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Ecological Studies of Wolves on Isle Royale, 1994-1995

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Annual Report

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Annual Report—1994-1995*

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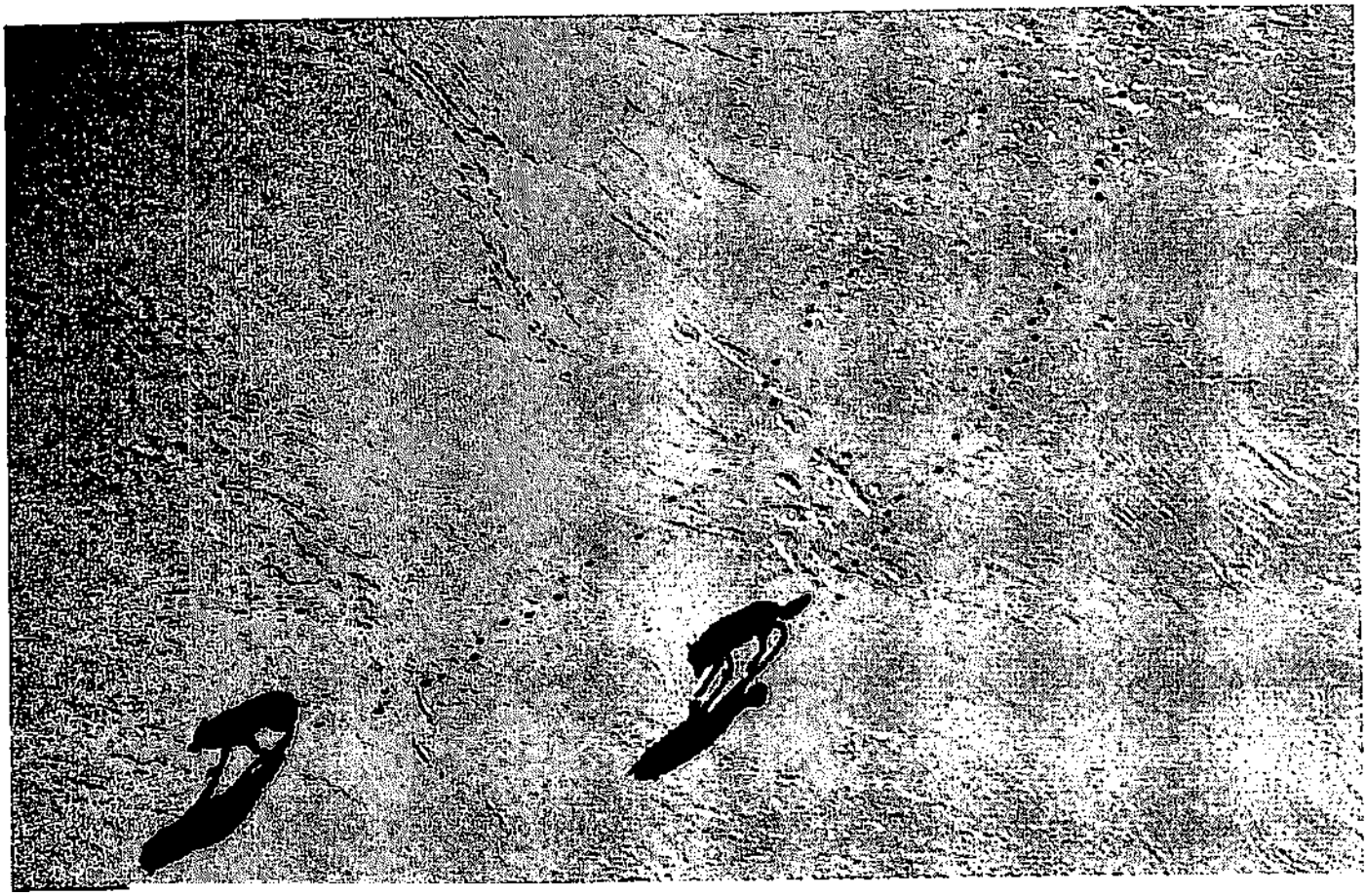
[Results reported here are preliminary, and in some cases represent findings of collaborators; please do not cite without consulting the author.)

Ecological Studies of Wolves on Isle Royale



"Animals are far more fundamental to our thinking than we supposed. They are not just a part of the fabric of thought; they are pari of the loom."... Peter Steinhart

Personnel and Logistics

In late April and early May 1994 veterinarian Mark lohnson (Yellowstone National Park) and David C. Soleim (Isle Royale National Park) assisted Rolf Peterson in wolf live-capture efforts. In summer 1994 Peterson directed ground-based field work, aided by David P. Bach. Nicholas A. DeCovich. Kathy M. and Jeffrey). Holt. Brian E. McLaren. Carolyn C. Peterson, leremy D. Peterson. Trevor S. Peterson, Douglas W. Smith, John A. Vucetich. and loseph R. Zanon. Radio-collared wolves were tracked in summer with air support from Superior National Forest and Voyageurs National Park.

In 1995 the annual winter study extended from lanuary 15 until February 28. Peterson and pilot Don Glaser participated in the entire study, assisted by: graduate students Brian E. McLaren and Mary L. Hindelang. volunteers Edith N. Greene. Cynthia D. Carter and Elise |. Lawson; and the following personnel from Isle Royale National Park—William 1. Coponen. David C. Soleim. Jack G. Oelfke. and Robert K. Whaley.

Summary

In 1994-1995 the wolf population at Isle Royale remained stable, with 16 animals counted in lanuary 1995. while the moose population increased to an estimated 2.400 animals (Fig. I). Annual wolf mortality (18%) was near the long-term average and reproduction fell back to the low level prevalent since the late 1980s. The wolf population is in an important transition as one generation is replaced by the next. After the 1995 winter study there remained only one wolf (a male) that had ever reproduced, yet there were 11 wolves less than four years old with ample numbers of males and females ready to assume alpha positions which permit reproduction. In the past year (lanuary 1994 to lanuary 1995) two aging alpha wolves died and another established alpha wolf perished during the 1995 study. Only one of the three territorial packs reproduced, yielding two surviving pups.

Isle Royale is now free of important wolf diseases and wolf food supply (old moose) will increase steadily during the 1990s. We hope to resolve questions about the impact of genetic isolation on reproduction by monitoring the next generation. If the next generation of wolves reproduces at rates similar to the last, then genetic decay will probably remain the only reasonable explanation for low reproduction which is preventing expansion of wolf numbers.

Growth of the moose population was furthered by "easy winters" during the past two years. There was little starvation mortality in.spring 1994 and little is expected in 1995. During the 1995 winter study we recorded a few moose deaths from malnutrition and accidents, but wolf predation was responsible for almost 90% of the moose mortality we recorded.

The wolf decline of the 1980s and 1990s revealed the importance of wolf predation in the dynamics of the Isle Royale "food chain". Released from top-down control by wolves, moose have now increased to historic high levels. Meanw.hile. tree-ring studies of forest trees heavily browsed by moose have revealed that tree growth in the regenerating forest declined in concert with the moose increase. The ecological significance of top carnivores in terrestrial food chains has probably been underestimated because they have been extirpated or reduced in number by human actions.

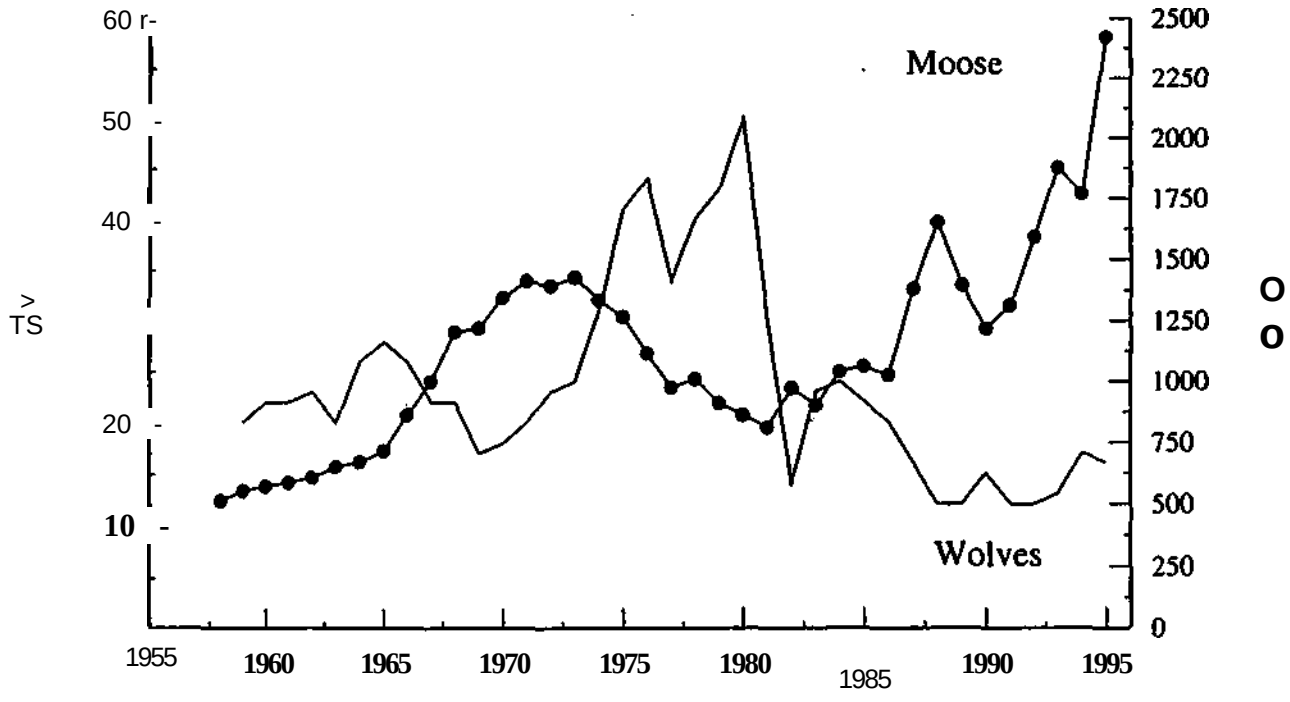


Figure 1. Wolf and moose fluctuations. Isle Royale National Park. 1959-1995. Moose population estimates during 1959-1981 are based on population reconstruction from recoveries of dead moose, whereas estimates from 1982-1995 are based on aerial surveys.

The Wolf Population

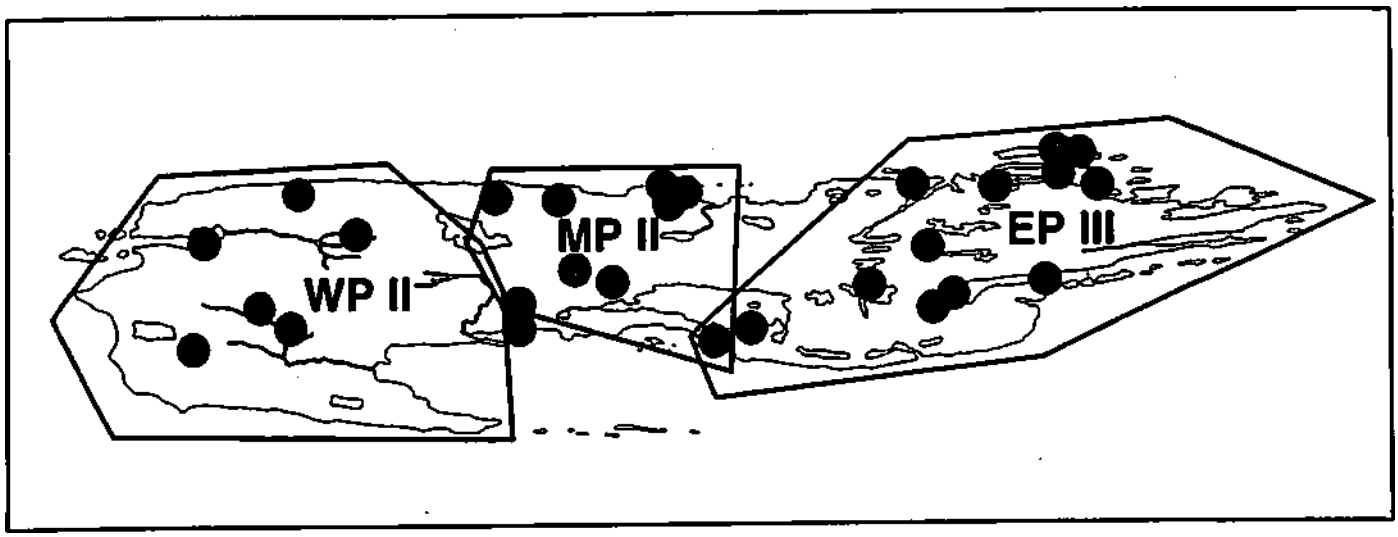


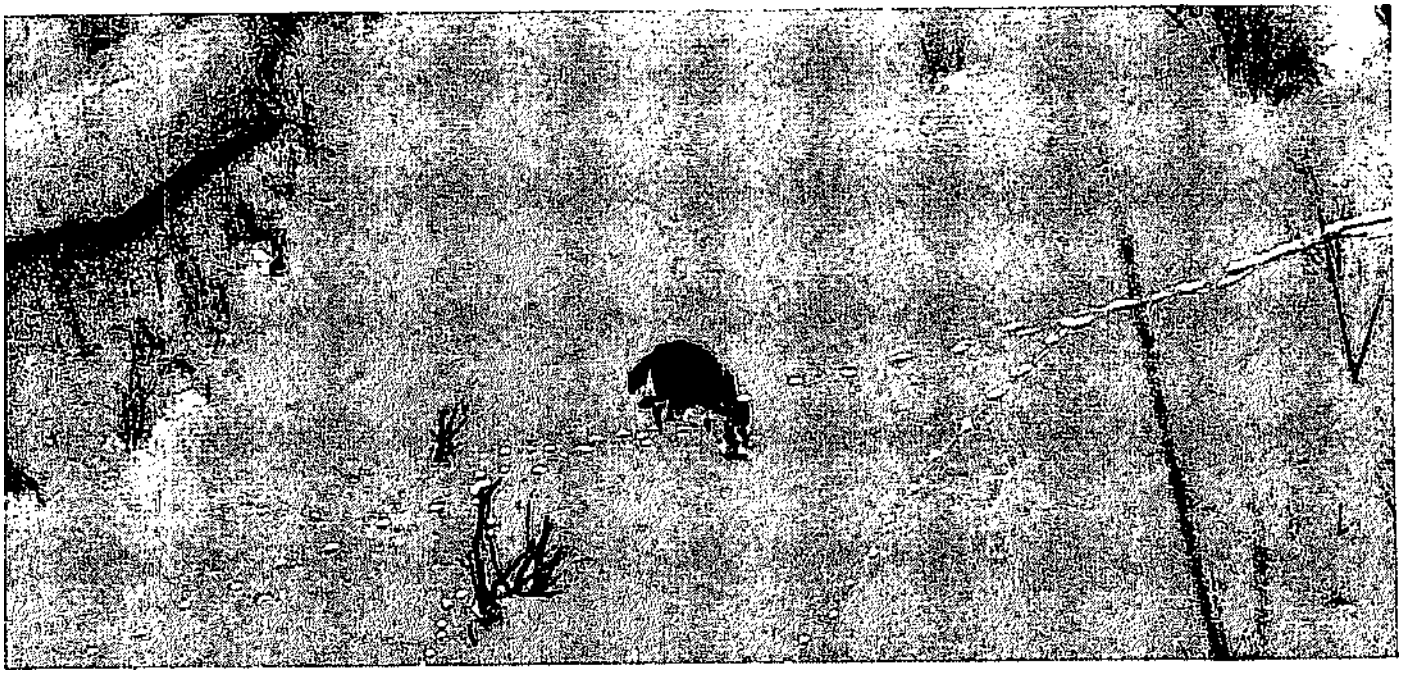
Figure 2. Wolf pack territories and moose carcasses during the 1995 winter study. West Pack II [WPII) was just an alpha pair, the Middle Pack II (MPII) had three wolves, and the East Pack 111 (EPIII) contained six wolves.

In 1995 the wolf population was organized as follows (Fig 2):

East Pack III	6
Middle Pack 11	3
West Pack II	2
1071 duo	2
singles	3
1994 total	16

The Middle Pack had two yearling wolves in alpha positions, the first breeding pair from the next generation. They were observed mating on February 22 after a month of courtship behavior. On February 21 vaginal bleeding (indicating estrous) was exhibited by the old alpha female in the West Pack II and a new alpha female in the East Pack.

Two yearling wolves in the Middle Pack (orphaned by the death of their parents when they were nine months old) were live-captured and radiocollared in spring 1994. and one of these died in February 1995. One of two additional radiocollared alpha males (wolf 430, West Pack II)



Male 490 ***became an alpha wolf as a yearling and here was busy inspecting scent posts in domain of the Middle Pack.***

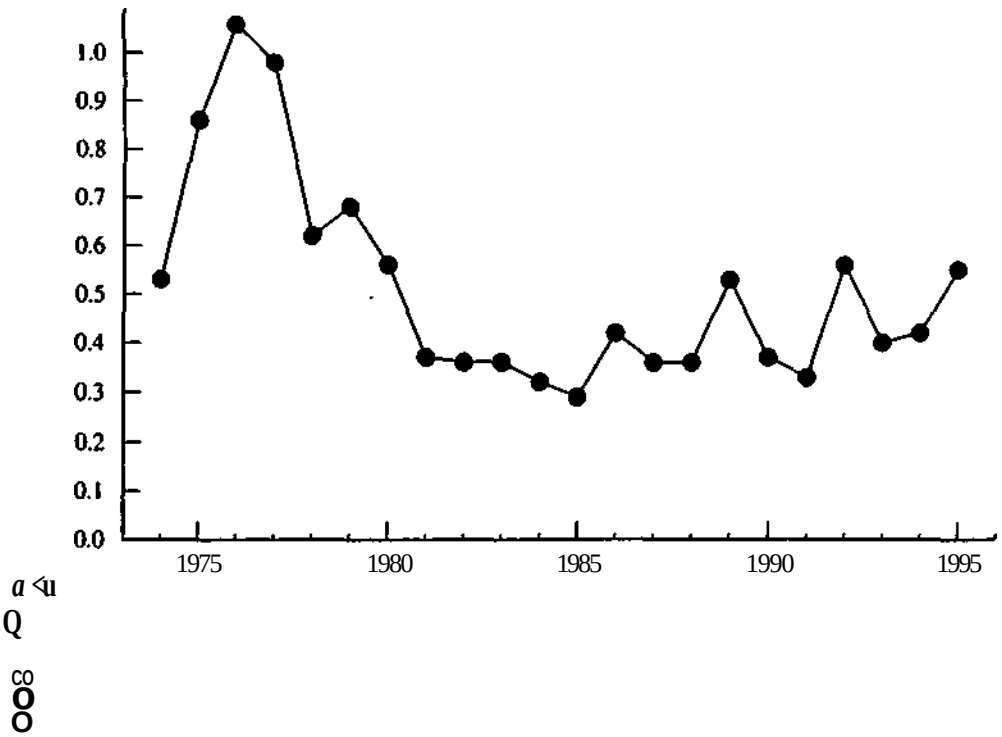


Figure 3. With low losses to wolf predation. moose mortality in winter has been constant or increasing only slowly in recent years.

ceased transmitting at the end of the 1995 winter study, leaving two radiocollared individuals in the population (alpha males in the East Pack III and in the Middle Pack II).

Thirteen wolves have been radiocollared on Isle Royale since 1988. Causes of death have now been determined for seven of these wolves. Two were killed by wolves, three died of "old age", and two probably died accidently. No diseases have been implicated in any wolf mortalities. and evidence of canine parvovirus (CPV) disappeared after 1988. Yet there is strong circumstantial evidence that CPV caused the wolf crash in 1980-1982 and probably contributed to chronic high mortality in 1982-1988. There is growing evidence that CPV is a significant factor in the dynamics of mainland populations of wolves and coyotes.

Wolf kill rate, indicated by moose mortality, was among the highest observed in 15 years, but still only half of the maximal rates of the mid-1970s (Fig. 3). Almost 40% of the wolf-killed moose were calves, near the long-term average. During observations in 1995 wolves succeeded in killing two of 24 moose that were tested. One yearling male was killed after being chased several miles (in two separate bouts) by two wolves in the West Pack.

Annual mortality for Isle Royale wolves in the past year was 18%. also near the long-term average level (Fig. 4). The three deaths recorded from lanuary 1994 to lanuary 1995 included the alpha male and female of the Middle Pack II. who both died of "old age" during the 1994 winter study. The third wolf that died in the past year was young. <4 yrs old. one of 8 animals born into the East Pack 111 since 1991.

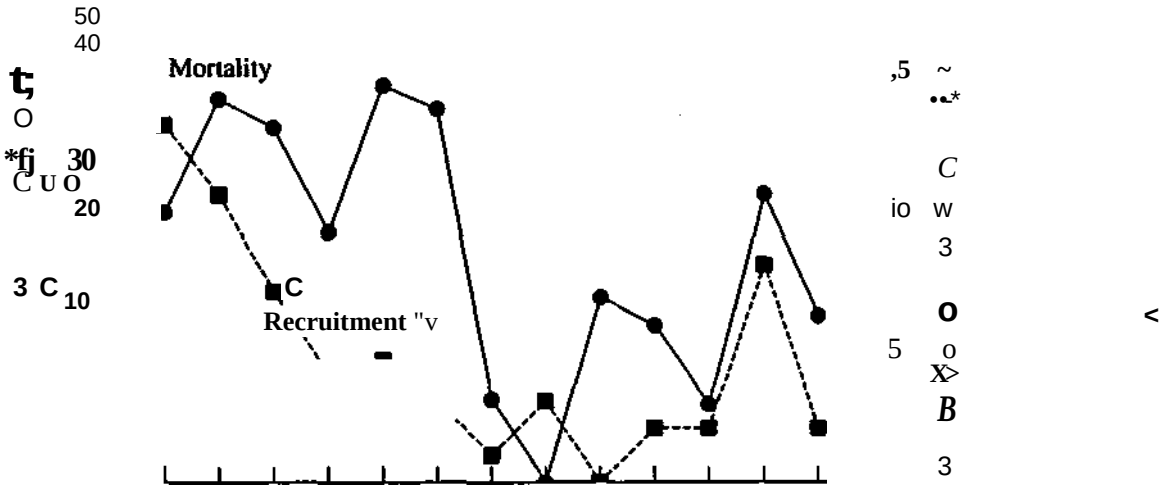


Figure 4. In the past

year, wolf annual mortality and reproductive success were both relatively low and wolf numbers changed little.

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In ***early May*** **1994. al** ***the age of one year, female*** **1071** ***was radiocoUared and evaluated for nutritional condition, genetic characteristics, and exposure to any diseases.***

Two additional wolves died during the 1995 winter study, a yearling female from Middle Pack (wolf 1071) and the elderly alpha female (wolf 450) from the East Pack. The young female was killed when she trespassed into East Pack range, and the East Pack alpha female then disappeared and is presumed dead, probably a victim of old age and the violence of her encounter with the Middle Pack female (see page 9).

As the "old guard" alpha wolves in three packs slowly succumb to old age they are being replaced by the next generation. Largely on the strength of the eight pups from two packs that survived in the 1993 cohort, there is a strong underclass of young wolves looking for opportunities to advance. At the end of the 1995 winter study there remained 11 wolves that were less than four years old; this group included three males, four females, and four wolves of unknown sex. Barring catastrophes, there should be ample wolves of both sexes to fill vacancies as they appear

Last year it was reported how four pups in the Middle Pack were orphaned at the age of nine months when their parents both died of starvation caused by extreme tooth wear and advanced age. In late April we located at least three, and probably all four, of the orphans still together in Middle Pack range. They were scavenging the carcass of a yearling moose that died of malnutrition. At that time two

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Female **1071** ***was killed and partially eaten by wolves in the Exist Pack in February*** **1995.**

Figure 5. Yearling female 1071. born in Middle Pack, explored East Pack territory at least twice in summer 1994. This photo of her was taken in luly by an automatic camera on a moose trail in East Pack territory.

of these wolves were radiocollared and during the summer of 1994 we found that they usually remained within traditional Middle Pack range. A visitor reported finding a wolf-killed moose calf in Middle Pack territory in August, the first evidence that the "orphans" had been able to kill moose. By that time the radiocollared female yearling had made occasional forays into East Pack territory, where she scavenged the carcass of a moose that died of malnutrition (Fig. 5). In January 1995 the Middle Pack yearlings were found, together with dispersing wolves from the East Pack. in two small groups in Middle Pack territory, and both groups were regularly killing moose.

In the past year the age at death was estimated (by M.S. student Carol Waite) for 31 Isle Royale wolves represented in the accumulated skull collection from the past 36 years. Mean survival was about 6 years and the oldest wolf was 11 years old. Female 450 was estimated to be 11 to 15 years old when she died in 1995, but she remained unrecovered. L. D. Mech reported that wolves in Minnesota have been known to live at least 13 years.

In the late 1970s, balsam fir emerged prominently in the forest understory at the east end of Isle Royale. Natural succession will slowly transform this forest from birch and aspen to spruce and fir. In order to investigate relationships between emergence of fir and moose (and wolf) population density, tree-ring width in balsam fir was recently studied by Ph.D. student Brian McLaren. Fir trees exhibited enhanced growth when moose were at low levels and wolves were numerous. It was clear from this study that wolves have indirectly determined forest growth patterns through their direct effects on moose abundance (Fig. 6).

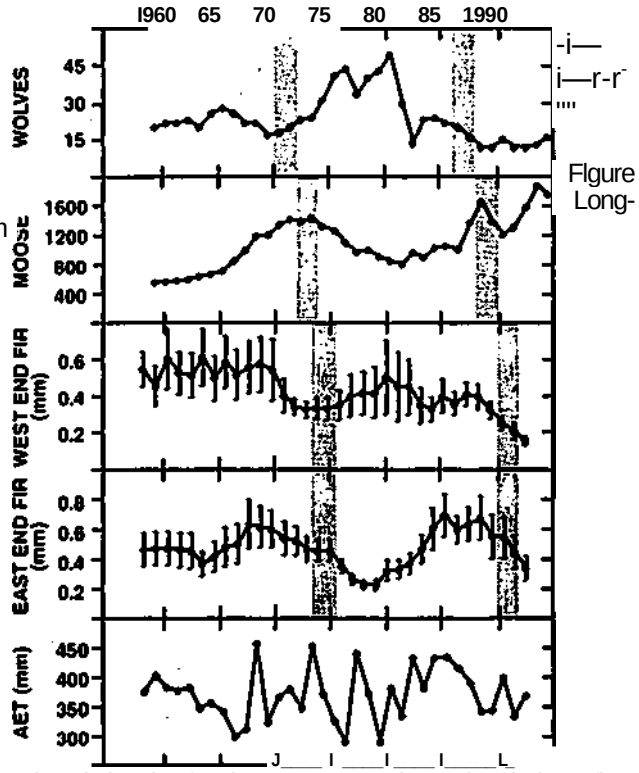

Figure 6. Long-term fluctuations in levels of wolves, moose and growth of balsam fir at Isle Royale suggest top-down control of this community by wolf predation. Trends in the wolf population (usually dictated by the number of old moose) were followed by opposite trends in moose numbers, which induced changes in regenerating fir trees (an important winter forage of moose). Fir growth was little-affected by weather (actual evapotranspiration, or AET) These data appeared in Science 266:1555-1558. December 2. 1994.

West *Pack alpha male* 430 *was born in* 1989 *in the East Pack, then moved to the other end of the island in* 1993 *and assumed the alpha male position in the two-member* West *Pack after the death oj the incumbent.* In *this view in* \anuary 1995, *he displayed an unusual view of his incisors as he had lost a portion oj his upper lip.*

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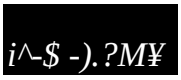

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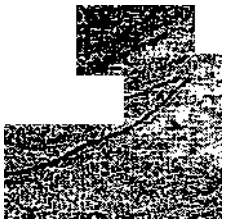

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Typical use o/a *moose carcass by* ls/e Royale wolves *in* 1995—*thorough but not extreme—indicates ample prey availability.*

Each year jn trie rr> id--1990s we carefully scrutinized the ,. East Pack for ferriitei 410. who%utlj?%j[he batteries in her radiocolla'r.. Sh^bec^ine progressively^ White With-age, and by J993wefexpecfed'rlerderriiseiatanytirnje.' Asa-rniddle-aged ' femajejn J9$g< sh&beaffie'|hejfirstwolf to,'Be^live-captured, -"" and radiocollaredtqnjisleRoyale; lb'previous annual reports , variouieven'te';Irt,he|ljfe;haxe'beench *f'*-

In Jafn^a^jI^.^i^JreKlinestTysuV^s^ fo.see her still alive, at H-i^^r^ofti^., Sh> seern^afto.be irj ppprcpndj- ' tion, gaunt wtthysfan^'p^ sJcefeton{ ; Her death s'eernW fn^ljleji^arld) weajily'Jioped." to -Feanf

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ued to lead her pack or six wolves. She sat out some of the extravagant chases, as when the alpha male and the younger members of the pack took off over the ice. Many of her former offspring had

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afte'ra passing fox.

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natal packjinj l^^and^iy^fhfi^lol^Wher sons returned to his.home territory, wiUf a< rad]bc6llare"d female wolf from r the adjacent Middl.e Pack? This pair killed a moose in. East Pack territory-and their-playful courtship-lent an optimistic cast to the future/fljis^as'exactly'the kind.of pairing we hoped for in wolvessof'th'e next generation, when we might learn the implications 'of genetic decay unfettered by low food supplyor disease.'

On January 30 fe'male 450 and her pack discovered a recent moose-kill from the newly-formed pair. A day later (when we were grounded by poor weather), the East Pack caught the pair several miles from the kill and they killed the Middle Pack female in a vigorous struggle. Twenty-four

- hours later, when we became aware of the event and arrived on the scene, only female. 450 remained at the carcass of the dead female. The old^Ipha female was carefully eating flesh from the jib cage ot the,dead: wolf;, the internal organs had already, been consumed; presumably-by raven and wolf. Never before;Had;tse%n'/a^wblf-eatjap6ther, even after killing it. Afidj obviously,, ojd-feniale 450 had;more spunk than I.

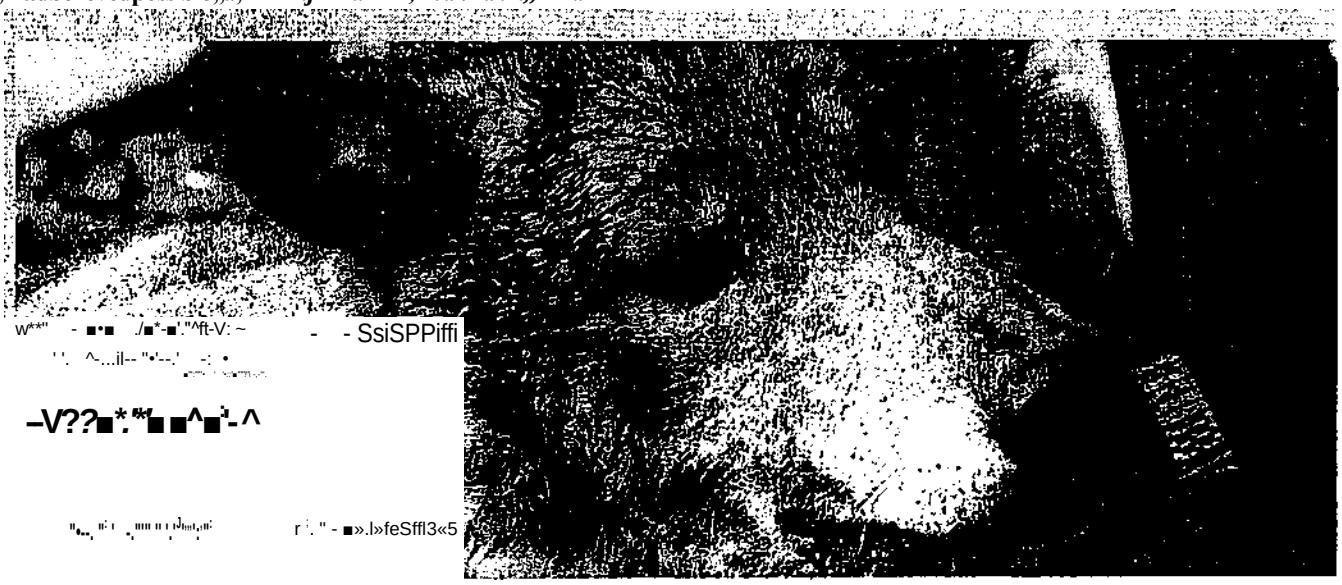
-; hadbelievedpossible;,..;^^"•' .j'i- f'.. '■■ ;■?..V '.. . -„;"" ..

_ We landed on a nearby lake and snowshoed to retrieve the dead wolf. As we emerged at the site a live wolf disappeared . into the shadows of the nearby forest. The kill site was a awe-some^spectade. ahd-we pieced together from tracks how the hapless-female had been chased off a low cliff, was caught below by the East Pack, and'died after a protracted struggle that left 30 - yards of'bloody snow and broken branches. - The young female had lasted a long tirrie; her attackers never succeeded in inflicting any mortal wounds aroufid.her vulnerable neck or head, and she'hsd crocked off two premolar teeth in her final effort.

.We^ were-never to'See;female 450 again! Killing her rival from #if fvUddte *Psek* Was Her last act', and it evidently ', clairried;,he1',flna,lr Reserve *tit* energy. Inihe nextmonth we searched diligently* for, heft.by-alrand on the ground, never finding a duel. For Us. another mystery:>we will search for her borjes.and worri'.radldcbllar under a tree or rock for many y&rs-tb come. She'was quickly replaced in the. pack hierar-chy by'a daughter, and the life of the East Pack resumed.

The alphamale in the East Pack'was left with only two pups and two of his'own,adult daughters in the pack, and mating and reproduction was uncertain in 1995. "Murder, cannibal-ism, and Incest", muttered a colleague, shaking his head. Henry Beston's words came to my own mind, "We need another and wiser and perhaps more mystical concept of ani-mals . .. For the animal shall not be measured by man . . . They are not brethren, they are not underlings; they are other nations, caught in... the splendour and travail of the earth."

Questions of immortality probably do not much interest wolves. But their quest to survive, reproduce, and secure resources for their offspring to carry on with life is unmistak-ably, powerful. the legacy of female 450 was much greater than that of the:"average" alpha wolf. It was her late-bloom-ing reproduction. modest though it was. that allowed the dramaUcexperlment of wolf survival to continue on Isle Royale into the^late 1990s. Though she would care not a whit."science owes'somethi rig.to.this old wolf, and to her. in a detached way, I am most grateful.



The Moose Population

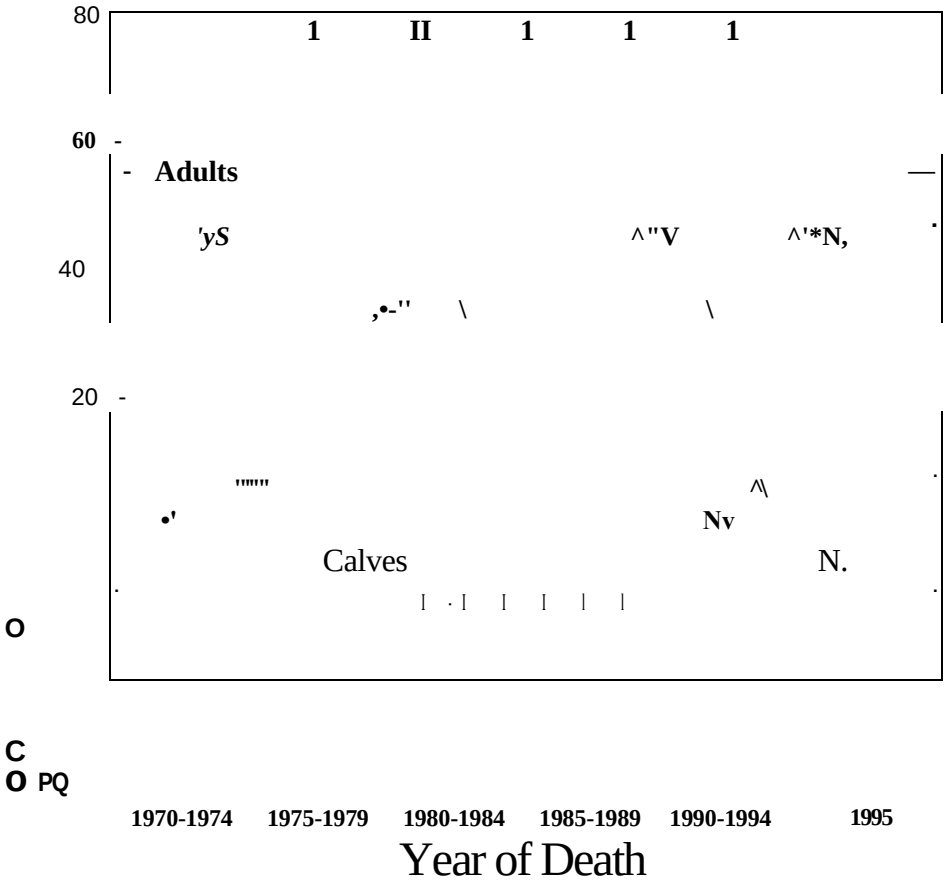


Figure 7. Long-term trends in moose bone marrow fat. Data for calves (which best reflect current conditions) represent mean levels. whereas adult data is the proportion with >70% marrow fat.

The moose of Isle Royale continued to increase during the past year, with population growth retarded little by the diminished wolf population. As moose density grows there is increasing evidence of malnutrition and retarded growth rates (in bone marrow fat levels— see Fig. 7—and measurements of moose calf leg bones, respectively). In the 1995 census many yearling moose remaining with their mothers for a second winter appeared to be little larger than calves of former days.

Even though moose calves are currently growth-retarded, they are still relatively numerous. In field surveys of the 1994 cohort in summer and winter we found that moose calves comprised 12% of the moose observed (Fig. 8).

The size of the moose population was estimated by aerial census in February, 1995, using intensive counts of

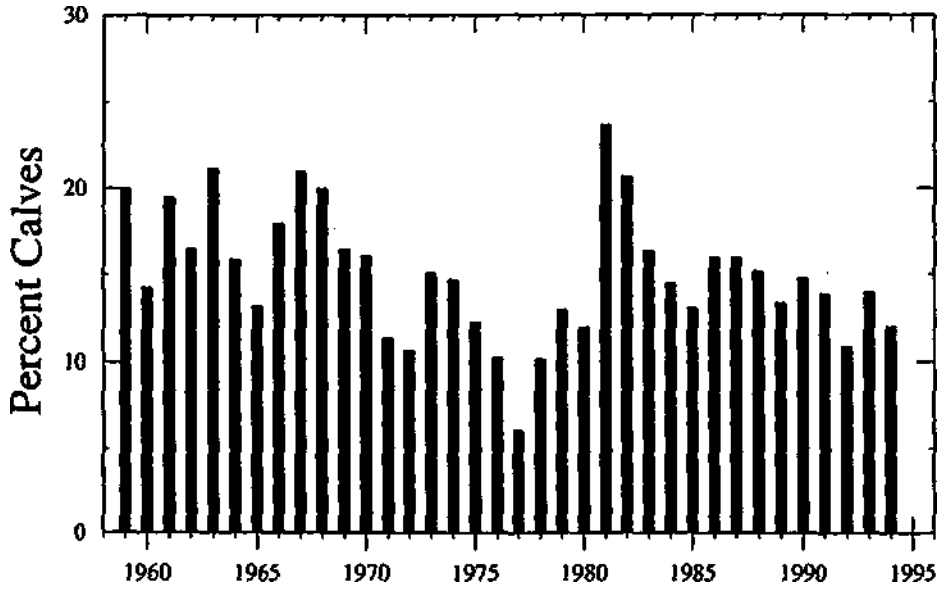


Figure 8. Moose calf abundance (at approximately six months of age) on Isle Royale, as a proportion of the total population. These are single best estimates, the mean of all available counts for each cohort (summer ground observations and aerial counts in autumn and winter).

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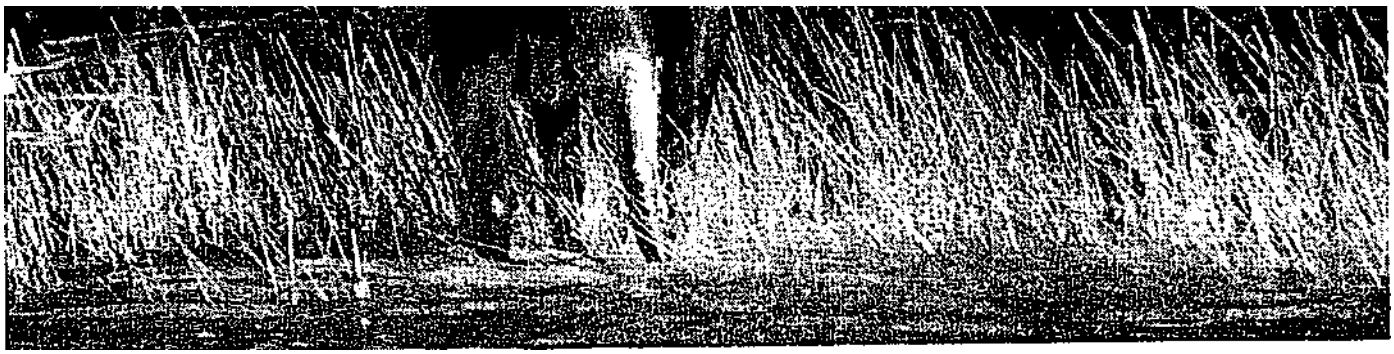
Figure 9. Moose distribution on Isle Royale during the aerial census in February, 1995

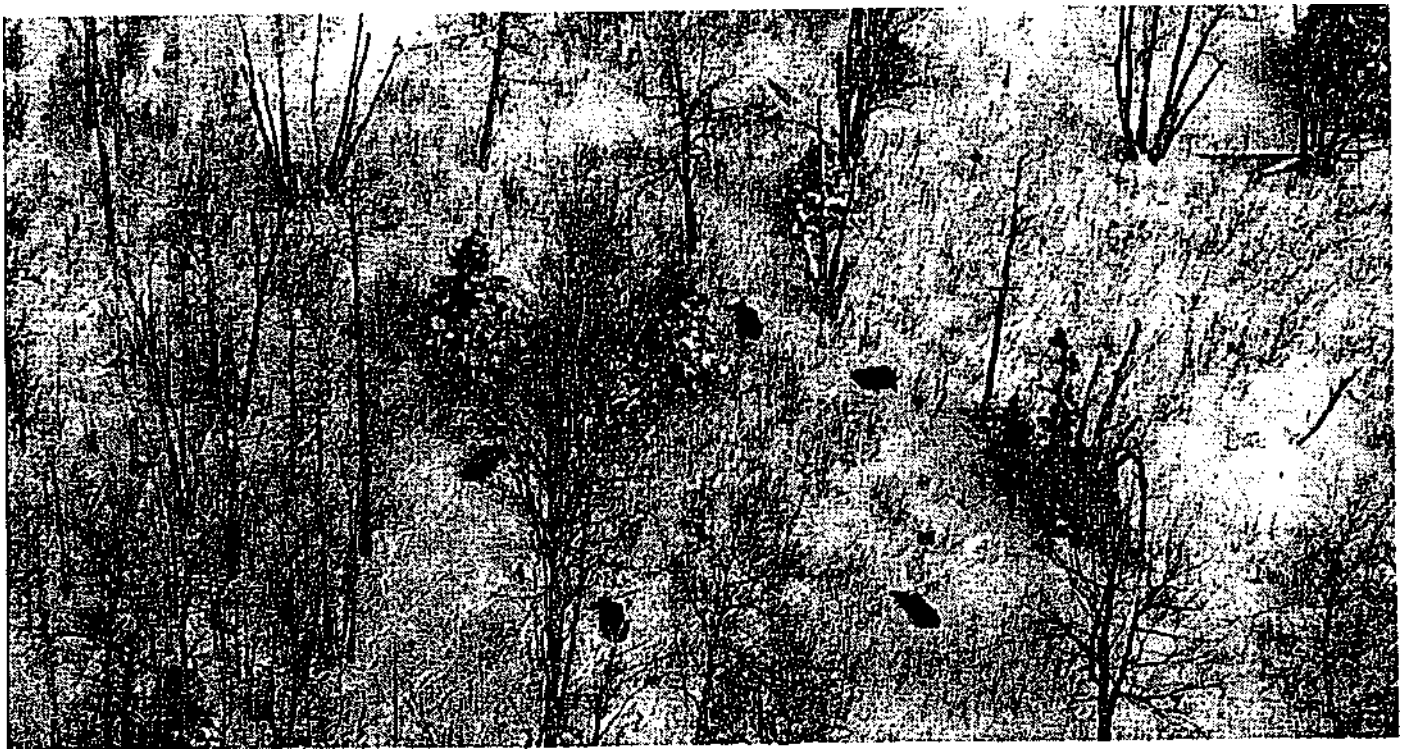
small plots totaling 17% of the island area (Fig. 9). On 10 of the 90 plots we counted 10 or more moose and one plot (one km^J in size) contained 28 moose! On all the plots 451 moose were counted, and we estimated 75% of the moose on the plots were seen. The resulting population estimate was 2.422 moose, with a 95% confidence interval of +/- 362 (15%). This is considerably higher than last year's estimate of 1,770 moose, although some of the increase may be caused by sampling variation.

The last two winters have been relatively easy for moose at Isle Royale. with low snow accumulations. Winter ticks, a potential source of mortality in late winter. have not been exceptionally abundant. Annual assessments of moose condition in winter from ureaxreatinine levels in snow-urine (in collaboration with Glenn Del-Guidice of the Minnesota Department Natural Resources) have shown no increase in catabolism of body protein in winter, suggestive of declining (at reserves. Continued growth of the moose population can be expected until mortality from ticks, starvation, or wolf predation increases. Winter and spring weather patterns might well dictate the course followed by the moose population.

A ***beaming and well-showered Earthwalch learn*** **I** ***poses with the*** **1994** ***moose bone collection.***



In *spile of extreme shortage of forage in winter, moose on* **Isle** *Royale can recover body condition in summer on a diet nch m deciduous and aquatic plants*



Wth low snow depths early in **1995.** *moose remained in open habitats much longer than usual. By February most moose had gravitated to thicker coniferous forest stands. This group was near Angleworm Lake.*

Other midlife

Red fox and snowshoe hare abundance (Figs. 10 and 11) were both relatively low in 1995, after an eruption of hares in 1988. Foxes appear to be in decline while hares may be increasing from a recent low. Following the hare increase in the late 1980s, foxes increased and then hares declined. We speculate that the wolf decline of the 1980s meant reduced food (from moose carcasses) for foxes and precipitated a decline in fox abundance in the middle-1980s. A snowshoe hare increase then followed, and since that time there is more evidence of regular fluctuations in fox and hare, in a classical predator-prey relationship. This suggests a indirect but influential role of one predator-prey system (wolf-moose) on another (fox-hare). As part of a long-term, park-funded monitoring program, a beaver census was flown in October 1994 by Douglas W. Smith, continuing the work begun in the early

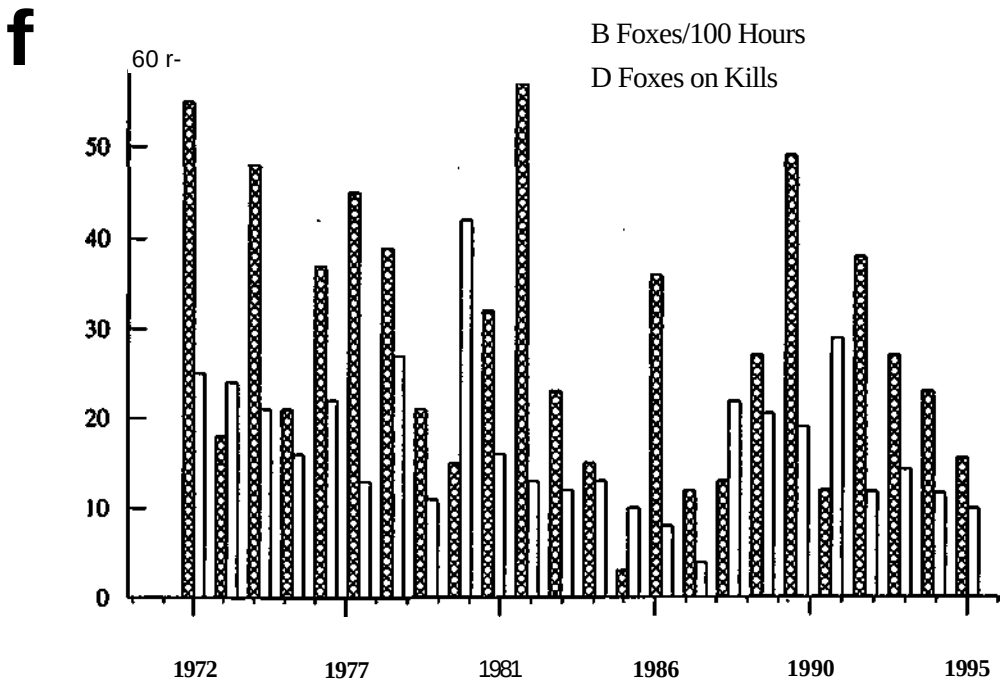


Figure 10. Relative abundance of red foxes from aircraft observations, 1972-1995. Hatched bar is the number of foxes seen away from moose carcasses/100 hours, while the open bar is the number of foxes seen on carcasses.

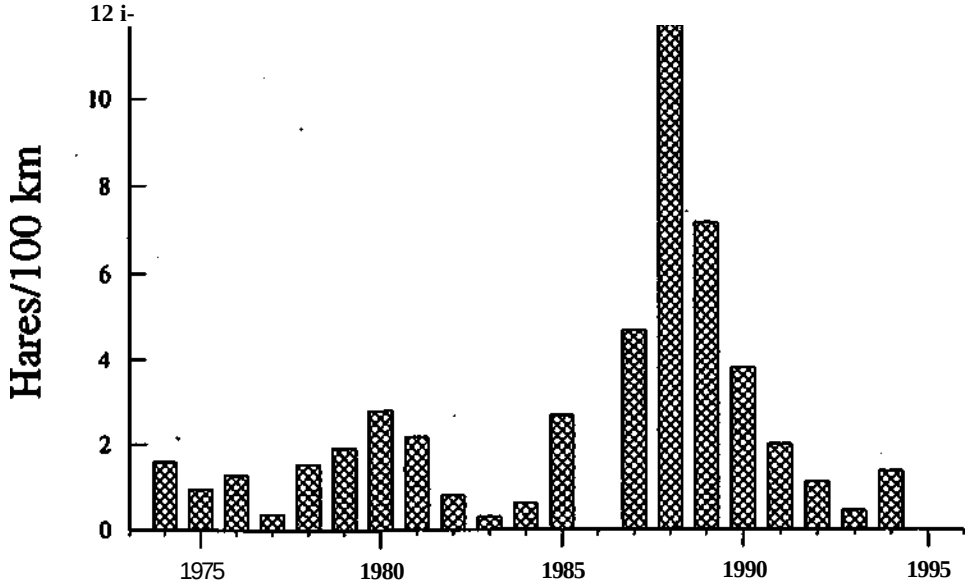


Figure 11. Snowshoe hares on Isle Royale have decline to very low levels after an population irruption in the late 1980s. Index is the number seen per 100 km hiked in summer.

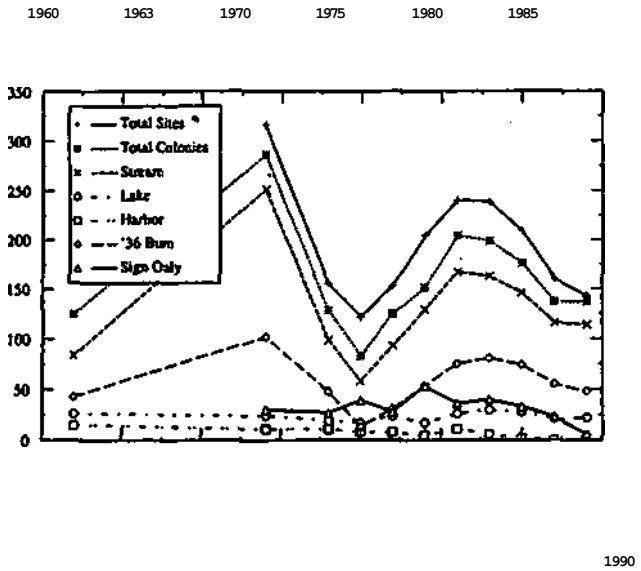


Figure 12. Beaver population trends on Isle Royale in specific habitats.

Figure 13. Mountain ash fruit remained heavy on trees in lanuary 1995, allowing mapping of this tree's distribution by aerial survey.

1960s by Philip C. Shelton. There was little change in beaver colony abundance in the last two years (Fig. 12), but there is evidence of continuing slow decline that probably reflects slow reduction in suitable habitat. The short-term beaver decline around 1980 was correlated with the peak in wolf abundance, suggesting limitation by predation which has now been relaxed.

Bald eagles and ospreys are slowly increasing at Isle Royale after disappearing completely in the in the aftermath of DDT use (nesting bald eagles were absent at Isle Royale from 1969 until 1985). In 1993 the National Park Service recorded six active eagle nests, probably fledging nine young, along with three osprey nests, at least one of which was successful. Eagles were seen several times during winter 1995. as little ice formed and there were ample foraging opportunities near open water in Lake Superior.

Mountain ash, a year-round favored forage plant for moose, also feeds foxes, ravens, and many other species with its fruit. The 1994 crop of fruit was unusually heavy and persistent (Fig. 13), allowing us to roughly map the distribution of this important but uncommon tree throughout the island (Fig. 14).

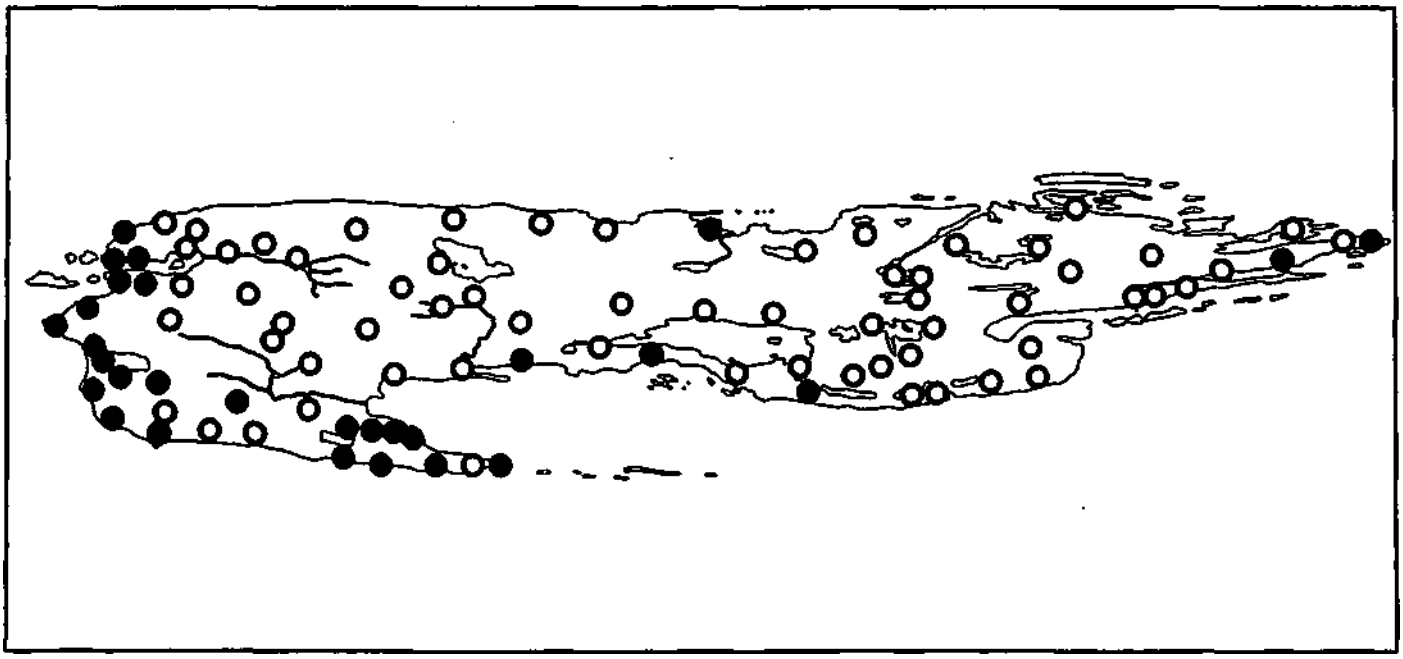
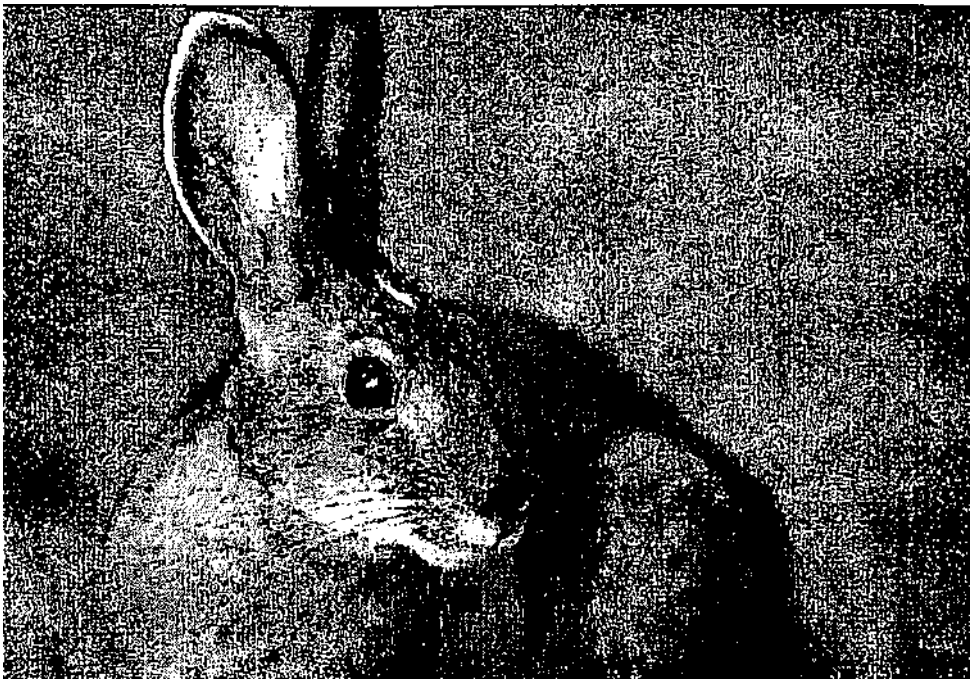
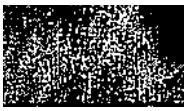


Figure 14. Presence (filled circles) or absence (unfilled circles) of mountain ash trees on moose census plots during a February 1995 aerial survey. Concentrations of these trees, usually along shorelines, were invariably associated with favored wintering areas for moose.





A/ter *reaching a peak in* **\ 988** *snowshoe hares became scarce for many years, but in* **1994** *there were indications of the beginning of recovery.*

Tfie red /ox al *Isle Royale relies almost entirely on snowshoe hares for prey in winter if wolf-killed moose are not plentiful. This may induce a* **classical** *predator-prey oscillation.*

Weather, Snow and Ice Conditions

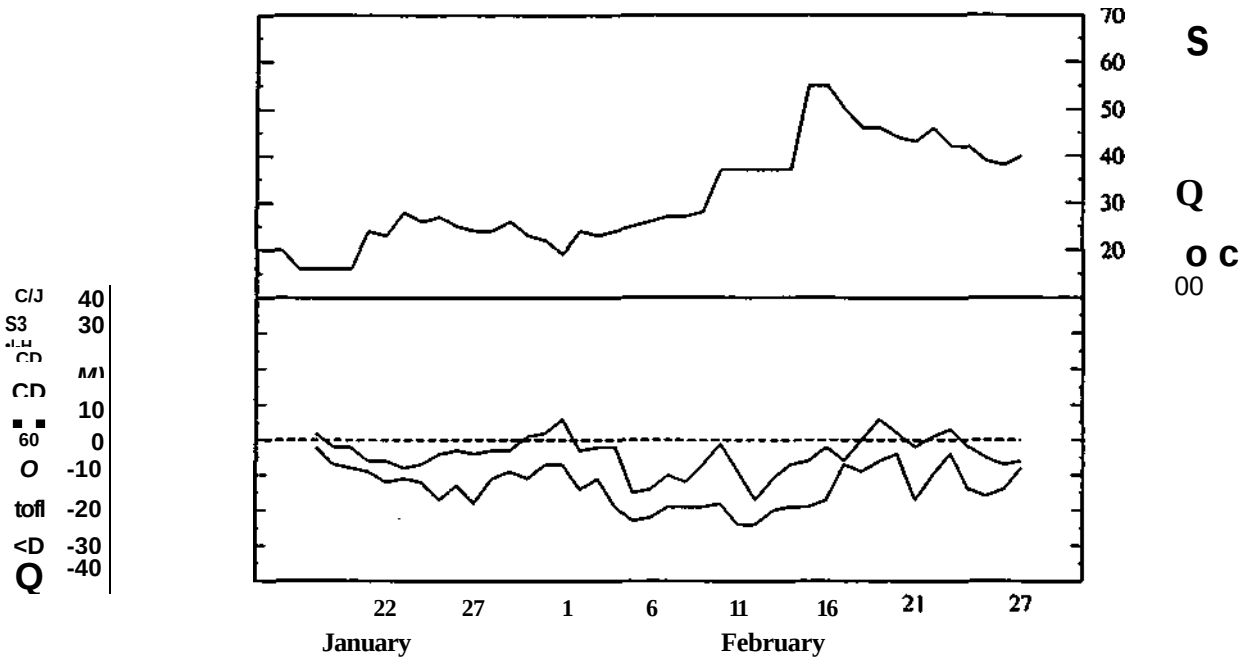


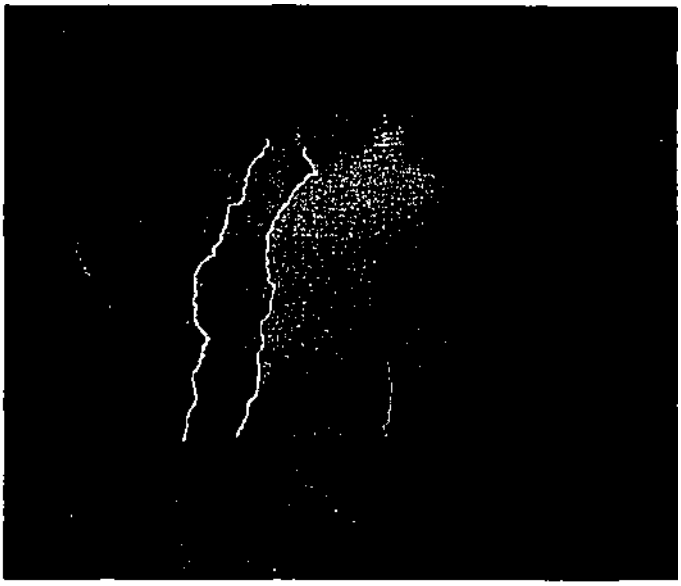
Figure 15. Snow depth (top) and temperature extremes during the 1994 winter study on Isle Royale.

In keeping with an El Nino year (anomalous warming ol the Pacific Ocean surface and resulting disruption of ocean currents and atmospheric jet streams). Isle Royale had a very mild winter in 1994-1995. Violent winds characterized lanuary and early February, often curtailing our aerial surveys.

Temperatures during the 1995 winter study were not tar above seasonal norms, but temperatures before and after the study were notably warmer than average (Fig. 15)

Snowfall was also very light, as in the previous winter. When we arrived on lanuary 15 there was only 20 cm of fresh snow and the ground had been mostly bare until that time. Snow depth gradually increased to a maximum of 50 cm in mid-February before declining during major daily thaws beginning late in February. An early spring was expected again in 1995. so moose mortality from malnutrition should be light

***Shoreline ice was almost completely absent around \sle Royale during the winter of* 1994-1995.**



A *thunderstorm crackled over Moskey Basin in* 1994, *a year with no significant naturally-ignited fires {a small bum resulting from lightning near Todd Harbor in \une did not gel far).*