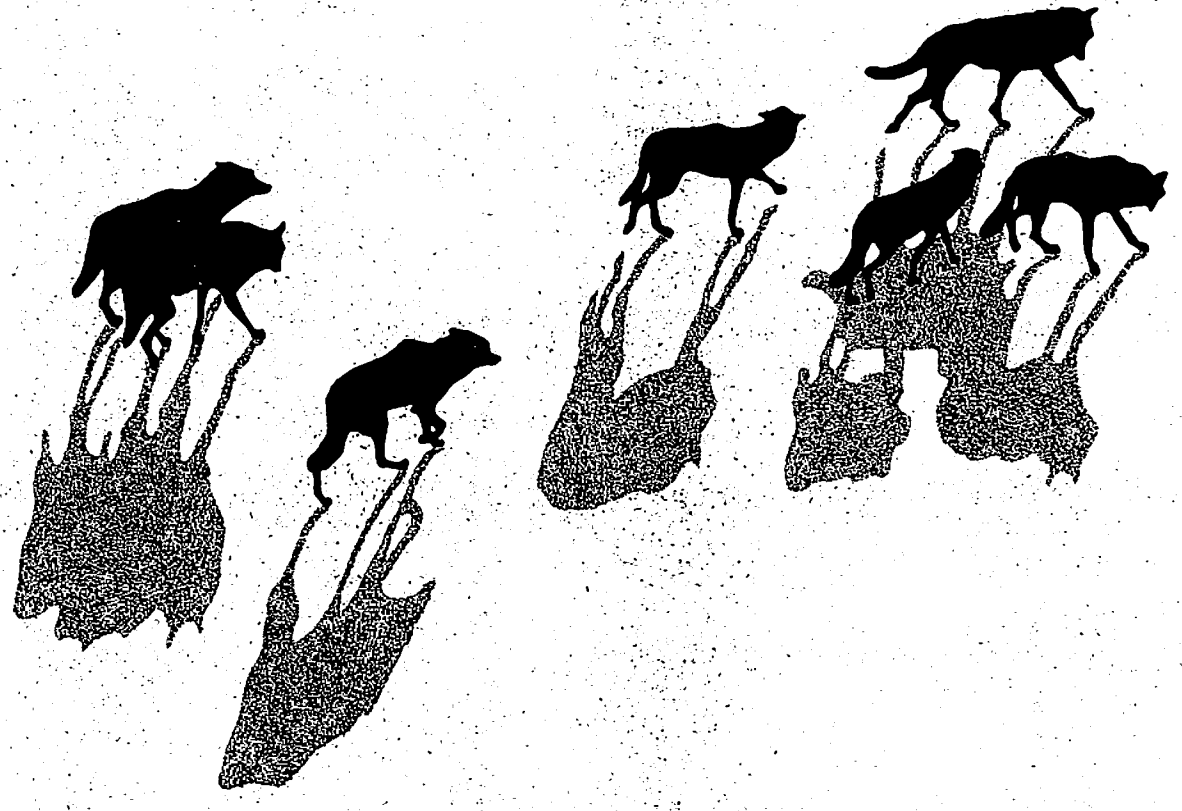
Ecological Studies of Wolves on Isle Royale

Annual Report

1990-1991



Ecological Studies of Wolves on Isle Royale*

Annual Report - 1990-1991

(Covering the thirty-third year of research)

by
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(prepared with the assistance of Joanne M. Thurber)

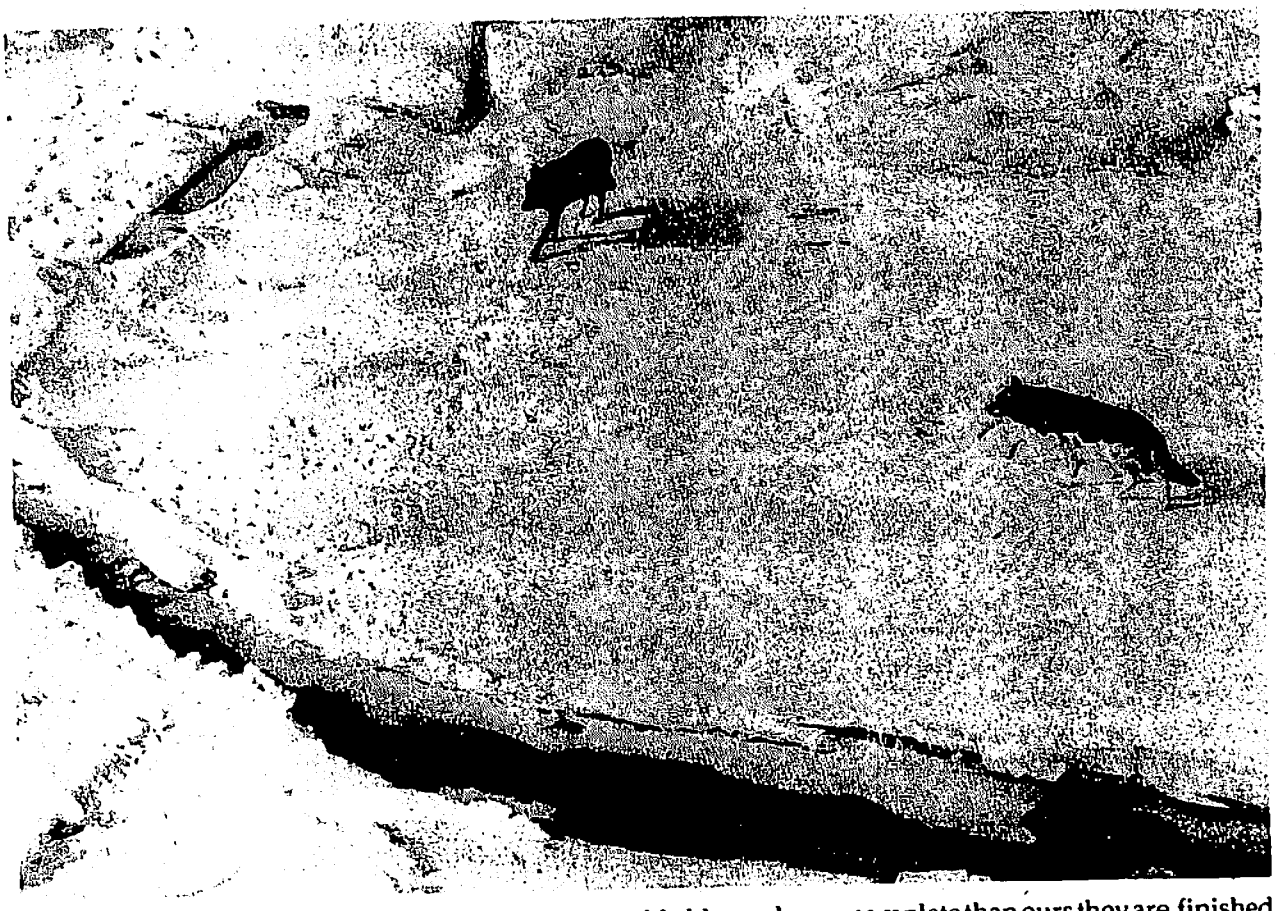
31 March 1991

*During the past year this research was supported by funding from the U.S. National Park Service (Coop. Agreement No. CA-6310-9-8001), U.S. National Science Foundation (BSR-8716095), National Geographic Society, and Earthwatch. Other donations were from Randall F. Absolon, Ameritech, Toxie E. Beavers, Dorthey L. Behrend, Jane Brackman, Greg and Janet Capito, Richard Cardy, Alison J. Clarke, The Conair Group, James A. Conant, Jr., James E. Deignan, Edith N. Greene, Gary B. Hansen, Frank B. Isaacs, Steve Magiera, Neil Proulx, Darcy R. Rutkowski, Billie E. Smith, John C. Varey, Atheline M. Wilbur, and students of Bangor Elementary School, Bangor, Wisconsin. Photos by R. Peterson and J. Thurber. Paper and typesetting were contributed by E. Greene. Robert J. Slater, of MTU Photo Services, provided special darkroom work. Cover and page 14 drawing by Fred Montague, RFD#5, Monticello, Indiana 47960. Special acknowledgement is due the 25 Earthwatch volunteers who participated in fieldwork and contributed funds to support the study:

TEAM 1: Tom Bull, Kent Davis, Stephen Humbert, Brian Krause, Don Pattillo, Michael Thomas
TEAM 2: Beverly Stencel
TEAM 3: Allen Todd
TEAM 4: Jane Brackman, Nancy Lombardo, Sam Pedigo, Adrienne Redd, Eric Rothman , Alex Shaimman, Chris Stephenson, David Trautman
TEAM 5: Daryl Brown, James Cottle, Margaret Howard, Chuck Johnson, Linda Masser, Naomi Schoenfeld, Rivka Schoenfeld, Kim Teugh, Michael Wilkinson

Tax-deductible donations to support continuing research on Isle Royale wolves and moose can be sent to: Wolf-Moose Study, Michigan Tech Fund, Alumni House, Michigan Technological University, Houghton, Michigan 49931. THANK YOU to all who have helped!

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



"For the animal shall not be measured by man. In a world older and more complete than ours they are finished and complete, gifted with extensions of the senses we have lost or never attained, living by voices we shall never hear. They are not brethren, they are not underlings; they are other nations, caught with ourselves in the net of life and time, fellow prisoners of the splendour and travail of the earth."

The Outermost House, Henry Beston, 1928

Personnel and Logistics

Field work during the past year was conducted from mid-May through early September 1990 plus a seven-week winter study beginning in mid-January 1991. Field assistants during summer were Daniel J. Fehringer, Carolyn C. Peterson, Douglas W. Smith, and Joanne M. Thurber.

During the 1991 winter study Peterson, Thurber, and research pilot Don Glaser participated for the entire seven weeks. National Park Service personnel who assisted during this time were: William J. Coponen, Larry A. Kangas, Robert J. Krumenaker, Elen H. Maurer, Timothy S. Cochrane, William O. Fink, and Stuart L. Croll. Winter supply flights to the island and summer telemetry flights were flown by the Ely Aviation Unit of Superior National Forest, and additional summer telemetry flights were flown by Jack Huhta (Hibbing, MN) and Portage Air (Ely, MN).

Summary

In 1991 the wolf population of Isle Royale National Park dropped to just 12 animals, equaling the lowest level recorded since annual censuses began in 1959 (Fig. 1). There was an unprecedented lack of reproduction, with no wolf pups detected in summer (1990) or winter (1991). In 1988-1989 the population stabilized and then increased slightly, during a brief respite from the high mortality rates (30-40% per year) which previously threatened the population. However, in the past year mortality returned to a more typical level (20%), and there was a corresponding drop in wolf numbers.

As part of an intensified study to understand causes of the wolf decline, eight of the 12 wolves alive in 1988 have now been live-captured, blood-sampled for disease and genetic studies, and released wearing radiocollars. During the past year we found no evidence that disease is currently an important factor in wolf dynamics, and their food supply should be increasing annually as the moose population ages. Loss of genetic variability and inbreeding in this small population may explain the low reproduction which currently endangers these famous wolves. Resolution of this question hinges on elimination of disease and food problems as alternative explanations.

The potential for wolf reproduction declined in 1991, as one of the four bonded pairs separated. During the 1989 and 1990 breeding seasons, four potential breeding pairs formed, yet only one litter of three pups was produced, in 1989. In 1991 there were three bonded pairs during the breeding season, and mating of one of these was observed. However, with perhaps one exception, all of these pairs have previously attempted reproduction and failed.

The largest pack in 1991 contained four wolves and, with the exception of two loners, the remaining wolves existed in pairs. Three wolves, all radiocollared, died in the 12 months prior to the 1991 winter study. One (female 490) was killed by wolves, one (male 421) died of chronic malnutrition/old age, and one (female 600, whose signal failed) disappeared from unknown causes. The signal from an additional wolf (female 670) disappeared during the 1991 winter study and she is also presumed dead, leaving a total of 11 wolves in March 1991. Notably, all three pups born in 1989 have survived.

In 1991 the moose population was estimated at 1,313 ± 303, or about 2.4 moose/km^2, suggesting that the population has stabilized after a 25% decline attributed to the influence of winter ticks. Ticks probably increased because of the unusually early spring in 1988, and a major die-off of moose was recorded in 1989. With wolves at such a low level, moose are expected to persist at high density until other sources of mortality intervene.

Presently there are no plans to reverse the wolf decline by human action, even though the possibility of extinction is relatively high. Thus far, it is felt that the scientific value of this natural experiment in population viability merits non-intervention. In the event of wolf extirpation, re-stocking of the island will be considered by the National Park Service (NPS).

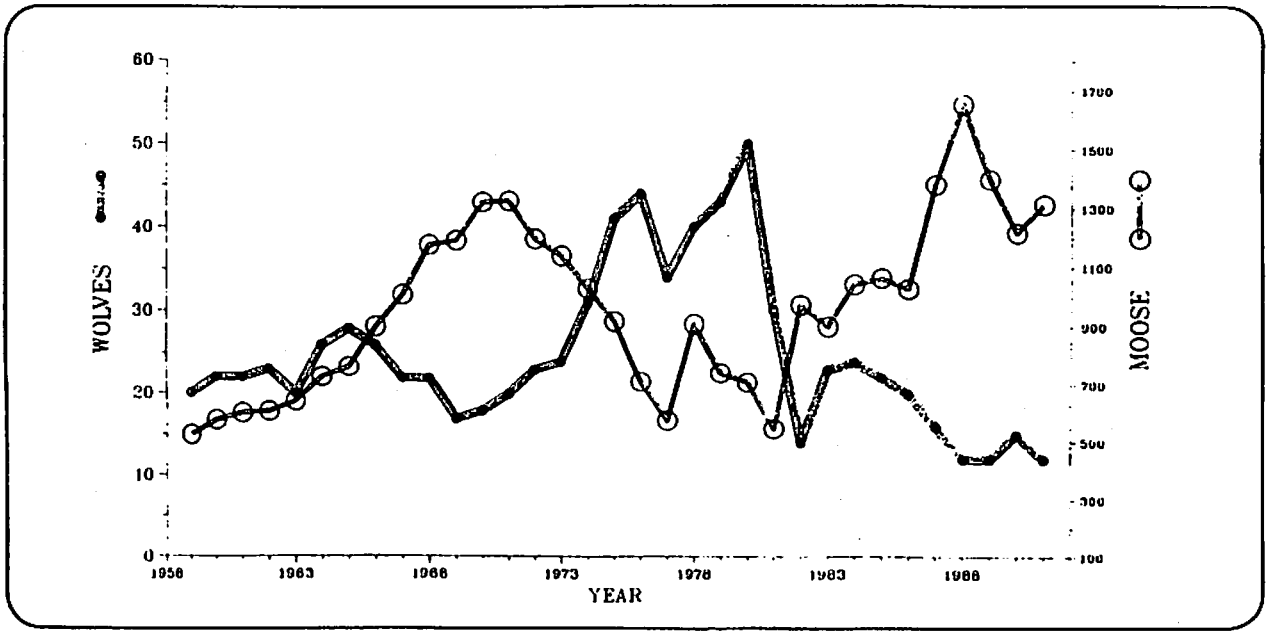


Figure 1. Wolf and moose fluctuations, Isle Royale National Park, 1959-1991. Moose population estimates during 1959-1976 have now been updated, based on population reconstruction from recoveries of dead moose.

The Wolf Population, 1990-1991

Three decades of study have pointed toward food supply as the ultimate regulator of wolf density on Isle Royale, in a "simple" system dominated by one species each of predator and prey. Lags in wolf response to changing moose density and vulnerability are thought responsible for the apparent oscillations in wolf and moose numbers. If these concepts hold in the 1990's it is expected that the Isle Royale wolf population should recover to around two dozen animals, near the long-term average level. Failure to do so will indicate that something else is driving wolf population change, and this wolf-moose system will then be in "uncharted waters".

Food shortage, new diseases, and genetic losses have all been advanced as possible causes of the recent wolf decline. Disease and genetic problems are potential factors which might now regulate wolf (and thereby moose) numbers. Isle Royale wolves are now known to be highly inbred and have lost genetic variability, possibly explaining the lack of reproduction which threatens their survival[1,2]. However, to be certain of this we must first rule out disease and food as contributing factors.

If a food shortage exists, because the moose population is dominated by vigorous young adult moose, all agree that wolves will see some improvement in food supply as the abundant moose population continues to age in the early 1990's. Disease questions are being addressed by thorough screening of wolves that are handled by researchers (on Isle Royale and elsewhere) and by monitoring survival of radiocollared wolves. Genetic studies of wolves on Isle Royale and the mainland are also continuing. Meanwhile, new details of wolf predation patterns and social relationships are emerging from close monitoring of radiocollared wolves, a technique which now supplements and enhances the traditional aerial snow-tracking employed at Isle Royale for the past 33 years. In winter 1991 radiocollars allowed us to readily monitor nine of the 12 remaining wolves. Two of the three uncollared wolves were observed only once during the 50-day study, in spite of our best efforts to locate them through snow tracking. Radiotelemetry is especially important now because otherwise single wolves and pairs are extremely difficult to find and identify.

Social Organization

In January 1991 there were 12 wolves alive on Isle Royale at the beginning of the winter study, including three yearlings born in 1989. One territorial pack of four wolves was present (450 Pack), and initially three other bonded pairs existed, two of which showed territorial behavior (Fig. 2). Two lone wolves rounded out the population, summarized as follows:

West Pack II (WPII) - a territorial, uncollared pair that formed prior to 1988; the male is at least seven years old and they last reproduced in 1988.

450 Pack - territorial pack led by female 450 and an uncollared alpha male, plus two yearlings.

550 pair - male 550 and an uncollared mate, this territorial pair first formed late in the 1990 breeding season; they were observed mating in 1991, and might represent the best hope for new reproduction (Fig. 3).

Pair - female 670 and male 470 - an "on-and-off" relationship in a non-territorial pair that lived within WPII territory, possibly had former ties to the WPII; 670 disappeared in February 1991 and is presumed dead.

Female 590 - recent loner who paired off with male 470 in March 1991; this pair failed to reproduce in 1989.

Loner - uncollared yearling of unknown sex, dispersed from the 450 Pack.

Through long-term identification of individuals, radiocollaring of Isle Royale wolves has enhanced our ability to understand wolf behavior in light of past relationships and alliances. For example, in 1991 we observed the 450 Pack, led by the alpha female 450, chase down and harass female

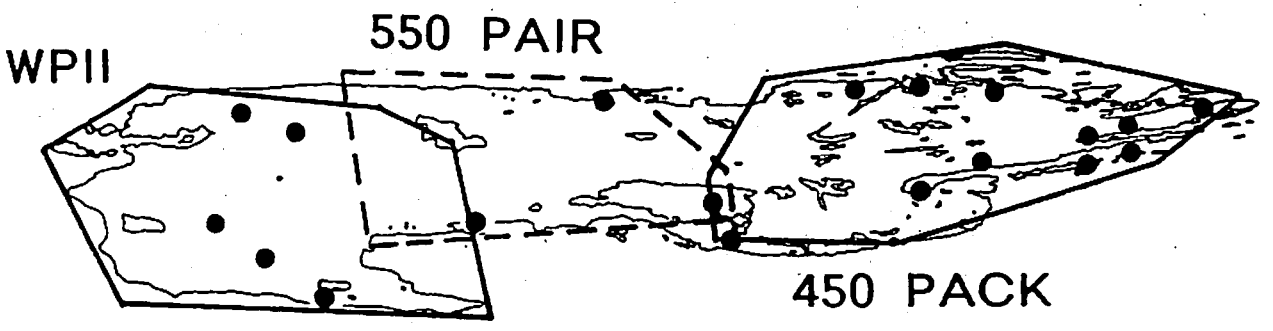


Figure 2. Wolf pack territories and moose carcasses during the 1991 winter study. WPII (West Pack II) and 550 Pack were just alpha pairs (male and female), while the 450 Pack contained an alpha pair and two yearlings.

590, a loner that spends most of her time in 450 Pack territory. The past histories of these two females probably explain why 590 was not simply killed outright—in 1988 and 1989 females 450 and 590 were virtually inseparable companions, until 450 appeared with pups born in 1989. These two wolves had been very close associates, likely kin to one another.

Reproduction

The decline in wolf reproduction that extended through the 1980's has persisted, as we found no pups among surviving wolves in winter 1991 (Fig. 4). Six adult female wolves, all potential reproducers, were alive during summer 1990, including four that were radiocollared and closely monitored beginning in early May. Yet all radiocollared wolves moved widely, and no dens or rendezvous sites were located. Ground coverage on foot of more than 1,500 km failed to confirm the presence of any pups, although small, possible pup tracks were recorded in three widely-spaced locations. At one of these sites we live-captured an adult wolf in August 1990, male 550, believed to be a two-year-old originally born into the West Pack II. Our optimistic expectation of pups in this group failed to materialize, and in winter male 550 traveled only in the company of an uncollared female and carved out a territory in the middle of the island (Fig. 2).

The remaining two territorial packs included the long-established West Pack II, now down to just the alpha pair, and the 450 Pack, consisting of alpha female 450, an uncollared mate, and two yearlings (Fig. 5). The third yearling from this litter, having dispersed prior to the 1991 winter study, remained separate from the pack throughout the study.

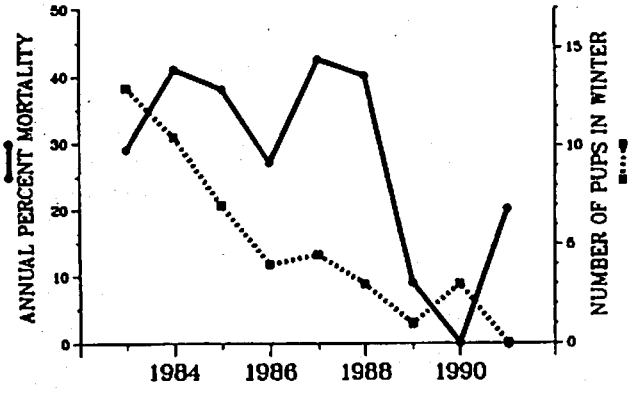


Figure 4. Wolf annual mortality and reproductive success on Isle Royale, 1983-1991.

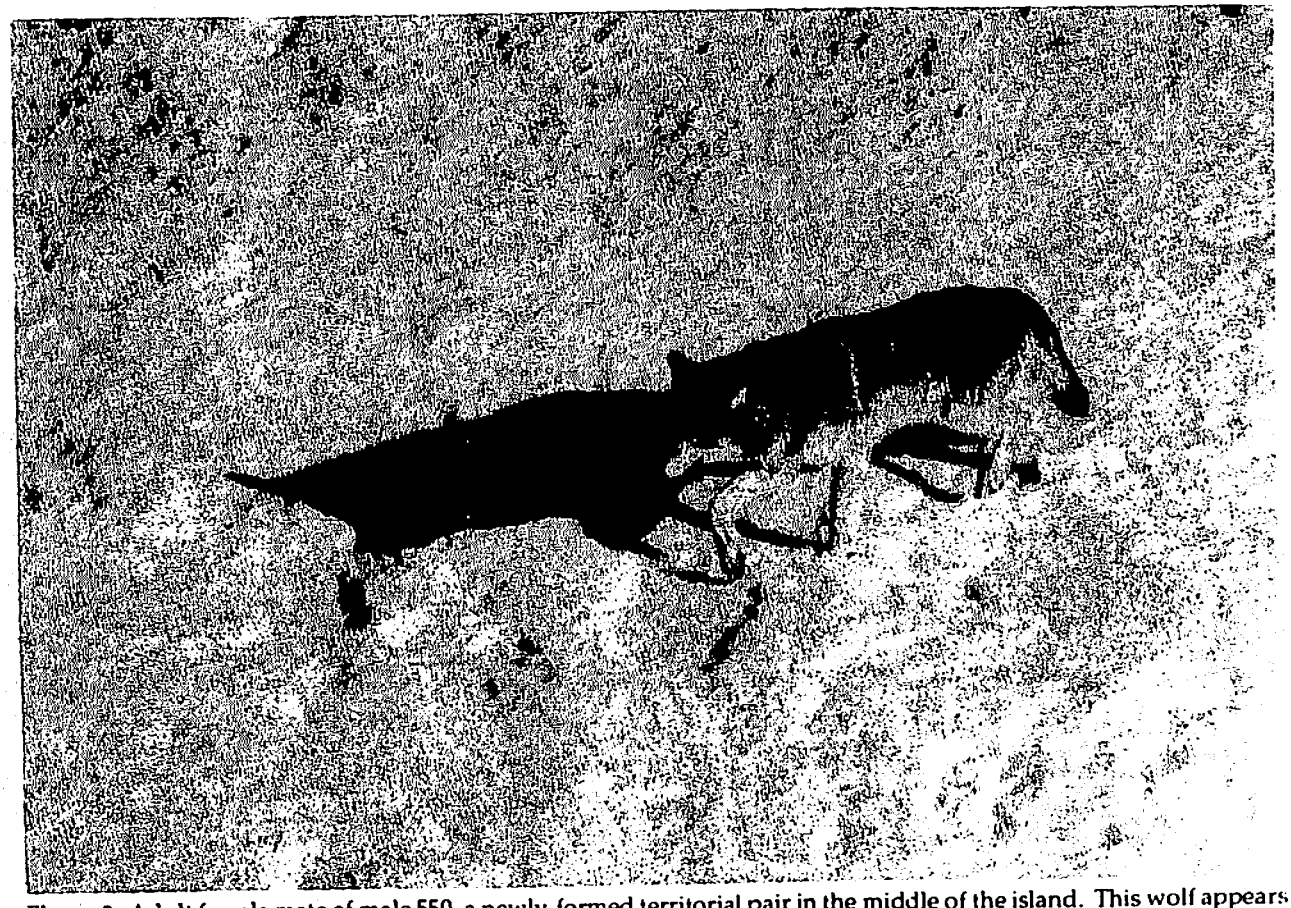


Figure 3. Adult female mate of male 550, a newly-formed territorial pair in the middle of the island. This wolf appears old, based on light pelage on its face, but she paired off with a two-year-old male beginning in 1990. This represents the only possibly "new" breeding pair on the island in the past year.

A fourth bonded pair, male 470 and female 670, existed during the past two years within WPII territory at the west end of the island. In 1991 they traveled together with few separations until mid-February, when female 670 abruptly departed and traveled quickly to the other end of the island, where her signal disappeared. Thereafter we found no trace of her and, more significantly, neither could 470, her former mate (see page 14). In early March, the closing days of the winter study, male 470 returned to former haunts at the east end and was last seen with female 590, whom he courted two years ago.

We confirmed that three female wolves (450, 550's uncollared mate, and the WPII alpha female) came into heat in late February, 1991, indicated by vaginal bleeding and active courtship by alpha males. Male 550 was observed mating with an uncollared female on 1 March 1991, five days after the female showed blood. Estrus bleeding by the WPII alpha female was observed during 23 February to 3 March. Female 450 was bleeding on 17 February, and was actively tended by the other three pack members, especially her two yearling offspring, during 18-26 February. Probably both of her offspring are males, and one actively scent-marked without reproach in the presence of the alpha male. This was reminiscent of a time in the 1970's when an aging alpha female in the East Pack allowed a subordinate female to mate with the alpha male.

Mortality

Unusually low mortality prevented further decline of Isle Royale wolves during 1988-1990, but this is not expected to continue (Fig. 3). Of the 15 wolves counted in 1990, three died prior to the 1991 winter study—female 490 was killed by the West Pack II in February 1990 and male 421, evidently a very old wolf, died of malnutrition in January 1991, a few days before the winter study commenced. Female 600 disappeared about the same time. After the count of 12 wolves was attained, female 670's signal disappeared and she is also presumed dead.

Eight of the 12 wolves alive in 1988 have been handled, and four of these are now believed dead. Last year we reported female 490's death from an attack by the West Pack II. Radiosignals from females 600 and 670 disappeared in December 1990 and February 1991—we found no evidence that wolf 600 was alive during the 1991 winter study, and she is presumed dead. Likewise, female 670 is

Figure 5. A yearling wolf "body-slams" its sibling in the 450 Pack. Such play might represent courtship, but these two wolves showed such intense interest in alpha female 450 when she was in heat that both were considered to be males. One of these yearlings was identified as a male by scent-marking posture.

assumed to have died after dispersing, in such a way that her radiocollar failed. Collars could have been damaged during a fatal attack by other wolves or, possibly, the animals perished after going through thin ice. On the day that female 670 disappeared, three other Isle Royale wolves were observed more than a kilometer from shore, traveling on thin "night-ice" that was gone a few hours later.

Male 421, who had remained a loner since his initial capture in 1988, continued to travel from end to end on Isle Royale during 1990 (Fig. 6). In May his scavenging rounds began to include campgrounds, and in in July he became a regular visitor at lakeside campsites, where he boldly sought out fish heads and entrails in full view of campers. When the winter study commenced in mid-January we found that he had died shortly before, just a few hundred meters from our usual winter residence at Windigo; his intact carcass was just outside a sheltered den he frequented beneath a fallen cedar (Fig. 7).

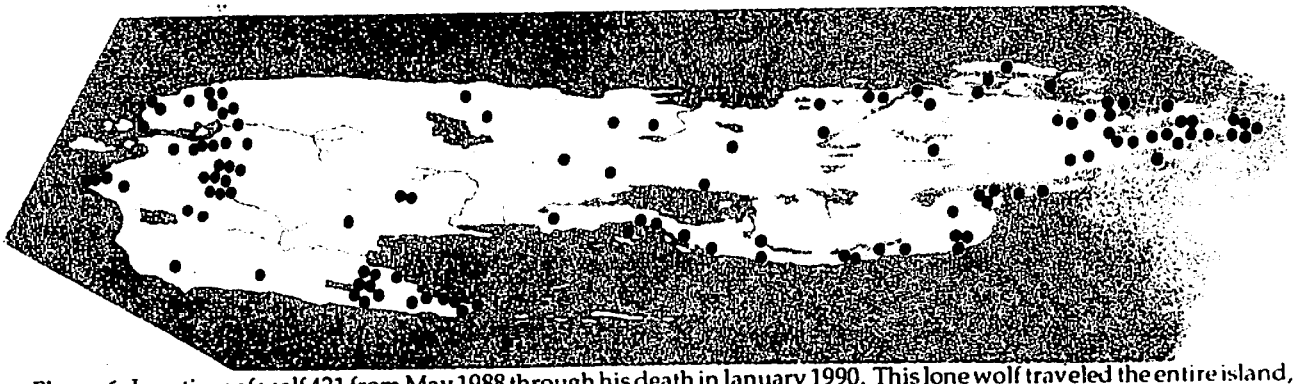


Figure 6. Locations of wolf 421 from May 1988 through his death in January 1990. This lone wolf traveled the entire island, but often concentrated his activities at its extreme ends. He was, at times, chased off his own kills by the West Pack II, but he either evaded them or was allowed to escape uninjured.

Figure 7. Final location of wolf 421, found dead in January 1991 in front of a den beneath a fallen tree (in background) he had been using in his final days. He appeared to have died of malutrition associated with old age; no diseases were implicated in his demise.

A full autopsy was carried out on male 421 by pathologist Nancy Thomas (U.S. Fish and Wildlife Service Wildlife Health Research Center), who found an emaciated and evidently very old wolf (Fig. 8)—we will attempt to determine his age from tooth cementum annulations and also from bomb radiocarbon residues in his teeth. During his final year tooth wear became extreme, and he had few usable teeth left when he died. Arthritis was evident in his spine, periodontitis was leading to progressive loss of bone around his remaining teeth, and he had heavy parasite loads of hookworm (*Uncinaria spp.*) and hydatid tapeworm (*Echinococcus granulosus*). We had live-trapped this wolf three times in 1988 and 1989 (the only wolf we've recaptured), and the resulting wounds to his toes, even though healed, must be counted among his many pathologies. However, he traveled normally and killed moose by himself as late as winter 1990, months after he was last captured. Surprisingly, he had suffered no broken ribs, a very common injury for wolves that kill moose. In this wolf we found no gross indications of any diseases of consequence to the population, although additional studies will be carried out on tissues recovered from his carcass. His hide will be mounted for interpretive display in the park.

Wolf Predation Patterns

During the 1991 winter study wolf kill rates were similar to the past several years (Table 1 and Fig. 9). Wolves in all types of social groups, from loner to pack member, actively killed moose. The age distribution of their kills showed the familiar predominance of calves and old moose, and recently there were some indications of a shift toward younger adult moose (Fig. 10). This is an expected consequence of aging within the moose population, bringing relatively abundant cohorts born in the early 1980's into the "high risk" group susceptible to wolf predation.

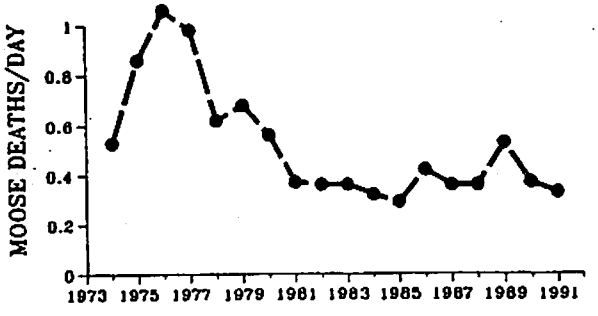


Figure 9. Moose mortality in 1991 was similar to levels of the 1980's.

Figure 8. Wolf 421 was autopsied at the U.S. Fish and Wildlife Health Research Center, Madison, Wisconsin. Pathologist Nancy Thomas (right) inspects the thawed carcass with Joanne Thurber.

Outlook for the Wolves

...in one word, "bleak," unless trends in reproduction are quickly reversed. Mortality from old age and direct killing by wolves can be expected to claim an average of 10-30% of the wolves each year. To offset this, and simply hold the population near its current precarious level, survival of about three pups each year is necessary. Population increase to a more secure level would require even higher pup survival. Recent trends in reproduction suggest this is unlikely. The genetics hypothesis for the wolf decline predicts eventual extinction. The food hypothesis predicts that the wolves will recover. The original disease hypothesis, that canine parvovirus is currently influential, has been rejected. As yet, there are no data to implicate Lyme or other diseases. At this point, because of low wolf numbers, random fluctuations in birth and death rates, and sex ratio, may decide the final outcome.

Thoughtful readers might wonder why, after more than 30 years of study, such a well-known wolf population would be allowed to dwindle to extinction, apparently just to test some scientific hypotheses. Justification may be found in the potential importance of our findings regarding the wolf decline, and our future ability to re-establish an extirpated species. If wolves and other large carnivores are subject to the same problems of genetic inbreeding as other species[2], then there are large implications for wolf conservation in the wild, both for harvested and endangered populations. By virtue of their low density (many prey are required to support a single predator), populations of large carnivores tend to be small and, like the Yellowstone grizzly, they may be isolated by human development. National parks and similar reserves, which provide some of the most intact habitats for endangered species remaining on Earth, are rapidly becoming ecological equivalents of islands. Learning about an extinction on an island will be useful for resource managers and, for the general public, extinction of such a high profile population will highlight the problems facing wildlife isolated in fragmented habitats.

Wolf extinction at Isle Royale, should it occur, may be remedied by reintroduction of new wolves. Of course, a new wolf population might encounter the same difficulties this one has, eventually requiring intervention to save or replace it. Although no such plan has been formulated, the National Park Service will be giving this matter serious thought in the near future. It is a sobering realization that deliberate management *by humans* is the only hope for much of the world's wildlife, even in a place like Isle Royale.

Table 1

Travel and kill rates for Isle Royale wolf packs.

	550 Pair, 1991	450 Pack, 1991	470 & 670, 1991	All Packs 1971-1990 average (sample size)
Pack size	2.0	4.0	2.0	7.5 (54 packs)
Travel rate (km/day)	6.3	9.0	-	9.1(1458 pack days)
Kill interval (days/kill)	11.0	5.6	12.5	7.7 (386 kills)
Travel between kills	69.3	50.6	-	49.4(304 kills)

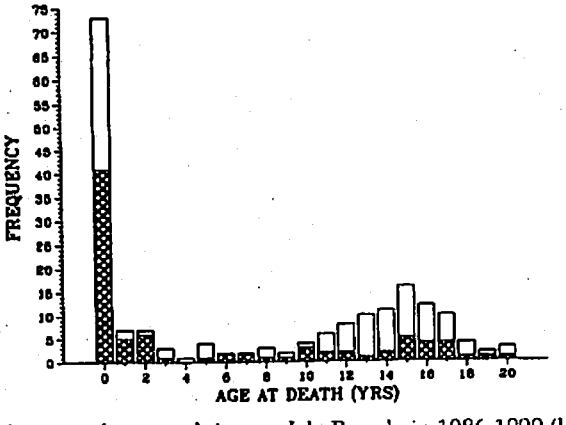


Figure 10. Age distribution of moose dying on Isle Royale in 1986-1990 (last two years highlighted). As the moose population ages, wolves have gradually been killing younger adult moose.

The Moose Population, 1990-1991

The moose population expanded rapidly during the 1980's, more than doubling in just seven years. After reaching almost 1,700 moose in 1988, the population dropped by some 25% as a result of high mortality in 1989, largely caused by winter ticks. Early snowmelt in the drought year 1988 apparently led to a rapid buildup of ticks at Isle Royale, similar to reports in Minnesota and many regions in Canada. In 1990 and 1991 tick-caused hair loss in moose declined at Isle Royale, and moose numbers appear once again to be rebuilding. It is unlikely that visitors to Isle Royale will see any winter ticks, which parasitize moose only in winter, but this small creature may compensate, in some respects at least, for the reduced presence of wolves.

Moose Census, 1991

A major thaw led to the appearance of much bare ground in early February, and we had to wait almost three weeks for new snowfall. The aerial moose census finally commenced on February 20, and good conditions prevailed until its completion eight days later (Fig. 11). Through intensive search over plots covering 19% of the island, we counted 260 moose. Assuming 75% of the moose on plots were detected, our final population estimate (and 95% confidence interval) was 1,313 ± 303 moose.

Moose Reproduction and Mortality

Recruitment of moose calves was relatively high, as was survival of older moose, leading to population growth. In winter moose calves comprised 19% of the moose counted on census plots, one of the highest calf counts in the past two decades (Fig. 12). With moose numbers also relatively high, there is obvious growth potential in the near future. Trends in bone marrow fat of dead moose suggest continued deterioration in the forage base for moose, after a period of improvement about a decade ago that coincided with a low point in moose density (Fig. 13).

Chronic poor nutrition, even if it reduces moose productivity, is apparently a weak stabilizing influence, and the moose population will probably continue to grow until a new source of mortality enters the picture. Wolf predation, at current levels, has been unable to stop growth in the moose population. Winter ticks can be very influential, but their populations may be driven by weather patterns which are largely unpredictable. Mortality from starvation alone has not been a powerful regulator of Isle Royale moose since the arrival of wolves in the 1940's. Prior to that, when moose declined from malnutrition, population density may have been more than twice the current level.

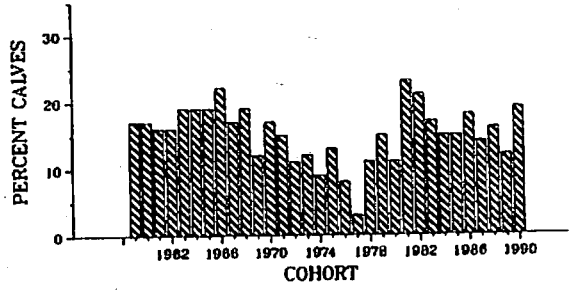


Figure 12. Moose calf abundance (at approximately six months of age) on Isle Royale, as a proportion of the total population. These are single best estimates, the mean of all available counts for each cohort (summer ground observations and aerial counts in autumn and winter).

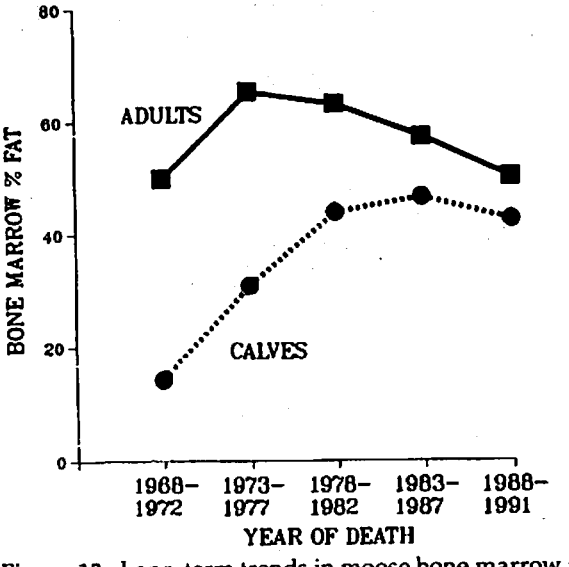


Figure 13. Long-term trends in moose bone marrow fat suggest deteriorating forage condition for moose in the late 1980's.

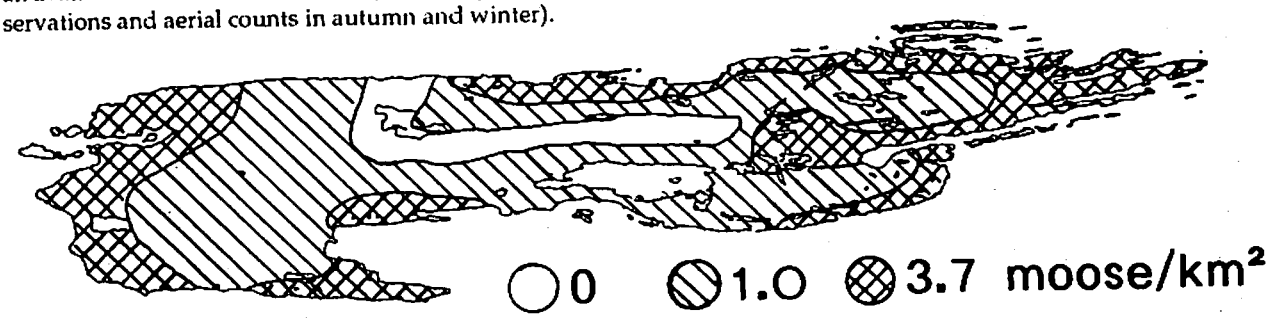


Figure 11. Moose distribution on Isle Royale during aerial census in Februrary, 1991.

During the 1991 winter study we located carcasses of 20 dead moose, including 16 that died during the 50-day study. This translates into a low mortality rate for moose, similar to the pattern observed through much of the past decade when moose population growth was rapid(Fig. 9).

Weather, Snow, and Ice Conditions

Even though Isle Royale is surrounded by the buffering influence of cold Lake Superior, CO_2-driven global warming may have subtle yet far-reaching impacts on Isle Royale wildlife in the future. Winter ice provided the avenue for wolves and other species to colonize the island, but the

Figure 14. A most unusual bull moose seen near Daisy Farm campground in June and in Lake Whittlesey in August. A.B. Bubenik, an authority on antler formation, points out that these unique antlers result from a lack of testosterone reaching the developing antler tissue, perhaps due to senescence or accidental castration.

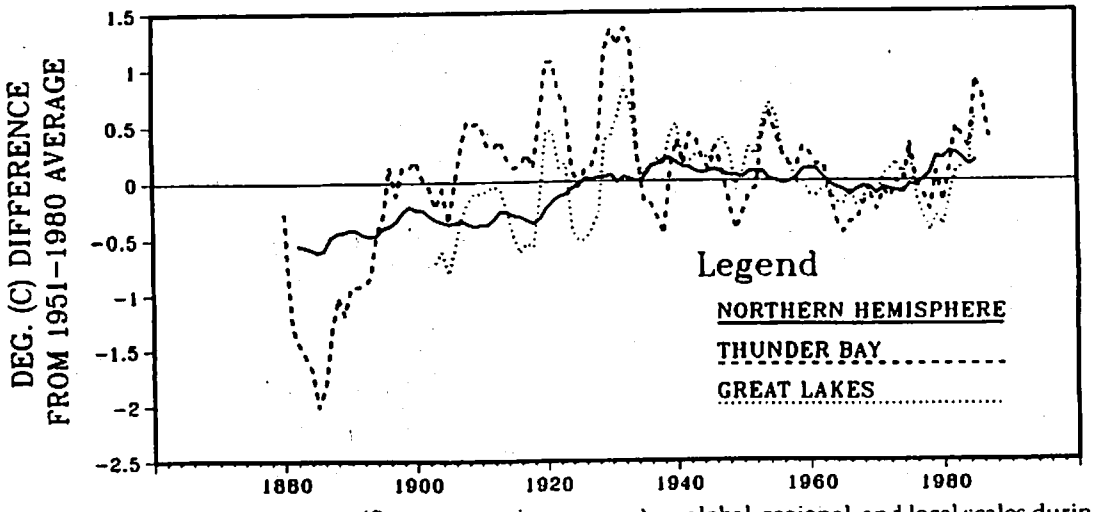


Figure 15. Annual average temperature (five-year moving average) on global, regional, and local scales during the past century reveal unusual stability from 1940 to 1980, but otherwise a strong warming trend. The Thunder Bay weather station provides year-round data closest to Isle Royale--this station was operated by a single individual, W.P. Cooke, for 59 years beginning in 1876.

Figure 17. Moose taking refuge on lake ice during a wolf encounter in early February 1991. Wolf 470, not in photo, was onshore. Moose normally seek refuge from wolves in heavy cover, but strong snow surface crusts following a mid-winter thaw created very unfavorable footing for moose in the forest.

Figure 18. More ice surrounded Isle Royale in 1991 than in most years in the previous decade, but an ice bridge to the mainland persisted for no more than two weeks.

most recent significant ice bridges were in 1977 and 1979. Weather also may be a driving force behind irruptions of influential arthropods, such as winter ticks and the spruce budworm. Finally, forest fires are likely to increase in frequency as spring and summer temperatures rise. Human influences on the global ecosystem will indirectly determine conditions for life on Isle Royale.

A century ago, when copper mines were active on Isle Royale and hundreds of people overwintered there, the mail was moved by dogteam across Lake Superior ice to the mainland. Today such an effort is unthinkable, but long-term temperature records reveal that the Lake Superior region was much colder 100 years ago (Fig. 15). They also point to the 1980's as a period without precedence in the previous century, with sustained warming both locally and globally.

Snow depth was slightly below average through most of the winter study of 1991 (Fig. 16). A brief thaw in early February was followed by a period of very strong surface crust, which supported wolves but forced moose to remain in areas of shallowest snow beneath coniferous trees. Here moose have the greatest security in the event of a wolf attack (see Fig. 17).

The winter of 1990-1991 was cold enough to provide secure ice around Isle Royale, necessary for landings of the research aircraft, and an ice bridge to mainland Ontario also formed in late February (Fig. 18). This ice bridge persisted for about two weeks, and it was intact when the winter study closed in early March. We were not aware of any wolf crossing during this time.

With shallow snow depth and another exceptionally early spring, conditions on Isle Royale in 1991 were similar to those of 1988, which preceded an impressive increase in winter ticks and a major moose die-off. Research by W. Samuel (University of Alberta) indicates that survival is enhanced for egg-laying ticks that drop from moose onto bare ground, instead of snow, in the spring. Because of the powerful influence of winter ticks on Isle Royale moose, weather patterns in the 1990's will take on new significance.

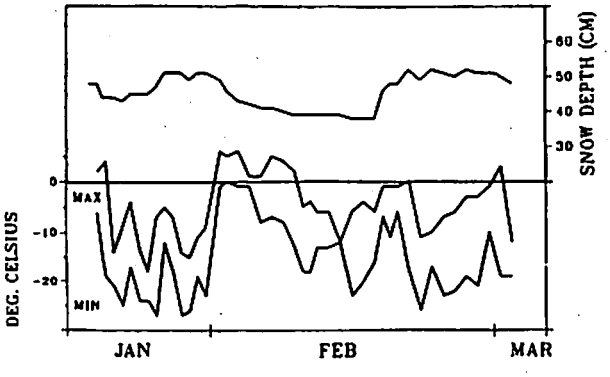


Figure 16. Temperature extremes and snow depth during the 1990 winter study at Isle Royale.

Other Wildlife Species

Last year snowshoe hares continued to decline, following a historic peak in 1988 (Fig. 19). Red foxes, which seem to have thrived during the years of abundant hares, have persisted at high population levels (Fig. 20).

Eagles and ospreys continue to succeed in small numbers, with one new eagle and three young ospreys fledged in 1990. This year, 1991, marks the fifth and final year of peregrine falcon releases by the NPS. Although no birds have returned to nest on the island, the release program, in its first four years, added 36 fledged birds to regional populations.

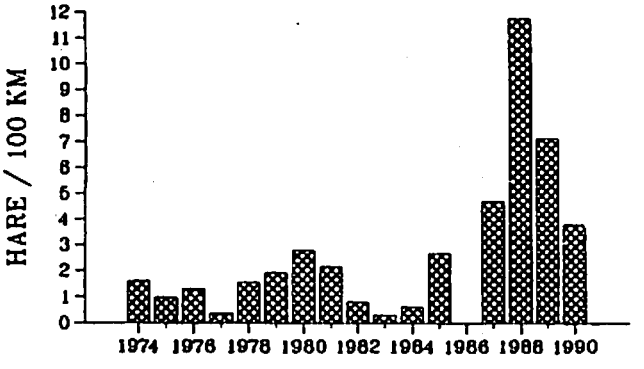


Figure 19. Snowshoe hares on Isle Royale continued to decline in 1990 from a recent historic high level (no data available for 1986).

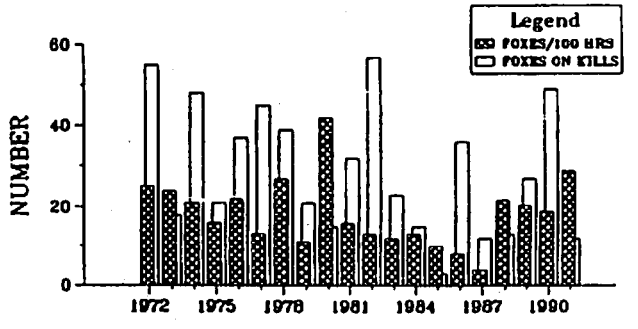
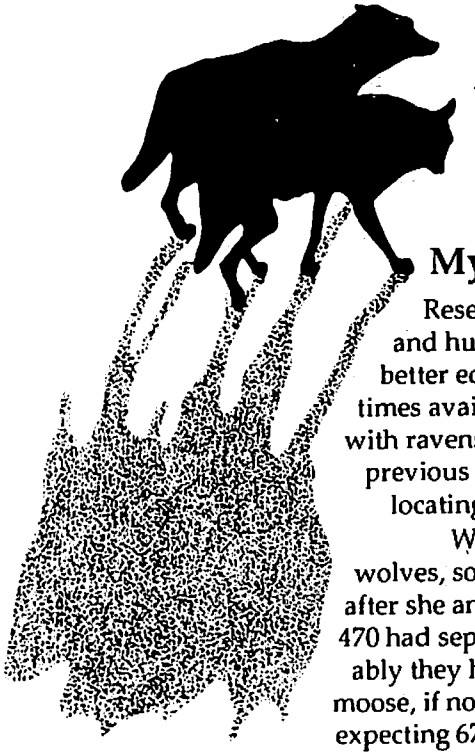


Figure 20. Relative abundance of red foxes from aircraft observations, 1972-1991. Hatched bar is the number of foxes seen away from moose carcasses/100 hours, while the open bar is the number of foxes seen on carcasses.

Footnotes

[1] Wayne, R.K. et al. 1991. Conservation genetics of the endangered Isle Royale gray wolf. Conservation Biology 5:41-51.

[2] Laikre, L. and N. Ryman. 1991. Inbreeding depression in a captive wolf (*Canis lupus*) population. Conservation Biology 5:33-40.



Mysteries Remain, Even for Wolves

Researchers are not the only creatures interested in the travels and hunting success of the Isle Royale wolves. Other species are better equipped to follow wolves than are humans, and we sometimes avail ourselves of their expertise. At sunrise we share the sky with ravens who are also in search of wolves and new kills made the previous night. Inadvertently ravens often provide us with help in locating obscure kills, and we occasionally return the favor.

Wolves, of course, have a finely-tuned ability to locate other wolves, so we hoped for some wolf assistance in locating female 670 after she and her radiosignal disappeared in February. She and male 470 had separated several times in the previous two years, but invariably they had rejoined into a pair that was at least effective in killing moose, if not in producing offspring. We carefully followed male 470, expecting 670 to show up, but soon it appeared that he was also searching for her, and with no better luck. A few days after she abandoned him, he traveled 60km to the northeast, killed a moose, and then remained alone around the kill for several days. He then abruptly returned to the west end and curled up on the pinnacle of a small island near a travel route he had often used with female 670. He spent two days looking over the harbor, and we presumed he was waiting for his mate to reappear. But she never returned, and male 470 then moved back to the northeast end and quickly found female 590, a wolf he had courted two years ago. By then it was early March, the very end of the breeding season, but perhaps not too late to reproduce.

And what was the final fate of female 670? Was she killed by other wolves? Did she fall through thin ice? The answer, like so many other details of wolves' lives, may never be known. The fact of female 670's existence may live longer in the annals of our research than in the memory of her mate, but he must wonder, at times, whatever happened to her.