WOLF-MOOSE INTERACTION IN ISLE ROYALE NATIONAL PARK

Final Report

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Abstract: Summarized here is a 27-year study of wolf and moose populations at Isle Royale National Park, undertaken in 1958 in order to clarify mechanisms of population regulation for this predator-prey system. Wolf numbers remained relatively static in the 1960's but moose increased to a level where moose foraging adversely impacted their food supply. A series of severe winters beginning in 1969 accentuated the food problem for moose, leading to increased moose vulnerability to wolf predation. Wolves increased in the 1970's while moose declined from the direct effects of predation and malnutrition. Wolf numbers remained at a high level from 1976 to 1980, but food level measured in winter steadily declined. When average food availability for some packs dropped to 3 kg/wolf/day some wolves died of malnutrition and there was an increase in territorial trespassing. During 1980-82 more than 50 wolves died and the wolf population crashed to a low level of 14 individuals. The spatial and social organization of the population was completely re-structured and the wolf population then recovered to a level near the long-term average. As soon as wolf numbers were reduced moose calf survival approximately doubled, leading to a sustained increase in the moose population during the first half of the 1980's. Food availability for wolves, estimated from their kills during a 50 day period in winter, provided an adequate basis for understanding wolf population fluctuations. Moose population size, in turn, was largely determined by wolf predation level, which was sufficient to hold moose for long periods below levels at which forage limitation was influential. Wolf predation, however, was not sufficient to maintain moose at a low, stable equilibrium; rather, moose slowly "escaped" to a higher population level where forage limitations brought about increased malnutrition and vulnerability to wolves. This scenario represents our most recent characterization of wolf-moose dynamics at Isle Royale, a long-term cycle lasting 30 years or more which can be attributed to interactions among wolves, moose, and vegetation. We think trophic interactions among all 3 levels must be integrated in order to adequately understand the Isle Royale system. Long-term study has proven essential to discovering critical aspects of wolf-moose dynamics. By comparison, our understanding of moose-forage interaction is in its infancy. Management recommendations can be summarized as follows: 1) minimize human influence of wolf-moose dynamics (primarily distribution and mortality of both moose and wolves); 2) continue to allow all naturally-occurring fires to burn unimpeded; and 3) continue monitoring and research efforts.

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Author's note: Certain data and conclusions contained herein are preliminary or part of ongoing research. Please consult the author before citing in scientific publications.

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CHAPTER ONE

WOLF AND MOOSE RESEARCH ON ISLE ROYALE

After 26 years of study of wolf-moose ecology at Isle Royale National Park, investigators have arrived at an important stage of synthesis, marked by development of new research hypotheses. Throughout this research program the major objective has been to clarify the nature of predator-prey interaction between naturally-regulated populations of wolves and moose, with emphasis on mechanisms of population regulation for these two species.

Based on an assessment of moose calf recruitment and wolf predation rates during 1959-61, Mech (1966) argued that wolf predation was maintaining a stable moose population below limits imposed by moose food supply. Subsequent periods of investigation concentrated on assessment of moose population trends and population dynamics of other Isle Royale mammals. Census techniques used throughout the 1960's did not allow accurate determination of moose population size, but by the late 1960's it was clear that it had perhaps doubled, with at least 1200 moose present. A series of severe winters beginning in 1969 accentuated the depleted food supply for moose, and set the stage for a major moose decline. During the early 1970's moose declined by 50%, while a previously stable wolf population began a sustained increase. Updating Mech's conclusions, Peterson (1977) felt that wolf predation controlled moose density, but only within limits dictated by food supply. He interpreted the moose decline of the early 1970's as a shift to a lower density equilibrium attributable to forest maturation, especially in the 1936 burn. From this conclusion followed the prediction that moose should remain at a lower density.

Moose were clearly held at a low level during the late 1970's by a record-high wolf population (Peterson and Page 1983). The increase of moose that followed the wolf crash of 1980-82 disproved the hypothesis of Peterson (1977) that wolf predation sensitively adjusts moose population levels to food supply (i.e. without lags). Peterson et al. (1984a) recently published a new hypothesis based on the idea that Isle Royale wolves and moose will continue to follow a long-term cycle with a period length of about 30 years.

This report presents a summary of conclusions based upon data collected through 1983. It reviews wolf population changes over the past decade, including data from 1984 (Chapter 1). It analyzes wolf population dynamics beginning in 1975. Peterson (1977) terminated his discussion with 1974 data. The report reviews response to declining prey density and wolf-prey dynamics in Chapter 3, and wolf regulation of moose in Chapter 4 (including a review of alternate hypotheses

of moose population regulation). We summarize the status of our understanding of moose-vegetation interaction on Isle Royale in Chapter 5 and provide management recommendations for Isle Royale National Park in Chapter 6. Finally, we include appendices summarizing aspects of the long-term data base now available for Isle Royale wolves and moose.

STUDY AREA

Isle Royale National Park is composed of 1 large island measuring 544 km^2 plus numerous off-shore islands with very little area, located about 20 km from the north shore of Lake Superior. The island has formed as the uptilted edge of numerous layers of metamorphosed bedrock of igneous and sedimentary origin, resulting in a long and narrow island with a high ratio of shoreline to area. Boreal forest vegetation dominates the island with white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), paper birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*) occurring in greatest abundance. At higher elevations on the southwest end of Isle Royale is a hardwood forest dominated by sugar maple (*Acer saccharrum*) and yellow birch (*Betula allegheniensis*). Glacial till is sparse and soils are thin and poorly developed on the northeastern 2/3 of the island, while on the southwestern 1/3, glacial till is thick and soils are more developed. North-facing slopes are steep, while south-facing slopes are quite gradual. Each winter, all interior lakes and protected harbors on the island's periphery are frozen from November or December until April. Extensive shelf ice commonly forms along most of the island's shoreline, and every 2-3 years a rough ice bridge to Canada forms briefly in mid-winter. Since 1971, exceptionally smooth ice bridges formed only during 1976-77 and 1978-79.

The island is usually snow-covered from December through March. During mid-January to early March snow depths in open areas are usually about 50-60 cm, with extreme depths occasionally reaching 100 cm.

About 2/3 of the mammalian species present on the adjacent mainland have never colonized Isle Royale. Only moose and beaver are prey for the Isle Royale wolves. In winter wolves are almost entirely dependent upon moose, with beaver available only occasionally during midwinter thaws.

In order to ensure a complete sanctuary for the wolf population, Isle Royale National Park is closed to visitors from November to mid-April. The only human inhabitants during the closed season are members of the research and monitoring crew, who gather data primarily from aircraft. During the summer visitor season, most human activity is restricted to hiking trails, with closures instituted in areas with a history of intensive wolf use (dens and summer homesites).

METHODS

Almost all wolf observations were made from aircraft during an annual winter study beginning about 20 January and extending for 7 weeks. National Park Service policies have not allowed handling of any wolves, precluding use of radio-telemetry to locate wolves for observation. Wolves were located by snow-tracking from light aircraft (Aeronca Champ, Citabria, or Piper PA-18 Supercub) on a daily basis if weather and snow conditions permitted. Wolves have become accustomed to the presence of the aircraft and exhibited virtually no avoidance behavior. Wolves were observed with 7X wide-field binoculars or, in 1984, with a gyroscope-stabilized monocular viewing device (Fraser-Volpe, Inc., Warrington, Pa.). Wolves were back-tracked whenever possible to their previous location, ideally providing complete coverage of travels and kills made since last observed.

Wolf packs were distinguished by size, location, and identifiable pack members (usually alpha, or dominant individuals). Packs were generally cohesive, and frequent observations allowed us to identify packs easily. Individual wolves were often recognized on a day-to-day basis by body conformation, pelage appearance, and, especially, tail characteristics. In rare cases, individuals were sufficiently unique that year-to-year recognition was possible. Social status of individual wolves was inferred from behavioral interactions among pack members (Peterson 1977).

Aside from major packs, single wolves and small, non-territorial packs numbering up to 5 wolves were tracked and observed opportunistically. A complete count of the wolf population was made at least twice during each annual study, more commonly several times.

During summer, ground personnel gathered data on wolf food habits and reproduction. Traditional dens and homesites were checked each year, and, if occupied, spontaneous and induced howling provided some data on the number of pups present. Abandoned sites were thoroughly examined for prey remains and scats, and additional scats were examined throughout the island during approximately 800 km traveled annually.

Prey populations (moose and beaver) were censused periodically throughout the study. A complete count of beaver colonies was made from aircraft in 1974, 1978, 1980, and 1982 by the same pilot and observer (Shelton and Peterson 1983). During 1969-83 moose population estimates were based on aerial sampling using stratified random quadrats (Peterson 1977), a winter aerial index (moose/hr) and a summer ground index (moose/100 km). Summer and winter indices were significantly correlated (r^2 = 0.52, p<0.001). The quadrat counts in 1970,

1980 and 1981 were used as alignment points for the summer index. The estimates based on the summer index, the longest data set, were used to convert the winter index to an additional estimate of moose density. Our annual best estimate was the average of all available estimates for a given year.

During 1971-84, as in previous studies of Isle Royale wolves and moose (Mech 1966; Jordan et al. 1967; Wolfe and Allen 1973), light aircraft were used to census and observe wolves and moose in midwinter, from approximately mid-January to early March. A total count of wolves was made each winter after the pattern established by Mech (1966). During daily flights, weather permitting, wolf packs and individuals were located by snow-tracking, and we tried to maintain, through back-tracking, a complete travel and predation record for the major packs on the islands. In some cases a complete kill record could be reconstructed in the absence of a complete travel record; complete travels were available for 66% of the time during which kills were recorded.

Virtually all kills were examined on the ground during winter or the following summer in order to gather data on age, sex, and condition of the victim. Since utilization of carcasses was highly variable and depended on the elapsed time between the kill and the examination, we estimated food availability based on assumed edible prey weights provided by Peterson (1977). Age was assigned to moose less than 18 months old on the basis of tooth eruption. For older moose we estimated age in years from growth annuli in ground molars (Wolfe 1969) or sectioned incisors (Sargeant & Pimlott 1959).

CHAPTER TWO

THE RISE AND FALL OF ISLE ROYALE WOLVES, 1975-84

The general correlation between wolf density and ungulate prey biomass (Keith 1983) reflects the fundamental link between wolf population dynamics and food supply. Packard and Mech (1980) have reviewed how social behavior directly influences wolf pack dynamics in relation to food abundance. Beyond these general concepts, however, lies substantial uncertainty over the relationship between wolf food supply and prey vulnerability (as distinct from density). Likewise, the significance of seasonal fluctuations in food supply remains largely unknown.

Research into natural population regulating mechanisms for wolves is hampered by continuing persecution by man. Isle Royale National Park provides the only site in the world where intensive studies of wolves have been carried out in the absence of important human influences. The natural prey population fluctuations of the past decade provide important data on wolf population response to changing food supply. In this chapter and the next are details of changes in the wolf population and predation characteristics in the face of a major prey decline. These are discussed especially in relation to natural intrinsic and extrinsic controls on wolf density.

PREY POPULATION STATUS

The major prey species supporting Isle Royale wolves are moose and beaver. From the early 1970's to the late 1970's both prey species declined, then stabilized, and finally increased during 1980-82 (Tables 1 and 2).

Beaver increased to peak levels by the early 1970's, with the highest colony count obtained in 1974 (Shelton and Peterson 1983). Subsequent surveys in 1978 and 1980 revealed a steady decline to a low which corresponded to peak wolf numbers. Following the wolf crash of 1980-82 beaver numbers recovered, increasing from a mere 29% of the 1974 peak in 1980 to 53% of the peak in 1984.

The inverse correlation between wolf and beaver numbers suggests a strong influence exerted by wolf predation on beaver density. Equilibrium beaver density, defined by long-term average numbers, still appears to be responsive to forage abundance. For example, beaver colony density in Voyageurs National Park in Minnesota is some 3 times higher than at Isle Royale (Peterson, unpubl. data). Voyageurs National Park supports young successional stage forests with abundant aspen stands while Isle Royale forests are old with a

high proportion of conifers. Wolf numbers and total land area are comparable in the 2 areas.

During the early 1970's moose numbers declined from a peak of at least 1,150. Jordan and Wolfe (1980) estimated that peak population size was 1,200-1,500. A low point of about 500 moose was reached by 1977, and moose remained relatively stable at this low level until 1982.

The large cohort of 1981 signaled the beginning of recovery for the moose population. Calf abundance in October averaged 23 calves/100 cows during 1972-80, a period of decline and stabilization. In October 1981, after the wolf crash was fully underway, calf abundance stood at an unprecedented 61 calves/100 cows. During 1982/84 this dropped to 30-35 calves/100 cows, sufficient to provide an annual growth rate of about 5% for the moose population.

We have hypothesized that wolves and moose at Isle Royale are fluctuating on a long-term cycle lasting about 30 years (Peterson et al. 1984a). As the single most important mortality factor operating on this moose population, wolf predation has obviously been responsible for major trends in moose numbers. In Chapter 4 we discuss alternative views on the role of wolf predation in regulating moose density.

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Table 1. Beaver population size in Isle Royale National Park, 1974-84.[a]

Year	Number of beaver colonies
1974	286
1978	129
1980	83
1982	125
1984	151

[a]Shelton and Peterson (1983) and P.C. Shelton (pers. commun.).

Table 2. Moose population size in Isle Royale National Park, 1969-84.

Year	Summer moose/100 km (pop.est.)	Winter moose/hr (pop.est.)	Quadrat estimate (+95%CI)	Best estimate, moose
1969	-----	-----	1150+266	1150
1970	22(986)	-----	945+242	966
1971	11(674)	-----	-----	674
1972	14(759)	-----	912+355	836
1973	16(816)	6.05(787)	895+261	802
1974	17(844)	5.23(705)	-----	815
1975	15(788)	5.86(768)	-----	778
1976	9(618)	4.82(664)	-----	641
1977	6(533)	2.98(480)	-----	507
1978	7(561)	3.42(524)	-----	543
1979	6(533)	4.22(604)	888+171	675
1980	6(533)	4.32(614)	585+164	577
1981	7(561)	4.85(667)	481+132	570
1982	6(533)	3.25(507)	729+209	590
1983	12(703)	6.48(831)	900+195	811
1984	-----	-----	781+187	781

WOLF POPULATION CHANGES

Wolf numbers and social organization

In 1972-74, just prior to the study phase reported here, the wolf population comorised 2 packs, reaching a maximum of 31 animals in 1974 (Peterson 1977). During 1975-80 the wolf population increased each year except 1977 and fluctuated between 34 and 50 individuals (Fig. 1 and Table 3). Additional packs became established during this period, until 5 were present in 1980 (Fig. 2). New packs appearing during this period were Middle Pack (1975), Southwest Pack (1976), and Harvey Lake Pack (1980). In 1979 the West Pack, recognized since 1968, finally disappeared.

Packs that were added during the increase phase resulted from growth of small packs or pairs that became established in areas not utilized by major packs. In 1975 the Middle Pack, which appeared to consist of an alpha pair and 5 pups, ranged over the middle of the island between the 2 established packs. The small, reddish alpha female resembled one of the Todd Duo wolves, present in the same area the previous 2 years. The Southwest Pack in 1977 contained a wolf that had traveled in the same area the previous year in a group of 3.

Over a period of 4 years (1976-79), the Southwest Pack became established in traditional West Pack territory and appeared to finally displace the West Pack (Fig. 2). In 1978, the final year in which it was recognized, the West Pack shifted into a portion of the island containing almost no moose in midwinter. In the following winter the 1978 West Pack range was virtually vacant, but 7 seemingly non-territorial wolves were found at the NE end of the island. The 7 wolves were initially seen together, but usually were split into groups of 3, 2, and 2 singles. Both the trio and duo traveled back to the old West Pack territory, and the duo remained there after killing a moose. The trio returned to the NE end of the island and traveled over areas not heavily used by the resident East Pack. It is possible that some of these wolves became successfully established at the NE end, as a small group resided there in 1980 and 1981.

A wolf "crash" occurred in 1980-82, when the population dropped from 50 to 14 wolves. One major pack, probably the Southwest Pack, disappeared completely, and all packs were greatly reduced. The only pack that we could trace with certainty from 1980 to 1981 was the Harvey Lake Pack. Both the West Pack II and the East Pack II used portions of the island similar to previously recognized packs, but the drastic changes in pack size and the lack of recognizeable wolves precluded a determination of their origin. The West Pack II utilized primarily the SW half of the island and was probably a remnant of the Southwest or Middle packs. This pack used a

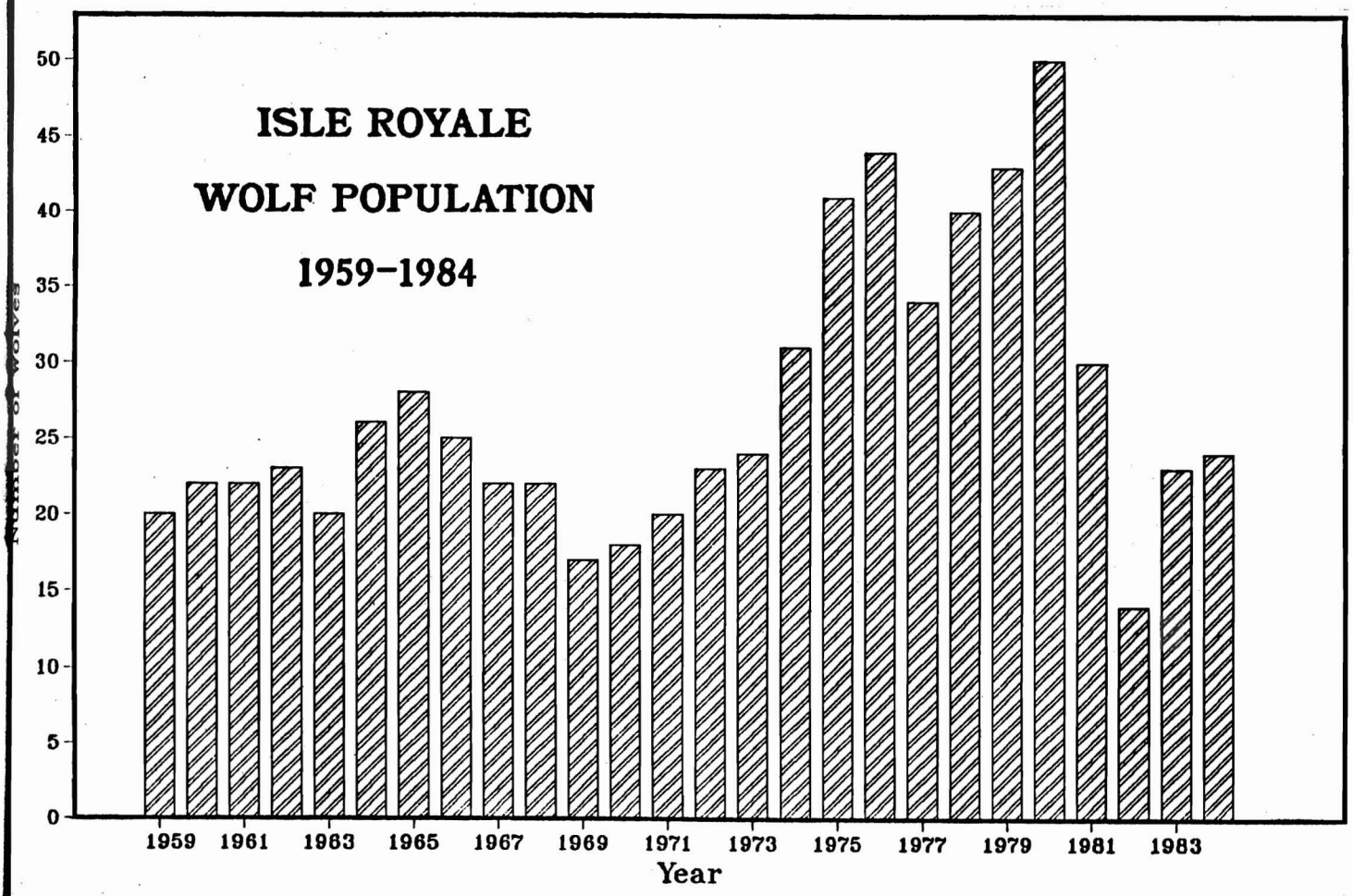


Fig. 1. Isle Royale wolf population fluctuations, 1959-84. Data from Mech (1966), Jordan et al. (1967), Wolfe and Allen (1973), Peterson (1977), and this study.

Table 3. Isle Royale wolf numbers and organization, 1975-84.

Year	Packs										Total
	Size of established packs					Size frequency distribution of other groups					
	East	West	Middle	Southwest	Harvey Lake	5	4	3	2	1	
1975	18	10	7	--	--	--	--	1	1	1	41
1976	17	9	4,3	3	--	--	1	--	1	2	44
1977	13	7	7	4	--	--	--	--	--	3	34
1978	12	8	11	7	--	--	--	--	--	2	40
1979	11	--	14	9	--	1	--	--	1	2	43
1980	10	--	14	7	4	--	1	--	3	5	50
1981	9	--	7	6	3	--	--	--	1	3	30
	East II	West II									
1982	2	4	--	--	2	--	--	--	1	3	14
1983	7	7	--	--	6	--	--	--	--	3	23
1984	5	10	--	--	6	--	--	--	--	3	24

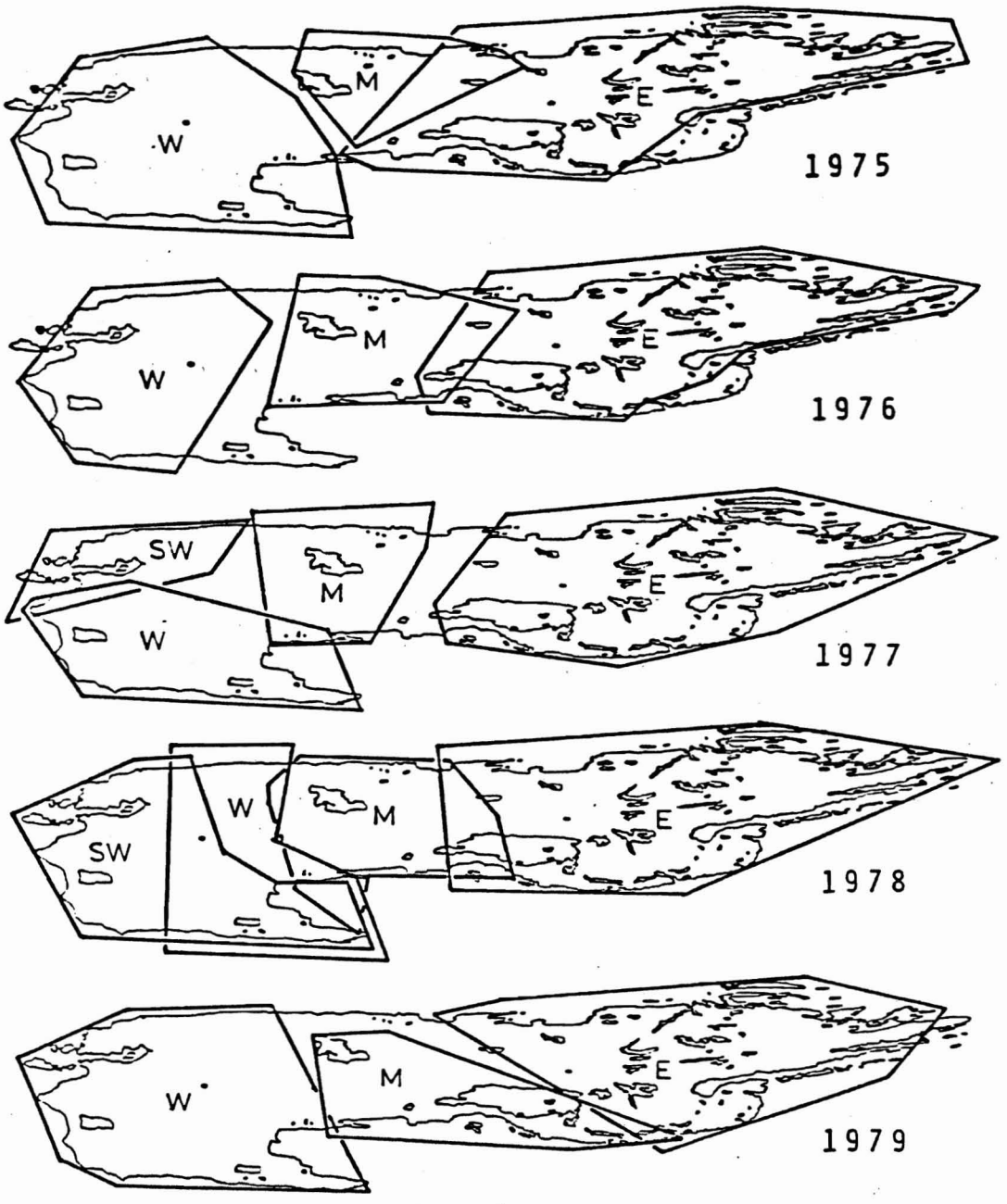


Fig. 2. Isle Royale wolf pack territories as indicated by midwinter movements, 1975-84. Pack abbreviations are as follows: W = West Pack, E = East Pack, M = Middle, SW = Southwest Pack, HL= Harvey Lake Pack, WII = West Pack II, EII = East Pack II, NE = Northeast Pack.

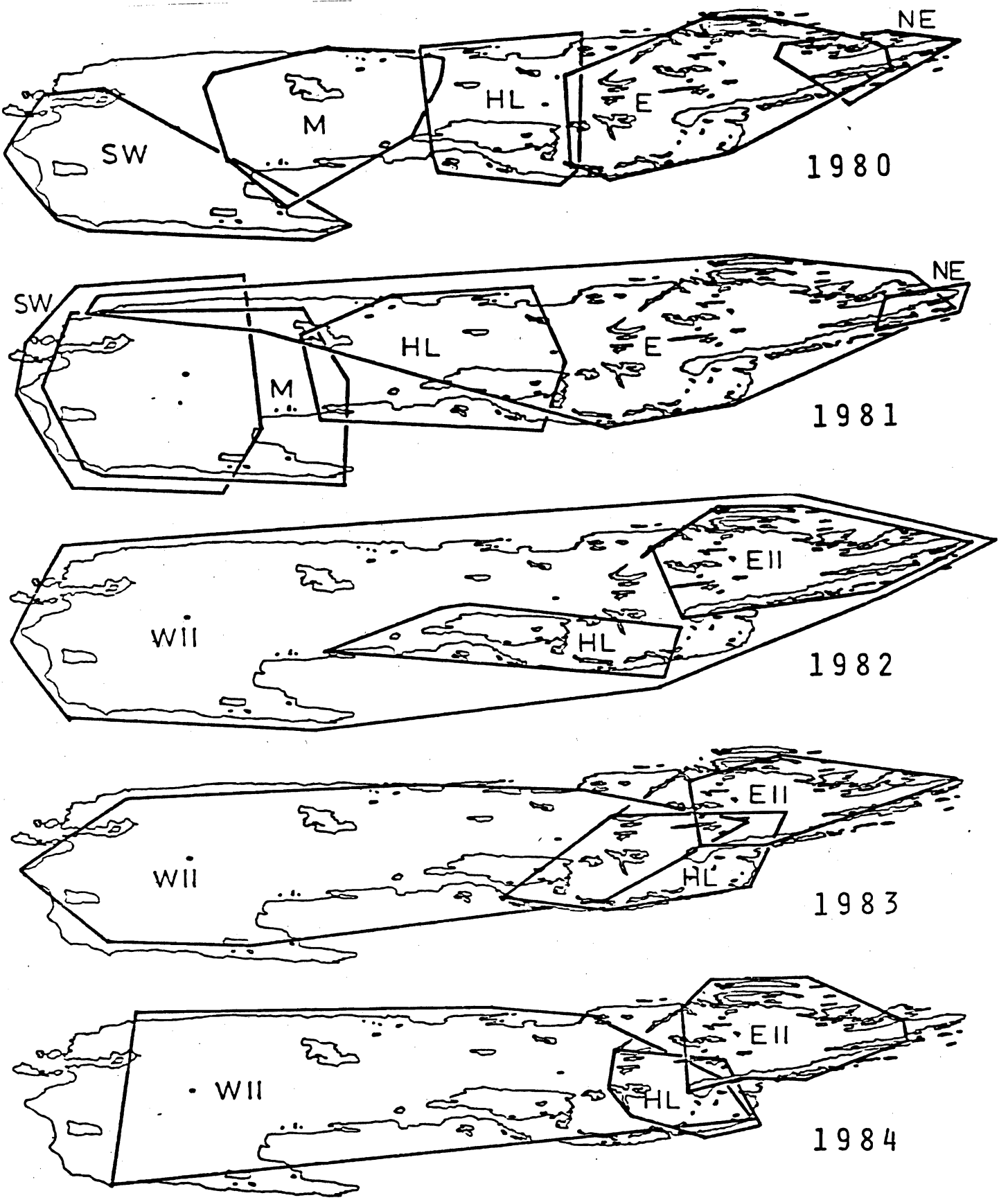


Fig. 2 (continued)

traditional Middle Pack summer homesite in 1983, suggesting ties with this former pack. The East Pack II could have originated from either the NE Pack or the East Pack. In 1982 and 1983 it utilized areas which had not served as summer homesites for the East Pack during the previous 9 years.

Spatial organization

The typical spatial organization for Isle Royale wolves in winter consisted of discrete and exclusive pack territories. Trespassing into another pack's territory was insignificant prior to 1981. In 1978, when the territories of the West Pack and the Southwest Pack overlapped, areas of intensive use were still separate. Territorial boundaries broke down in 1981, when the East Pack traveled the entire north shore of the island, and the Southwest and Middle packs showed extensive spatial overlap.

A complete break with the past was observed in 1982, when the West Pack II traveled the entire island, including areas used by both other packs. The following year the West Pack II still claimed 65% of the island. Meanwhile, the Harvey Lake Pack traveled extensively in territory used by its two neighboring packs, and in 1984 this pack was totally deprived of an exclusive territory.

As noted elsewhere (Peterson et al. 1984), territory size for Isle Royale wolf packs is correlated with pack size (Fig. 3). Peterson found that on the Kenai Peninsula in Alaska, 2 newly-established pairs of wolves claimed disproportionately large territories to accommodate at least a year of pack growth. Such a "superterritory" was documented for the West Pack II during its first 2 years, so these data points were excluded from the analysis of correlation.

Wolf food supply

Food supply in winter was indicated by the biomass of prey actually killed by wolves. Assumed prey weights and % utilization estimates follow Peterson (1977). Food supply per wolf showed a similar trend as food supply per pack except in 1982 (Figs. 4a & 4b). In that year, packs were extremely small but pack kill rates did not decline accordingly.

Overall trend in winter food availability in the 1970's was downward in approximately linear fashion. Food supply then stabilized at a relatively low level. There was no significant correlation between wolf food availability (a reflection of kill rate) and moose density. The longest data string for a single pack is the record of the East Pack II from 1972 through 1981. Food availability for this pack was consistently above that of other packs, although finally dropped in 1980. Food supply for East Pack members on a per wolf basis dropped to 4 kg/wolf/day as the pack increased to maximum size in 1975. The kill rate remained relatively

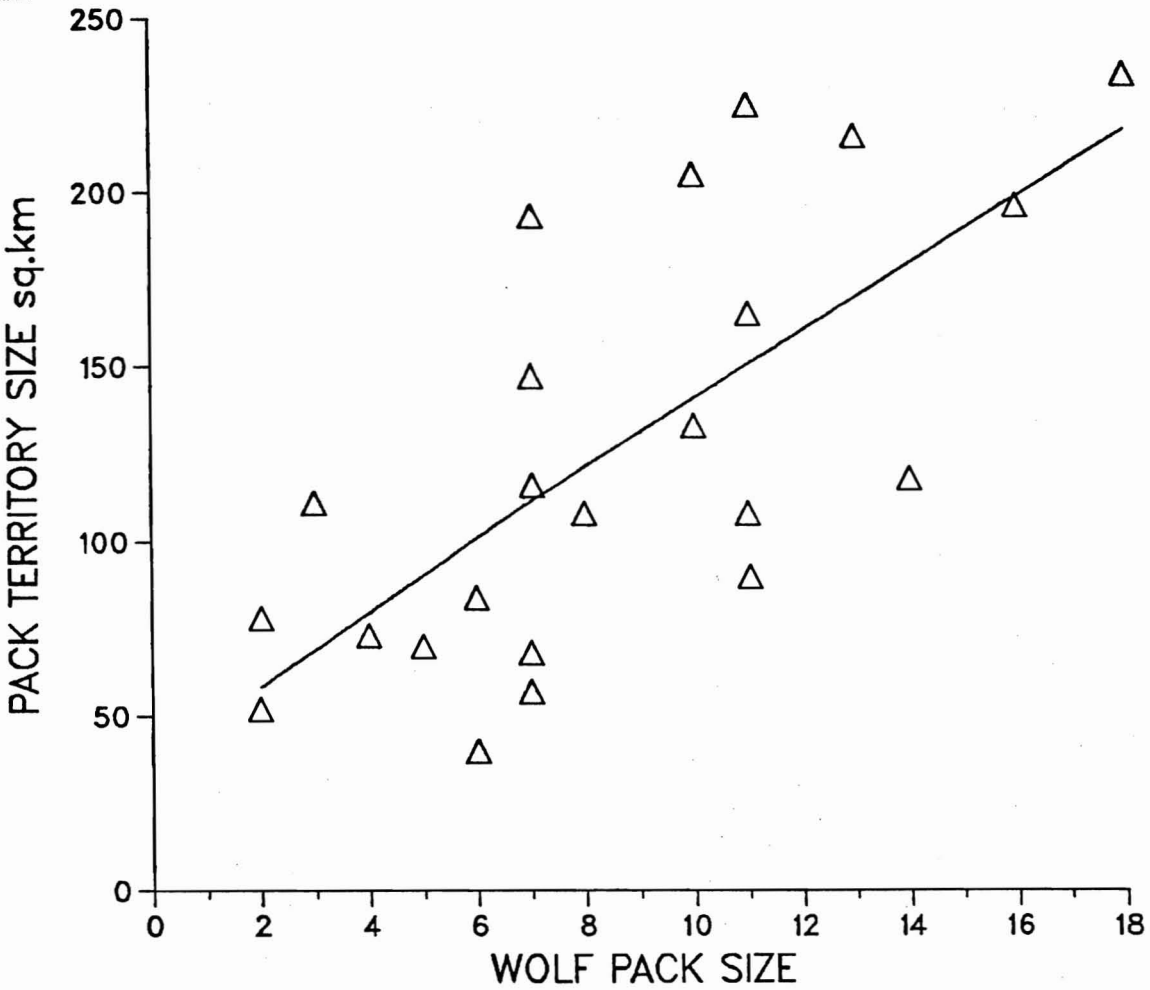


Fig. 3. Relationship between wolf pack size and territory size in midwinter on Isle Royale, 1975-84. Straight-line regression $Y = 9.97X+40.6$, $P<0.001$, $r^2 = 0.47$. Omitted from this analysis were data from trespassing packs (East Pack in 1981, West Pack II in 1982-84).

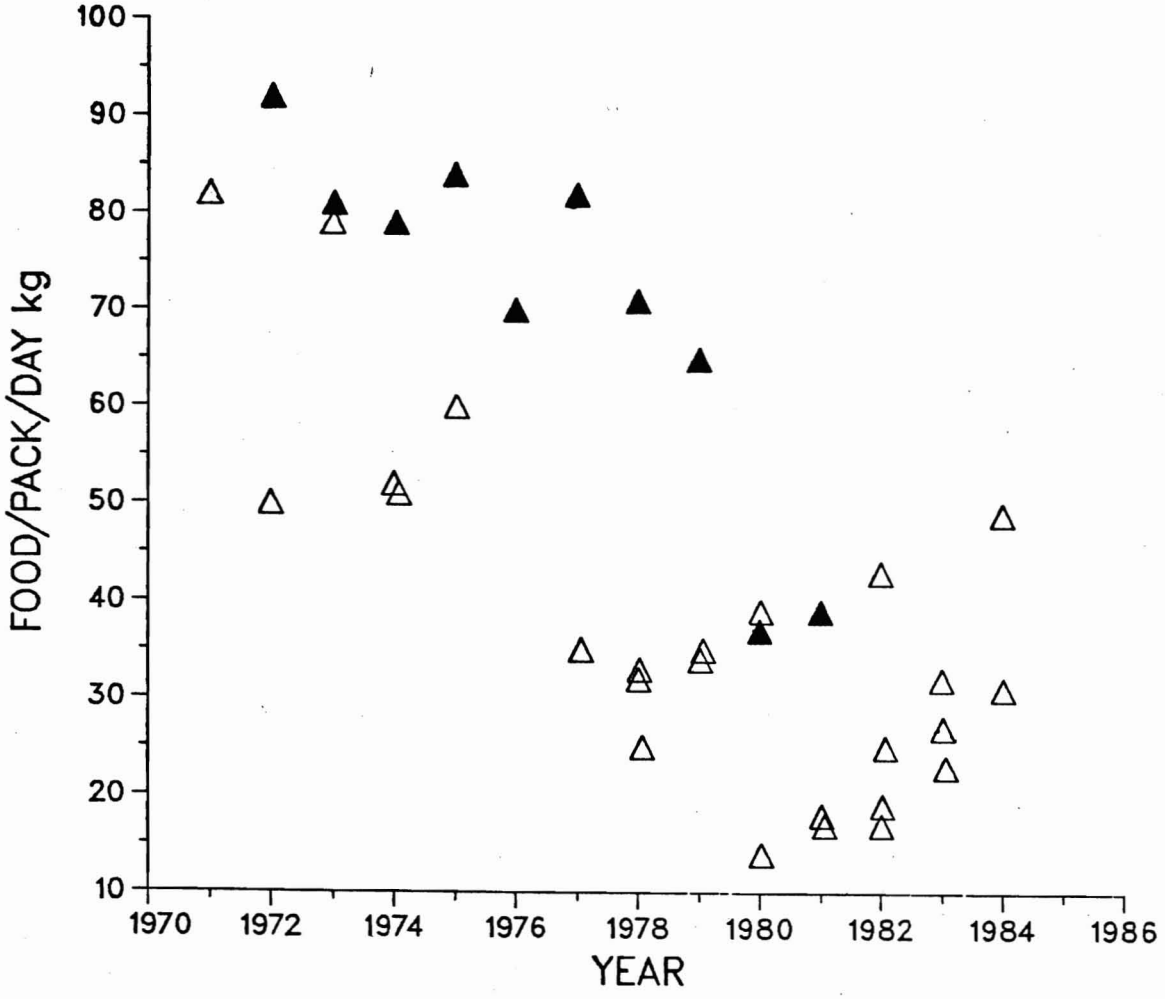


Fig. 4a. Trends in per pack food availability in midwinter on Isle Royale, 1971-84. Solid triangles represent the East Pack data points, open triangles derive from all other packs.

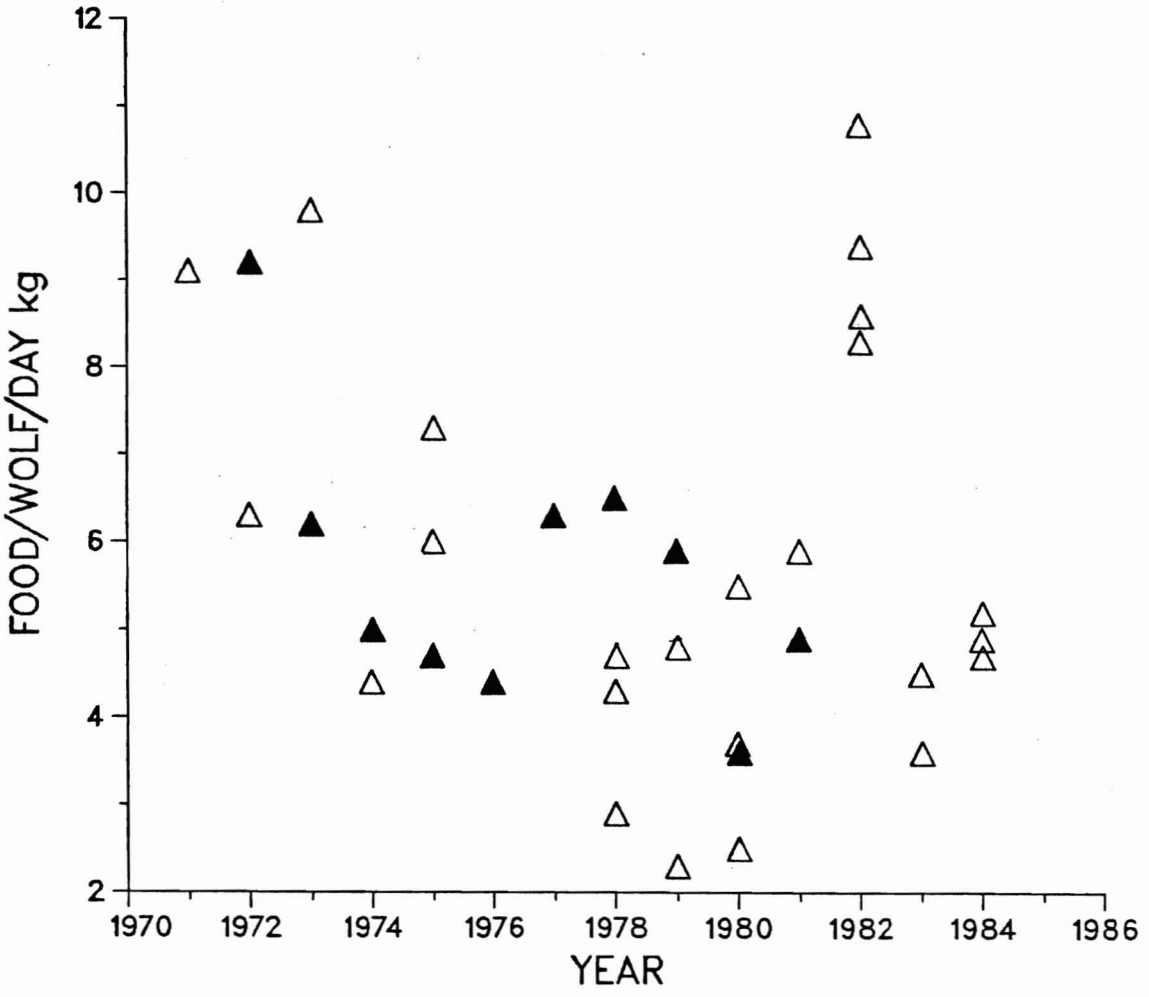


Fig. 4b. Trends in per wolf food availability in midwinter on Isle Royale, 1971-84. Solid triangles represent East Pack data points, open triangles derive from all other packs.

constant when the pack size dwindled, resulting in an increased food supply per wolf. By 1980 East Pack food supply on both a per pack and a per wolf basis dropped to the same low level exhibited by other packs. In 1981 the pack trespassed extensively, and in 1982 the pack no longer existed as a recognizeable entity.

There is a general consensus among ecologists that top predators such as wolves will ultimately be regulated by food supply. For wolves, ultimate regulation by food is mediated by social and physiological influences (Packard and Mech 1980) which constitute proximal controls. We examined correlations between food supply and wolf finite rate of increase (λ), the ratio of population size in two successive years. The correlation between food/pack and was not significant ($P<0.50$). The correlation between food/wolf and , however, was significant ($P<0.05$). However, food/wolf explained only 26% of the variation in wolf (Fig. 5).

From 1973 through 1980 wolf scat analyses showed beaver and moose to occur with roughly equal frequency in summer (Fig. 6). During this time an average of 82% of the moose occurrence was provided by calves. However, percent occurrence accurately reflects neither relative number of prey taken nor prey biomass (Floyd et al. 1978).

Floyd et al. (1978) demonstrated that small prey tend to be overrepresented by percent occurrence in wolf scats through feeding trials with captive wolves. They provided a conversion equation that can be used to convert percent occurrence data on scat contents (Table 4) to estimates of relative biomass of prey ingested, which can in turn be converted to relative numbers of prey taken (Table 5). The results reveal that, from the stand-point of biomass ingested, Isle Royale wolves rely more heavily on beaver than other wolf populations feeding predominantly on moose. Yet moose typically provide over 80% of summer food for Isle Royale wolves. Although adult hair in scats is uncommon compared to that of calves, adult moose provided approximately the same prey biomass as moose calves. Data on relative numbers of prey taken reveal that the wolves kill more beaver in summer than any other prey species, and that about 6 moose calves were killed for every adult killed. When data from all 2,648 scats examined between 1975 and 1983 are grouped and compared to samples examined in 1958-61 and 1973, there is remarkably little change, except in the proportion contributed by beaver (Table 5).

Beaver proportion increased from insignificance in the late 1950's to a prominant prey item when the beaver population peaked in the first half of the 1970's. It has since declined as the beaver population itself dropped. Previous conclusions that beaver constituted half of the wolf

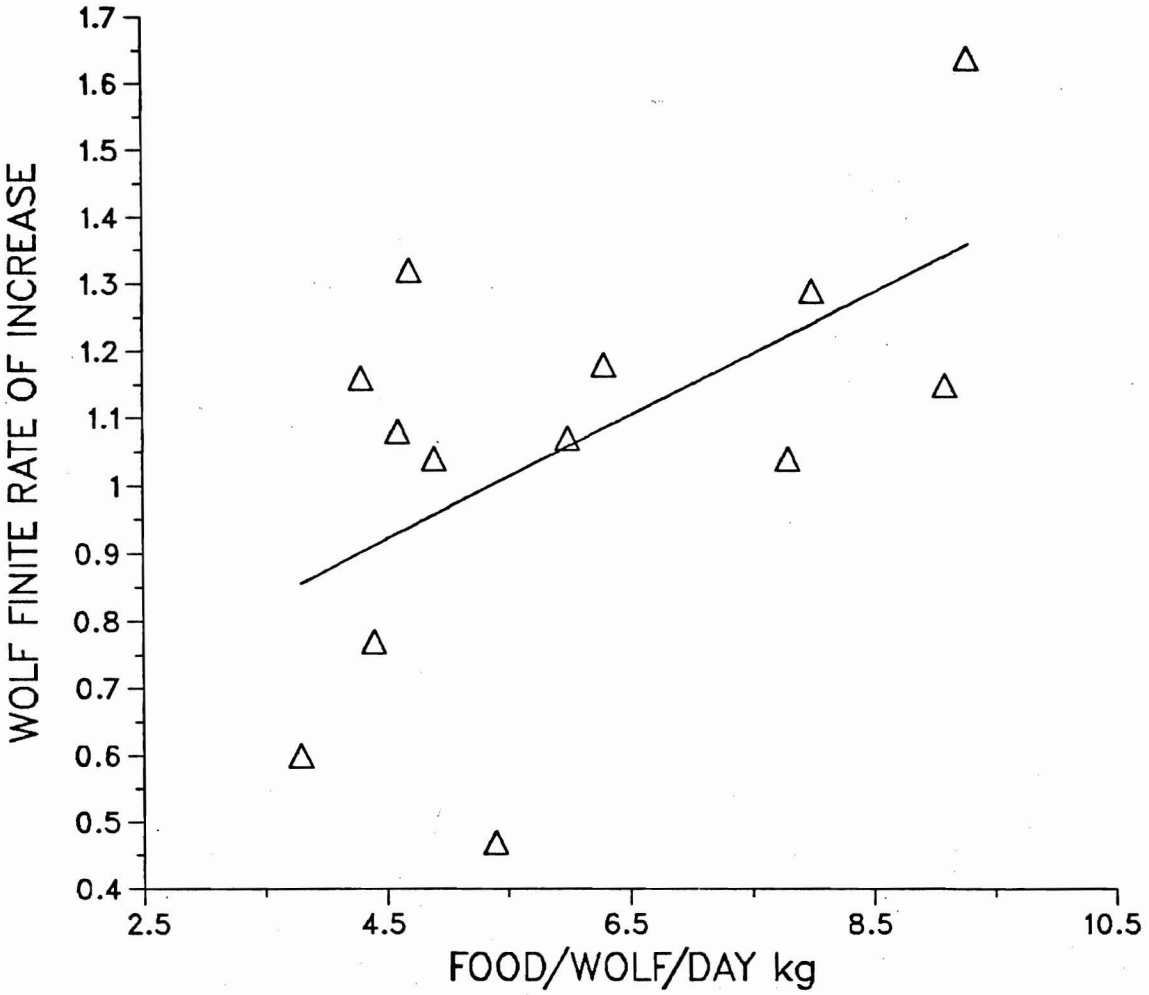


Fig. 5. Relationship between per wolf food supply and population rate of increase. Straight-line regression $Y = 0.092X + 0.508$, $P < 0.05$, $r^2 = 0.26$.

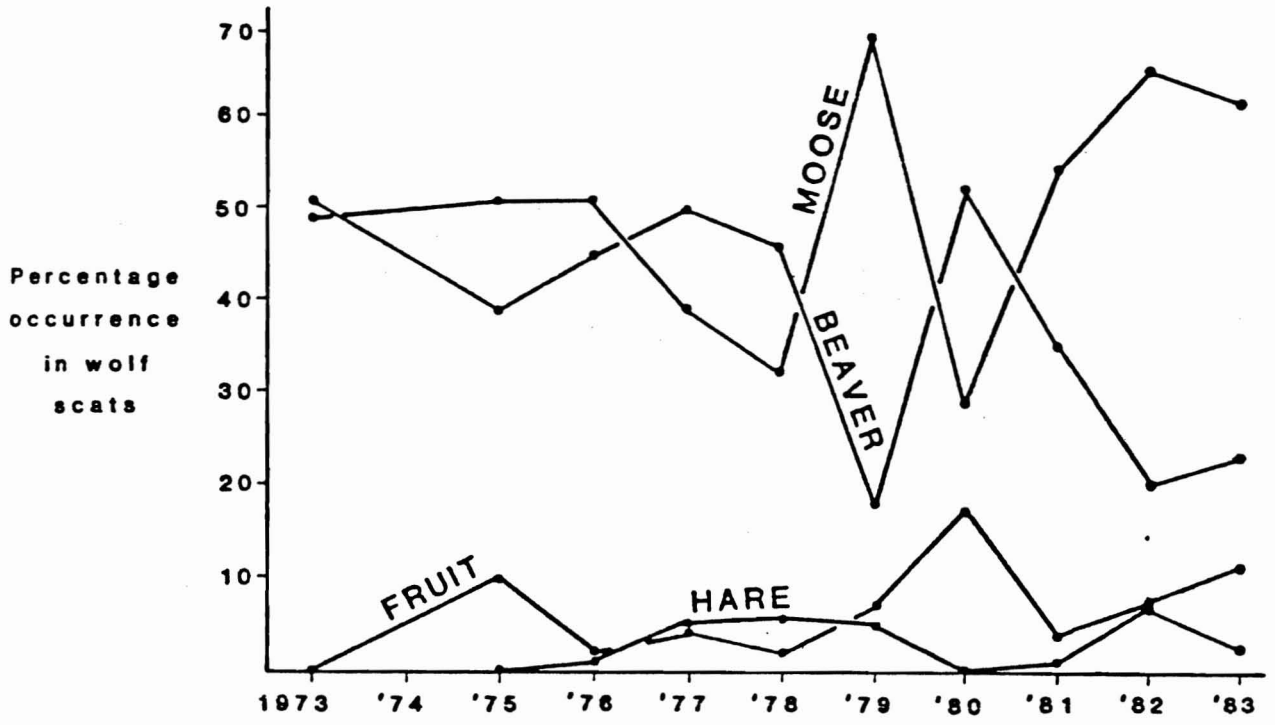


Fig. 6. Summer diet of Isle Royale wolves, based on percent frequency of occurrence of prey remains in scats.

Table 4. Frequency of occurrence of prey remains in summer (May-Aug) scats of Isle Royale wolves, 1975-83.

			% prey occurrence					
Year	Scats(N)	Occurrences(N)	Moose	Beaver	Hare	Fruit	Other	Unkwn.
1975	727	736	52.2	46.2	0	1.1	0.3	0
1976	641	675	51.0	45.0	0	2.0	1.0	2.0
1977	191	205	39.0	50.0	0	4.0	5.0	1.0
1978	206	222	32.0	46.0	0	2.0	6.0	14.0
1979	382	392	70.4	19.4	5.1	6.4	0	0
1980	118	118	28.6	52.9	0	18.5	0	0
1981	110	110	53.6	35.0	1.0	4.0	7.0	0
1982	115	115	65.0	20.0	7.0	7.0	1.0	0
1983	158	158	62.0	23.4	3.2	11.4	0	0
Total:								
	2,648	2,731	50.4	37.5	1.8	6.3	2.3	1.9

Table 5. Comparative prey use by wolves during summer (May-Aug) in area where moose constitute the principal prey, indicated by scat analyses[a].

Characteristic and study area	Adult moose	Calf moose	Beaver	Snowshoe hare
Percent prey occurrence in scats				
Kenai Peninsula, Alaska[b]	34	41	5	14
Nelchina Basin, Alaska[c]	9	44	13	14
Alberta, Canada[d]	30	14	34	13
Isle Royale, 1958-61[e]	12	62	11	4
Isle Royale, 1973[f]	7	42	51	0
Isle Royale, 1975-83	9	41	38	2
Relative number of prey				
Kenai Peninsula, Alaska[b]	1.00	1.33	0.28	5.10
Nelchina Basin, Alaska[c]	1.00	5.40	2.76	19.20
Alberta, Canada[d]	1.00	0.91	3.56	6.27
Isle Royale, 1958-61[e]	1.00	5.59	1.71	3.91
Isle Royale, 1973[f]	1.00	6.45	13.60	0
Isle Royale, 1975-83	1.00	5.96	9.78	2.54
Percent biomass of prey				
Kenai Peninsula, Alaska[b]	79.3	17.9	1.0	1.8
Nelchina Basin, Alaska[c]	47.1	43.0	5.9	4.0
Alberta, Canada[d]	74.3	15.0	9.0	1.6
Isle Royale, 1958-61[e]	48.5	46.8	3.8	0.9
Isle Royale, 1973[f]	36.3	40.8	22.9	0
Isle Royale, 1975-83	44.8	38.1	16.6	0.4

Table 5. continued

[a]Only moose, beaver, and snowshoe hare were considered; where some occurrence of moose was not classified as adult or calf, it was apportioned on the basis of the adult:calf ratio in the rest of the sample. Assumed whole prey weights (kg), based on Fuller and Keith (1980) and Franzmann et al. (1978), and prey weight (kg) represented by each occurrence in scat (calculated by the method of Floyd et al. 1978) were as follows: adult moose (350, 7.38), calf moose (50, 1.38), beaver (13.3, 0.64), snowshoe hare (1.33, 0.41). Consumable prey weight was estimated at 90% of whole weight for all prey except adult moose (75%), as in Fuller and Keith (1980). Moose, beaver, and snowshoe hare composed the following proportion of all prey occurrences: Kenai Peninsula (94%); Nelchina Basin (81%); Alberta (92%); Isle Royale, 1958-61 (88%); Isle Royale, 1973 (100%); Isle Royale, 1975-83 (90%).

[b]Peterson et al. (1984b).

[c]All scats totaled (Ballard et al. 1981).

[d]Means for different packs (Fuller and Keith 1980).

[e]All fresh scats totaled (Mech 1966).

[f]All scats totaled; adult:calf ratio for moose derived from scats deposited before calf molt (Peterson 1977).

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diet in summer were based solely on percent occurrence data; when these are converted to relative biomass it is clear that Isle Royale wolves continue to rely on moose in the summer as well as winter. It should be noted that muscle tissue from beaver has a higher caloric value (A.B. Bubenik, pers. commun.) and that beaver remain prominent in scats because they are the prey most frequently taken by the wolves in summer.

In 1981-83 wolves apparently switched to a diet of primarily moose in summer. This accompanied a dramatic rise in calf numbers on both an absolute and proportional scale. Significantly, beaver density increased between 1980 and 1982 after a significant decline since 1974 (Table 1).

Behavior

Wolf activity was recorded each time wolves were observed, thus these records reflect daytime behavior of a predominantly nocturnal predator. Mech (1977) found that a Minnesota wolf pack rested and slept more as food supply dwindled, suggesting a possible adaptation to conserve energy. There were no clear trends in activity of Isle Royale wolves over the last 12 years, although there is a suggestion of reduced travel in the mid-1970's, when pack sizes and kill rates were high (Table 6). Taken together, sleeping and resting accounted for 50% of observed activity, with traveling composing an additional 29%.

Wolf activity showed significant trends through the day (Fig. 7). Wolves were most apt to be sleeping in the first hours after sunrise. Hunting, composing only 4% of total activity, was typically begun in late afternoon and probably continued through the night.

Scent-marking was indicated by raised-leg urination, squat urination, and scratching (Peters and Mech 1975), with a directional component. Scent-marking behavior was analyzed beginning in the late 1970's, as the population approached a crisis in available food. Scent-marking was completely the prerogative of the alpha male and female, as demonstrated by Peters and Mech (1975). During 1978-81 scent-marking frequency was about 1-3 marks/hour (Fig. 8). The marking behavior of the aggressive West Pack II was most obvious, but the other 2 packs also marked extensively. During the next 2 years marking frequency fell to about 4-5 marks/hour.

During the most recent phase of the study, intraspecific aggression increased among packs and probably a significant role in the wolf collapse of 1980-82. Wolves killed by other wolves were recovered in 1976 (1 recovered, 1 lost in Lake Superior), 1981 (2), 1982 (2), and 1984 (1). In addition, 2 direct observations were made of wolves attacking but then

Table 6. Observed activity of Isle Royale wolves, 1972-83.

		Frequency of observed activity (%)						
Year	N	Trvlng.	Slpng.	Huntng.	Rstng.	Feedng.	Playng.	Crtshp.
1972	99	33	31	7	8	11	5	4
1973	85	30	33	9	6	11	4	7
1974	162	31	42	3	10	13	1	1
1975	97	14	42	7	7	11	4	13
1976	153	25	47	1	12	5	4	6
1977	113	33	44	2	4	11	4	3
1978	155	21	42	5	13	15	2	2
1979	222	34	31	3	22	8	0	3
1980	102	28	36	6	17	9	2	2
1981	56	41	27	4	13	16	0	0
1982	71	27	44	8	4	13	0	4
1983	53	34	26	4	13	11	8	4
Total								
	1,368	29	38	4	12	11	2	4

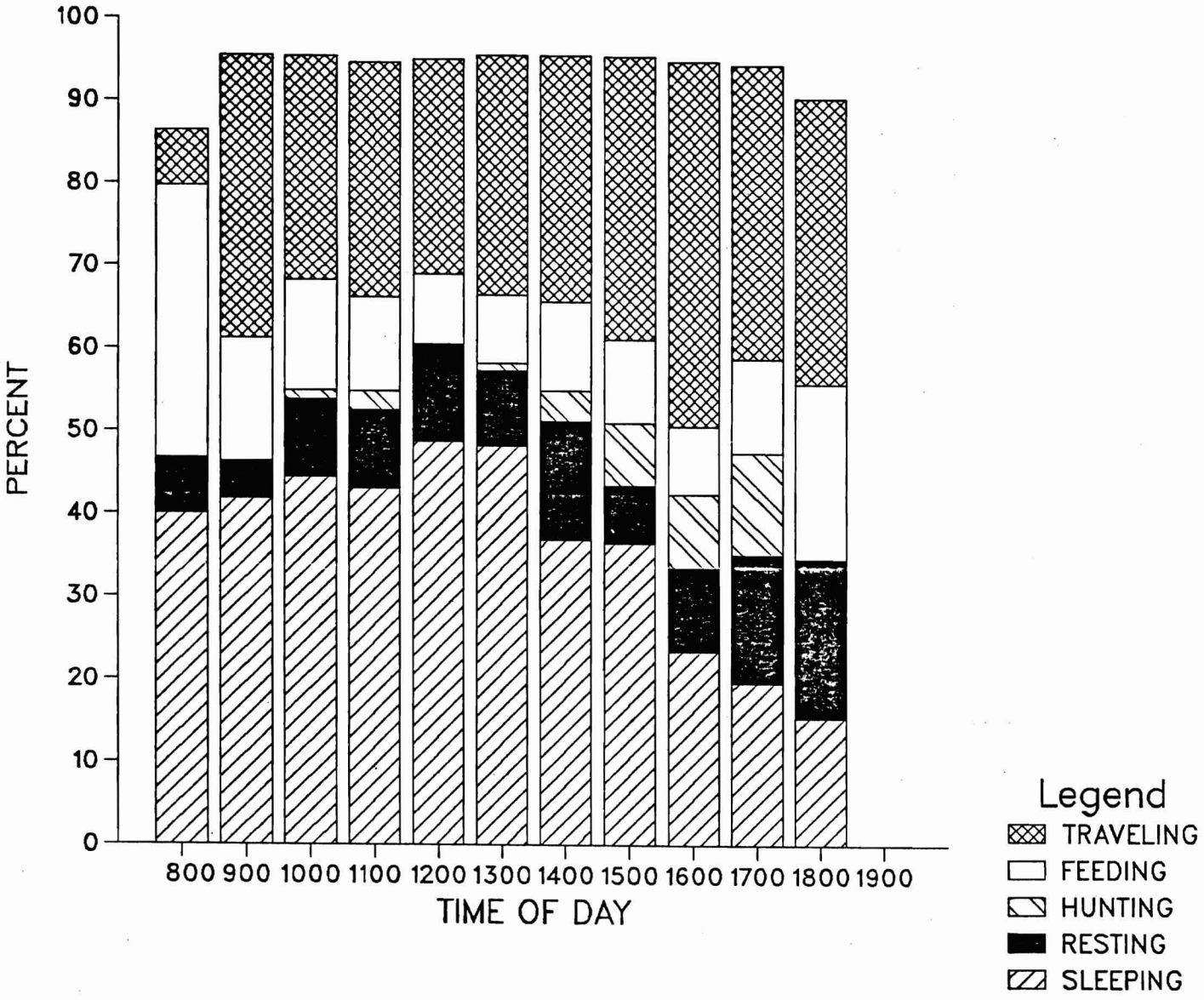


Fig. 7. Daytime wolf activity patterns in midwinter on Isle Royale, based on behavior when first observed from aircraft (N = 1,773) during 1972-83.

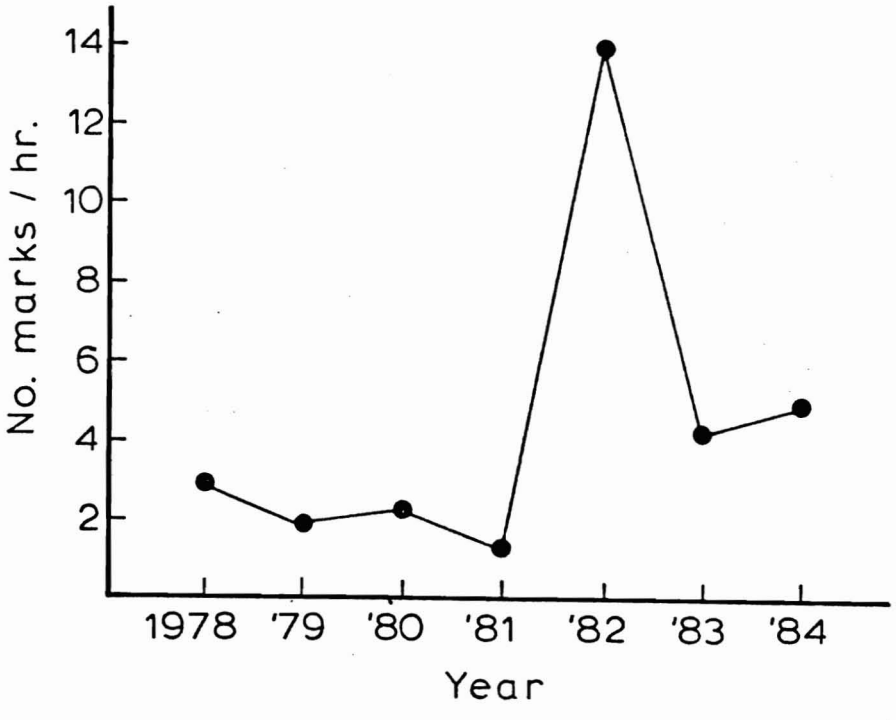


Fig. 8. Scent-marking frequency of Isle Royale wolf packs. Excluded from this analysis were all observations during periods of intensive hunting.

releasing single wolves. Since intraspecific aggression is a poorly understood phenomenon, detailed accounts follow of the known circumstances surrounding each case.

In 1976 the wolf population stood at 44, higher than ever before. Territorial packs were large, and several smaller groups persisted without clearly defined exclusive territories. A group of 4 wolves moved into the extreme northwest corner of the island. The group contained 3 "rope-tailed" wolves that shared many characteristics of East Pack pups (Peterson 1977) and 1 full-tailed female. On the first day the pack was observed it was attacked by the resident West Pack II of 9 wolves. Two of the 4 wolves were fatally wounded. A third wolf was bleeding several days after the attack but survived at least 2 weeks. The attack was not witnessed but was easily reconstructed from tracks and other sign. After bleeding extensively on a shelf of ice, one of the wounded wolves died and slipped into Lake Superior. A second wolf lived for several hours and moved alone along the shore for 1 km, then died at least 6 hours after the attack as result of severe lacerations in the throat. The carcass of this wolf was recovered and showed numerous canine puncture wounds, especially in the rear hindquarters.

In 1981 a wolf was killed by the SW Pack in an area of overlap with the Middle Pack; fragmentation of the Middle Pack precluded identification of the victim's origin. Also, the East Pack attacked a single wolf, but during observation the wolf was allowed to submissively retreat to cover and escape. Five days later, a very old, malnourished wolf was recovered dead a few miles away near a moose carcass. The wolf died in a bedded position and had a freshly broken rib surrounded by inflammation, probably inflicted by a moose. Several other ribs had been previously broken and healed.

During summer 1982 two wolves washed up on the south shore of Isle Royale after dying on the ice the previous winter; one still retained hide that contained numerous puncture marks, and both were probably killed by other wolves.

The behavior of the 4 wolves in the new West Pack II in 1982 was strongly aggressive toward other members of the population. In spite of a record-high level of food abundance, the 19 km/day average travel rate for this pack was almost twice the long-term average and higher than any other Isle Royale pack. For this pack, feeding and hunting appeared to be secondary to patrolling the new territory --- once the pack made a kill at night and fed briefly, but the next morning the pack was several kilometers away, actively following the trail of a lone wolf. As noted elsewhere, a high rate of scent-marking was documented for all packs in 1982, but it seemed to be an especially significant activity for the West Pack II. Their behavior is consistent with our inference that direct killing was prominent during the wolf crash of 1980-82.

In 1983 the Harvey Lake Pack, lacking an exclusive territory, was chased off its own kills by both the West Pack II and the East Pack II. In one observed encounter the West Pack II caught up with the Harvey Lake Pack, passed a pup and then brought down the alpha female. West Pack wolves crowded around her and bit and threatened her, while she assumed a submissive posture but snapped at her attackers. Suddenly the attack ceased, and she was allowed to escape. In 1984 the Harvey Lake Pack was once again attacked by the West Pack II, and this time the alpha female was killed.

Breeding and reproduction

Almost all known matings of Isle Royale wolves have occurred during February, especially during Feb. 21-25 (Table 7). During the most recent phase of the study, breeding behavior generally remained the prerogative of the alpha pair. Five matings involving subordinate wolves were recorded, although in no case was it determined if pups were born to a subordinate female. Peterson et al. (1984b) related an incident in Alaska in which a subordinate female with a litter was forced to den away from the main focus of pack activities, and all her pups died.

On 2 occasions an alpha male mated with a subordinate female. In the first instance, occurring in the SW Pack in 1977, the subordinate female was subsequently chased across an ice bridge to Canada (Peterson 1979a). The second occasion involved the East Pack in 1979, and in this case courtship behavior by a subordinate female was tolerated by the aging alpha female (> 9 years old). Notably, the subordinate female could easily have been her daughter.

From howling responses in summer we were often able to determine the number of litters of wolf pups (Table 8). Packs with sedentary pups focused their activities on dens or rendezvous sites, usually occupied until September. Such sites were often reused and were typically in remote portions of the island. Homesite distribution revealed a distinct avoidance of areas within 1 km of trails or campgrounds (Fig. 9).

Mortality

Deaths of Isle Royale wolves have been recorded only rarely. The high mortality of 1980-82 was unprecedented, but only fragmentary information was gathered on its causes. During 1980-82 the wolf population declined from 50 to 14, in spite of the addition of 16 pups in 1980 and 1981. Throughout this period dispersal from the island was impossible due to lack of ice. Thus a minimum of 52 wolves perished in 2 years.

Table 7. Copulation dates for Isle Royale wolves, 1959-83.

Date	Recorded Matings (N)[a]
Before February 1	0
February 1-5	2
February 6-10	6
February 11-15	2
February 16-20	4
February 21-25	9
February 26-March 2	4
After March 2	1

[a]Copulation observed or deduced from characteristics tracks of "tied" wolves.

Table 8. Wolf pup production on Isle Royale 1974-83.

Year	Packs with confirmed litters	Estimated number of pups	Comments (where applicable)
1974	East Pack	5	Direct observation
	West Pack	unknown	5 seen next winter
	Middle Pack	unknown	5 seen next winter
1975	East Pack	4-5	
	West Pack	4-5	
	Middle Pack	2	
1976	East Pack	4	
	Southwest Pack	1-2	
	Middle Pack	3	
1977	East Pack	3	
	Middle Pack	3	
	+2 additional litters	unknown	
1978	East Pack	unknown	
	Middle Pack	unknown	
	+2 additional litters	unknown	
1979	Southwest Pack	3-4	
	Middle Pack	3-4	
	East Pack	3-4	
1980	Southwest Pack	3	
	Middle Pack	4	
	East Pack	0	
1981	East Pack II	3	No survivors in winter
	Harvey Lake Pack	3	No survivors in winter
	West Pack II	3	0-2 survived in winter
1982	East Pack II	4	5 present in winter
	Harvey Lake Pack	3	4 present in winter
	West Pack II	2	4 present in winter
	Duo (Southwest Duo)	1	No survivors in winter
1983	East Pack II	unknown	3 present in winter
	Harvey Lake Pack	2	2 present in winter
	West Pack II	unknown	5-6 present in winter

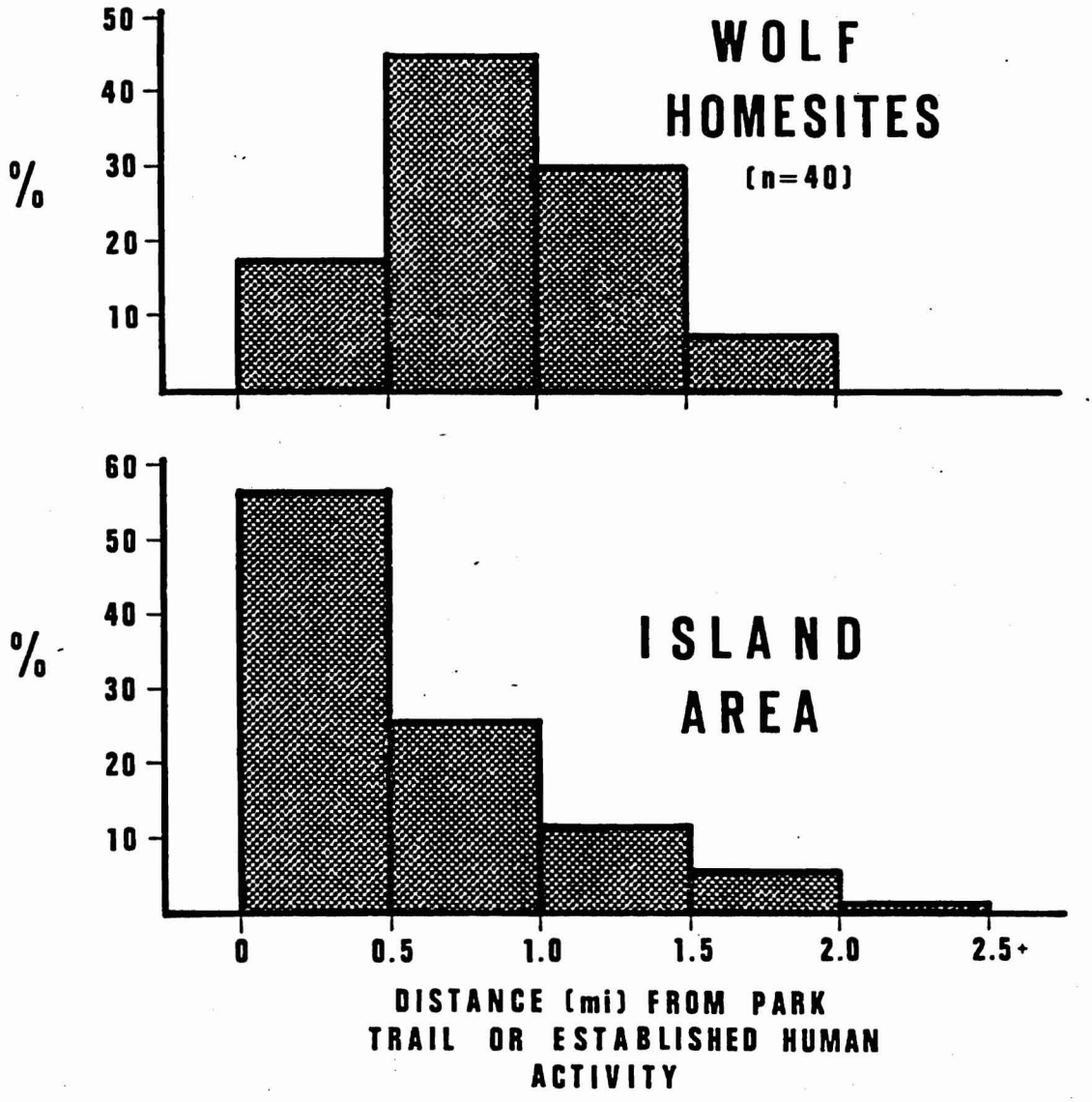


Fig. 9. Distribution of Isle Royale wolf homesites (dens and rendezvous sites) in relation to human activity.

Carcasses of only 5 wolves were recovered during the 2-year crash:

-#1516 - adult wolf, sex unknown, killed by other wolves near Checker Point in February 1980. Carcass mostly consumed by scavengers before detailed examination was possible.

-#1521 - aged adult male, died of old age and malnutrition in Five Finger Bay in February 1980. Total weight was 57 lbs, about 2/3 normal weight, and femur marrow fat contained only 16% fat. This wolf died 5 days after the East Pack attacked and released a wolf on Angleworm Lake, but there was no definite evidence confirming that this wolf had been the victim. The only recent wound was an infected broken rib that was partially healed.

-#1565 - an old adult male, weighed about 58 lbs (soaking wet). Recovered in July 1980 from a water-filled mine pit near Daisy Farm. The wolf had evidently paused to examine a remnant moose bone from an animal that had died several years before, then fell into the pit. Sloping sides would have proved no problem for a normal individual, but this wolf was too weak to crawl out. When boiled, the carcass produced no trace of fat. The kidneys were strangely lobed, and there was a freshly-broken rib, accompanied by inflammation. Again, cause of death was considered to be old age/malnutrition.

-#1667 - skeleton of adult wolf with small pieces of flesh. Discovered partially buried in beach gravel at Butterfield Point. The bones were smoothed by rocks, suggesting that the carcass had been washed onshore after the wolf died on the ice the previous winter. Probable cause of death was considered to be killing by other wolves.

-#1757 - decomposed carcass of adult male wolf. Discovered washed ashore near Long Point. The hide revealed several puncture wounds, indicating a death caused by other wolves on the ice the previous winter.

Other observations suggested that malnutrition probably played a significant role as a direct agent of mortality. During 1980 there were 11 non-pack-members -- one that was photographed at close range on Siskiwit Bay showed the graying muzzle and lower sides characteristic of aging wolves plus the outline of bones emerging through hide. During the following summer a notably gaunt wolf became a campground nuisance at Malone Bay. It had allegedly received handouts of fish the previous week and boldly approached humans on several occasions. After several days the wolf disappeared from the area and no additional incidents were reported. In 1981 few single wolves remained in the population.

Aside from malnutrition and intraspecific killing, the only other significant cause of mortality during the wolf crash could be disease. During August 1981 there was an

outbreak of canine parvovirus among domestic dogs in the Houghton area on the Upper Michigan mainland (jumping-off site for park visitors). Although mammalian pets are prohibited on the island, the disease could have reached Isle Royale via more indirect routes (e.g., on the soles of hikers' boots). In this regard, it may be significant that only 0-2 pups survived from a total of at least 9 born in 1981. No surviving wolves could be handled to see if they had been exposed to parvovirus, although blood serum samples from 2 red foxes examined at Windigo in 1983 and 1984 proved negative for parvovirus. Several wolves we checked in northern Minnesota exhibited antibodies to parvovirus and one of these animals died after steadily losing weight (L.D. Mech, pers. commun.). These preliminary data suggest that parvovirus may indeed have contributed to the wolf die-off of 1980-82.

There is circumstantial evidence suggesting that during 1980-81 most adult wolves lost were peripheral animals on a marginal economy, while during 1981-82 there were large losses among presumably vigorous pack members. Thus malnutrition and possibly disease were significant in 1980-81 while direct killing of wolves by other wolves may have been dominant in 1981-82.

Estimates of annual mortality for Isle Royale wolves were generated from data on summer (and occasionally winter) pup occurrence (Table 9) combined with annual changes in total wolf numbers (Table 3). These estimates ranged from 4% to 64% annual mortality between 1974-75 and 1983-84. When the finite rate of increase of the wolf population, λ , is regressed against the highest 5 mortality estimates, the point where the regression line crosses $\lambda = 1.00$ should indicate the maximum sustainable mortality in a stable wolf population (Fig. 10) The indicated value is almost 40%, which is discussed below in terms of wolf response to harvest by humans in populations that are hunted and trapped.

POPULATION REGULATION IN WOLVES

The recent history of the Isle Royale wolf population has revealed much about the ultimate controls on wolf abundance. Our interpretation of events since 1975 supports the view that the wolf population is food-limited. Data from Isle Royale best demonstrate the responses to food that are manifested in spatial organization of packs and interpack aggression.

The number of wolves in any area is controlled by 2 fundamentally different types of processes -- intrinsic control (those mechanisms that actually regulate numbers) and extrinsic controls (those factors which influence the amount of available food). The means of internal self-regulation of wolf populations are wolf pack territoriality, which regulates the number of packs (reproducing units), and individual

Table 9. Estimates of annual mortality among Isle Royale wolves based on successive winter counts plus pup production.

Year	Estimated number of pups	Population change	Comments	% Mortality
1974-75	15	+10	Lost minimum 5 of 46	11%
1975-76	10-12	+3	Lost minimum 7 of 51	14%
1976-77	8-9	-10	Lost minimum 18 of 52	35%
1977-78	6	+6	Lost minimum 0 of 40	0%
1979-80	9-12	+7	Lost minimum 2 of 52	4%
1980-81	7	-20	Lost minimum 27 of 57	47%
1981-82	9	-16	Lost minimum 25 of 39	64%
1982-83	13	+9	Lost 4 of 14	29%
1983-84	10-11	+1	Lost 9-10 of 23	39-43%

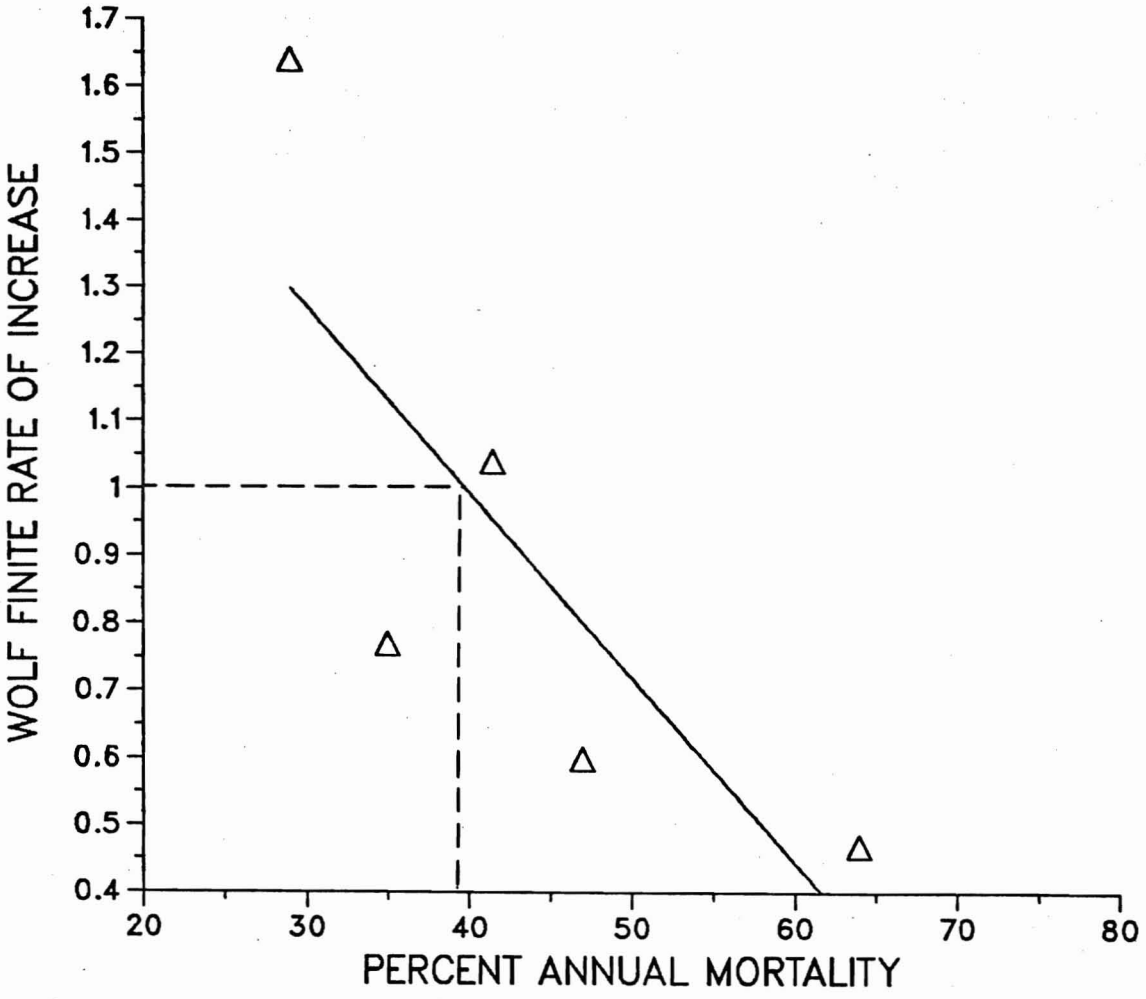


Fig. 10. Relationship between documented high rates of mortality and population rate of increase for Isle Royale wolves. Dotted lines indicate maximum mortality rate that can be sustained without population loss (see text).

dispersal from packs, which regulates pack size. Extrinsic controls are number of prey available, vulnerability of prey, size of prey, and diversity of prey types. Disease, competition from other predators, and harvest by humans can also be significant in specific cases. Extrinsic controls can, over evolutionary time, affect intrinsic controls.

Intrinsic control

Territoriality. A prominent feature of wolf dynamics and social structure is the formation of territories that are exclusively held by the members of the pack. Wolf territories are actively defended from conspecifics, are frequently patrolled, and are marked with species- and individual-specific signs. About 2/3 of the variation in territory size for Isle Royale wolves is explained by food availability (Fig. 11). While food availability on Isle Royale in the late 1970's was greatly influenced by prey vulnerability during a period of relatively constant moose density, on a macro scale wolf pack territory size is affected fundamentally by prey abundance. Thus Peterson et al. (1984b) found that wolf pack territories were more than 3 times larger on Alaska's Kenai Peninsula, where moose density is approximately half that of Isle Royale.

Territorial boundaries may or may not respond quickly to changes in food supply. The relationship between territory size and food availability for Isle Royale wolves is weakened considerably if data from the early 1970's is included -- this may reflect the imperfect response of wolves to high moose density coupled with high winter severity. Conversely, when available prey declines, a pack may be slow to trespass into another territory because of the risk involved to alpha wolves. Because of a lag in response wolf density remains high as prey decline and, if kill rates are maintained, proportional loss to predation increases; thus prey declines may be accentuated by wolf predation.

Any increase in the number of packs in an area is contingent upon more wolves being available to form a new pack. This surplus is provided by dispersers, wolves that leave their original pack.

Dispersal and Group Size. The size of a wolf pack is determined by the number of pups born to the pack, survival of wolves within the pack, and dispersal of wolves out of the pack. Immigration into established packs is not significant in pack dynamics. On Isle Royale (and elsewhere) one breeding pair per pack is the norm. While litter size at birth is usually 4-6 (Mech 1970), the number of surviving offspring 6 months later is often 2-4 (Harrington et al. 1983). Very little is known about pup production and survival patterns for Isle Royale wolves. Research in Minnesota indicates that pup

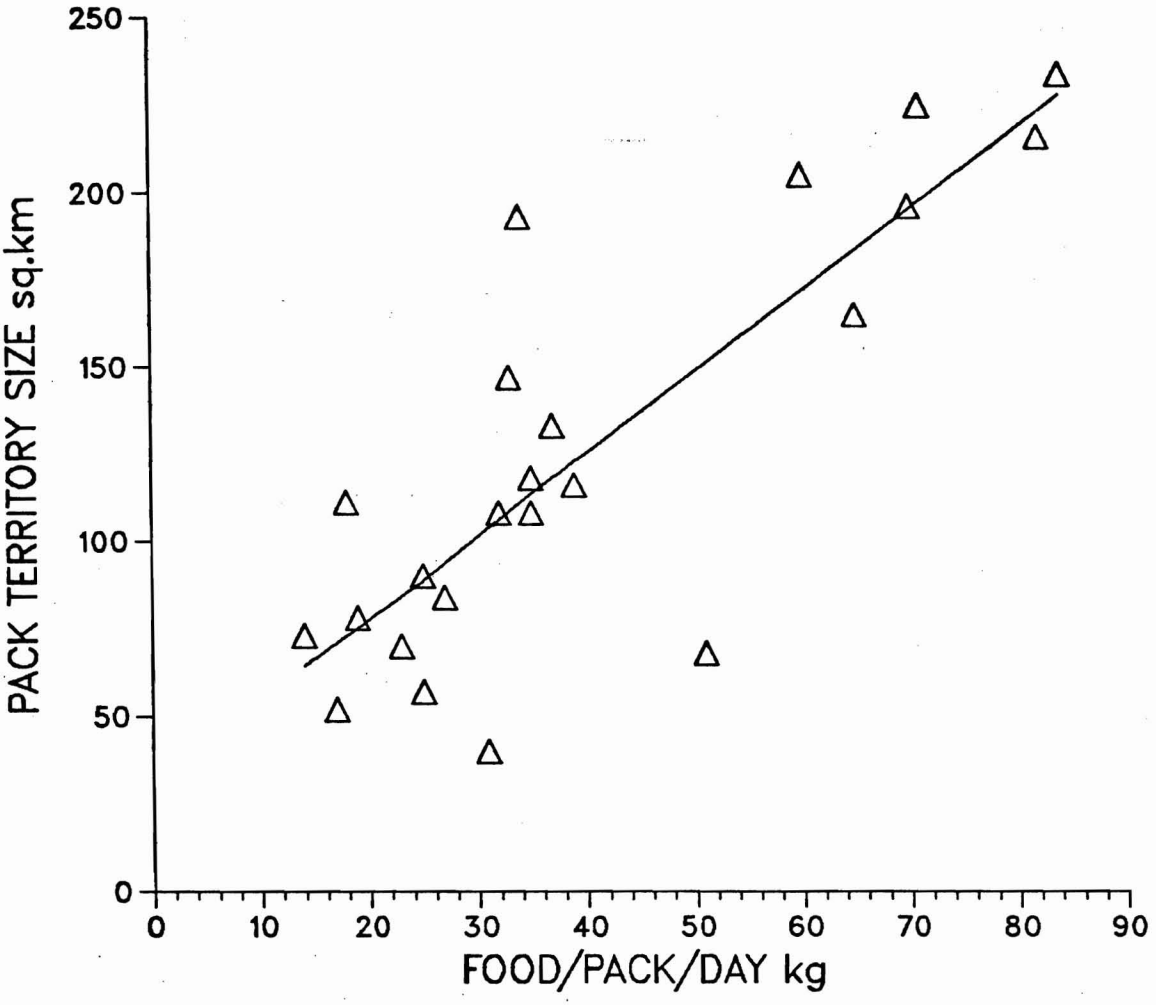


Fig. 11. Relationship between per pack food availability and pack territory size, 1975-84. Straight-line regression $Y = 2.35X + 30.7$, $P<0.001$, $r^2 = 0.67$. Omitted from this analysis were data from trespassing packs (East Pack in 1981, West Pack II in 1982-84).

survival is related to pack size, but the relationship can be either positive or negative and seems to be linked to food availability. Where prey availability was high and the wolf population was increasing, the correlation between pack size and pup survival was positive; conversely, where prey were scarce and the wolf population declining, pack size and pup survival were negatively related (Harrington et al. 1983). These findings were discussed in relation to the amount of help provided to pups by auxiliary pack members, but there is too little knowledge in this area to allow more than preliminary hypotheses. There is certainly an empirical basis for concluding that pup survival is largely dependent on food supply (Kuyt 1972).

How many wolves should there be in one pack? Empirical data indicate that average pack size increases as prey size increases, with pack sizes of up to about 7 prevailing for wolves preying mainly on deer, 8-10 for packs feeding on elk, and 10-12 or more for packs relying on moose (Peterson 1977). Maximum food/wolf will be achieved, theoretically, at relatively low pack sizes, since even for moose only about 4-6 wolves are typically playing a major role in detection and killing of prey. From the standpoint of food/wolf, 2-3 wolves per pack is probably optimal for deer and 3-5 wolves per pack for moose (Nudds 1978). Isle Royale data supports the view that food/wolf is maximized at small pack sizes (Fig. 12). Packs are usually larger than this, however. Individual fitness is greater at these relatively low pack sizes, but inclusive fitness (defined by Alcock 1984:476 as "the total genetic success via personal reproduction and effects on relatives' reproduction") is increased at high pack sizes because of the very high relatedness of wolf pack members (assuming that "extra" pack members contribute to pup survival). Most members are full or half sibs, and can pass on their genetic heritage by helping raise offspring of relatives. Inclusive fitness probably does not decrease until 8-10 wolves/pack with moose as the dominant prey. At greater levels, food availability per wolf begins to approach minimum levels necessary for survival. Large packs develop only under very favorable food regimes.

Zimen (1976) believed that the dispersal rate for individuals from a pack was food-related. Aggressive behavior within a pack increased as food declined, prompting some subordinate individuals to choose to leave. Packard and Mech (1980) viewed dispersal as a mechanism to maximize individual fitness (personal reproduction), and identified 2 strategies by which individual fitness is maximized.

Wolves can either bide their time ("biders"), waiting for an opening in the alpha position which would allow them to reproduce, or they can disperse, taking their chances in

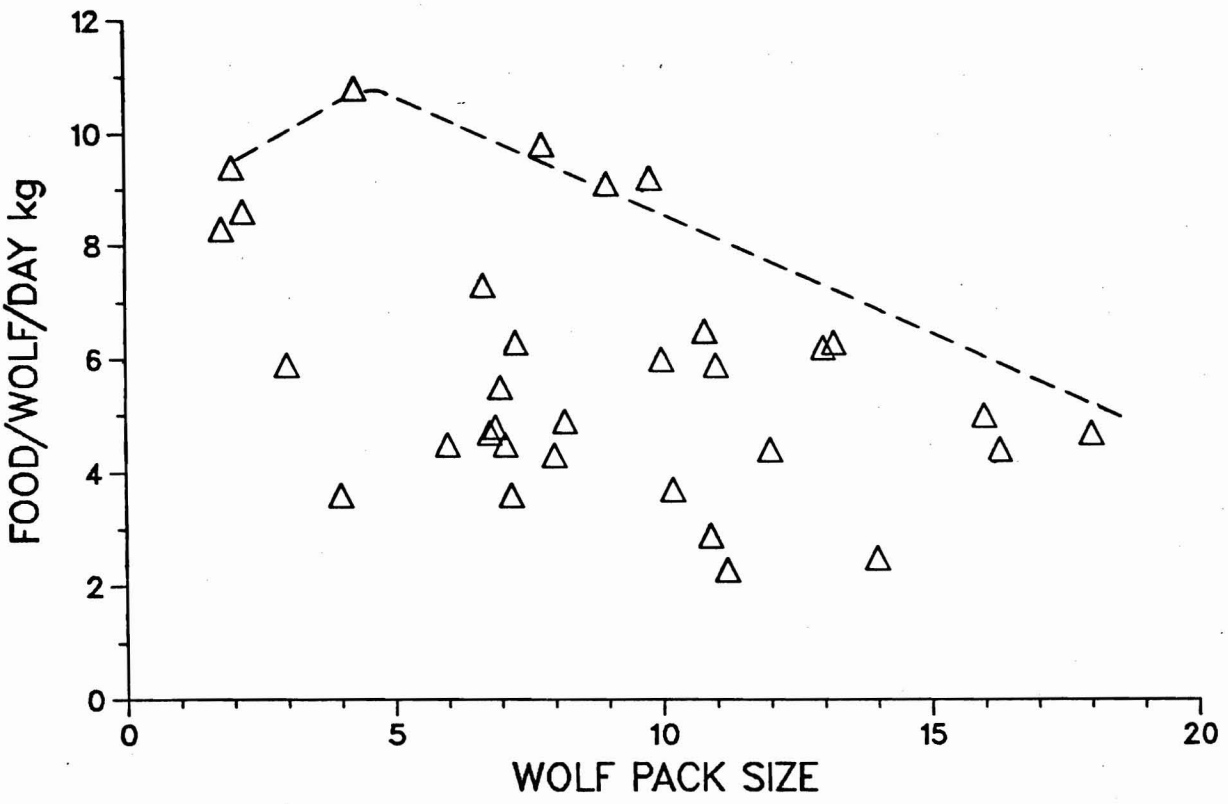


Fig. 12. Relationship between wolf pack size and per wolf food availability on Isle Royale, 1971-84. Dotted line was hand-fitted to indicate maximum observed values for specific pack sizes.

unfamiliar areas while attempting to find a mate and a vacant territory. Dispersers typically have a much higher mortality rate than resident wolves, and increased mortality appears to be a risk whenever a wolf leaves its original territory (Peterson et al. 1984). Dispersal is a poor strategy in a saturated wolf population with few openings, but in a colonizing situation or heavily harvested population vacancies are readily found and dispersal may represent the best option for subordinate wolves. Peterson et al. (1984) found a wide range of dispersal behavior (cf. Van Ballenberghe 1983), from abrupt long-distance departures to gradual dissociations accompanied by considerable exploratory travel outside the original territory. Some individuals returned to their home packs after absences of several months.

Extrinsic control

Food availability. The food available to a pack is the prime determinant of pack size (see below), and food availability is determined by prey biomass and vulnerability. Prey numbers affect the encounter rate of a pack with a prey animal. The types of prey available and prey condition determine the vulnerability of prey to wolf attack. Changes in prey vulnerability affect actual food availability given the same prey biomass (see Ch. 3). Size of prey determines the handling time and the return per kill. Wolf kill rates (which are equivalent to food availability for Isle Royale wolves) are thus determined by the interaction of encounter rates, success rates, and prey size.

These factors are the proximal controls of food availability, which operate within the short term to determine wolf numbers. The long term integration (in evolutionary time) of these short term variations determines equilibrium densities.

Correlations among territory size, pack size and food availability

Wolf pack territory size on Isle Royale is positively correlated with pack size and food availability (Figs. 3 & 11), while pack size is positively correlated with food availability (Fig. 12). We interpret these findings in the following way. Pack territory can be considered as an elastic disc, responding to changes in food supply so as to provide an adequate resource base. There may be lags in responses which will contribute to instability (Peterson et al. 1984a). The lack of correlation between territory size and food supply per wolf suggests that food supply per wolf will be largely independent of territory size -- i.e., wolf packs of all sizes attempt to maintain a minimum food supply of 3-4 kg/day/wolf. A larger territory is associated with a larger food base that will support a larger pack. A wolf pack will grow in a fixed

territory if food supply expands. Likewise, a pack will grow on a fixed food supply if it is able to enlarge its territory and food base. If food supply shrinks, pack size seems to be more responsive than territory size, as evidenced by the decline in pack size in the late 1970's while spatial organization remained unchanged (with the decline of the West Pack a notable exception). The usual response to a marginal food supply for a subordinate pack member seems to be dispersal, which limits pack size in relation to the food base.

Notable lags are characteristic of wolf-moose systems and may be the primary cause of instability exemplified by cycling populations. The causes of these lags include delayed changes in prey vulnerability in response to density changes and inherent stability of wolf pack spatial organization. These phenomena arise from the long life spans of wolves and moose, which are fundamentally linked to large body size (Peterson et al. 1984a).

The final mechanism by which Isle Royale wolf density was finally brought into line with food supply involved a drastic reorganization which involved either reductions and/or elimination for all packs. Unusual behavior was manifested by intensive patrolling of new territories (including high rates of travel and scent-marking) and intraspecific killing. While such killing has been observed infrequently in northern Minnesota and elsewhere (Mech 1977b), in no other study has the magnitude of change been so large as at Isle Royale. It is likely that the "fence effect" of Isle Royale was important in preventing dispersal which would have been the natural "relief valve" for this population if it existed on the mainland. A dispersal sink for wolves (in which dispersers are systematically removed) does not normally exist, leading to unusual population pressures that were resolved only by an extreme mechanism such as violent encounters between packs. We believe that mortality from malnutrition (possibly interacting with disease) and intraspecific killing played a significant role in the wolf crash -- there is not sufficient evidence indicating which of these mortality factors predominated. Empirical data suggest that some wolves were dying of malnutrition when average winter per capita food levels fell below 3 kg/day. A minimum maintenance diet for a large canid such as a wolf has been estimated at about 2 kg/day (Mech 1970). The wolf population showed a positive rate of increase when per capita food level ranged from 4.3 to over 9 kg/day. Declines followed years when per capita food ranged from 3.8 to 5.4 kg/day.

The population dynamics of Isle Royale wolves have revealed basic characteristics of the reproductive potential or this species which apply to managed wolf populations. Peterson et al. (1984b) indicated that the maximum rate of

increase (λ) documented for a wolf population was 1.32, which supported their conclusion that maximum sustainable yield (annual kill) for their study population was 30-40%. The recovery of Isle Royale wolves from 14 to 23 indicates a λ of 1.64, undoubtedly a maximum record for the species. Peterson et al. (1984b) believed that the primary influence of harvest on a wolf population was the lowering of average pack size. In their study territory size was well-correlated with pack size, and territory size reductions accompanied declines in pack size caused by harvest. The population increased as new packs (reproducing units) became established in vacant areas. Thus harvest resulted in smaller, more numerous packs, each producing a litter of pups annually. Under conditions of a constant food supply (Isle Royale data suggest that this may be rare), we would expect that rate of increase for a wolf population would tend to be inversely proportional to average pack size. Since mean group size for Isle Royale packs in the year prior to 64% growth was 2.7 (compared to the absolute minimum value of 2.0 -- one male and one female), it seems unlikely that a higher empirical value for will be forthcoming.

Aside from the unusual circumstance of population growth cited above, a review of Isle Royale wolf population response to a range of high mortality suggests that population equilibrium will probably not be possible if annual mortality exceeds 40%, contrary to the conventional wisdom that 50% of a wolf population can be killed annually without leading to a population decline. The conclusions based on the Isle Royale data support those of Peterson et al. (1984) and Keith (1983).

What is the future for Isle Royale wolves? The continued low food supply in 1983 and 1984, the continued interpack aggression, and the history of this population suggest that it is unlikely that the 3 packs that were present in 1982-84 can all persist and grow. The West Pack II has obvious growth potential and will undoubtedly develop into the preeminent pack on the island. It is possible that a second pack of moderate size could operate successfully on the remainder of the island. The East Pack II has exclusive territory, has not been attacked by other packs to our knowledge, and has previously chased the Harvey Lake Pack. These facts lead us to predict that if a pack is indeed lost, it is likely to be the Harvey Lake Pack. Fulfillment of this prediction would mean a return to a wolf population similar to that of 25 years ago, a change that would be in accord with our "cycle hypothesis" (Ch. 1) for wolf-moose fluctuations on Isle Royale (Peterson et al. 1984a). Lest we take encouragement from this, one should note that in the past our greatest advances in understanding this wolf-moose system have followed incorrect predictions based on incomplete knowledge.

CHAPTER THREE

THE INFLUENCE OF A PREY DECLINE ON THE FORAGING EFFICIENCY OF WOLVES

Wolf-prey relationships continue to be the focus of considerable research in North America as competition between humans and wolves for prey rises. Whereas mammalian predators do not regulate prey populations as a rule, there has been increasing evidence that wolves do not exactly fit the usual pattern. This was suggested long ago by Errington (1946), the champion of predation as a compensatory form of mortality. Pimlott (1967) and Keith (1974) argued that wolf predation does not simply substitute for other forms of mortality and that wolves tend to regulate the numbers of their prey.

Wolf research intensified in the 1960's, in general a period of increasing prey numbers throughout boreal forests of North America. Moose populations, in particular, seemed to be in a synchronous increase that has been attributed to extensive forest fires in the 1930's, followed by conservative moose hunting regulations and intensive wolf control. Isle Royale moose reflected the general pattern of moose in many parts of Canada and Alaska, and the decline of Isle Royale moose in the 1970's mirrored declines occurring elsewhere (Peterson 1979b).

In the 1970's there were a number of studies which documented the important demographic influence of wolf predation on prey populations. Mech and Karns (1977) found that wolves were largely responsible for a virtual elimination of deer in a large area in NE Minnesota. In a wolf removal experiment in Alaska, Gasaway et al. (1983) found that moose calf survival was significantly increased after wolves were reduced, reversing a moose population decline. Other studies of moose calf mortality revealed that black bears (*Ursus americanus*) and brown bears (*Ursus arctos*) killed a high percentage of moose in the first 6 weeks of life, compounding the influence of wolf predation. Bergerud (1980) has argued that wolves have generally held caribou populations below the level at which food influences their population dynamics; more recently, the same claim was extended to wolf influence on moose (Bergerud et al. 1983).

While the role of wolf predation in regulating prey populations is not completely understood, there is a clear need for wildlife managers to develop some guidelines for determining the influence of predation in specific cases. Gasaway et al. (1983) pointed out that lack of such an ability led to serious management mistakes in interior Alaska -- low calf abundance was taken to be an indicator of a moose population at the limits of habitat carrying capacity, while actually predation was responsible for low calf survival. Management response to this case was to increase hunting

pressure to lower moose density relative to forage, which lowered moose:wolf ratios and exacerbated the predation problem.

The recent literature has emphasized wolf:prey ratios as a means of estimating predation impact. This is similar to Mech's (1970) conclusion that wolf predation will generally limit prey populations if there is less than 25,000 lb prey biomass per wolf. Gasaway et al. (1983) argued that wolf predation will cause declines in moose populations when moose:wolf ratios are less than 20:1. For ratios between 20:1 and 30:1, moose populations will probably remain stable or decline, while for ratios higher than 30:1 moose will remain stable or increase. Criteria that have been applied by Alaska Department of Fish and Game are that wolf predation will often prove to be an important limiting factor if moose:wolf ratios are less than 40-50:1. Data from Isle Royale in the 1970's were used by Gasaway et al. (1983) to develop his recommended moose:wolf ratios. Keith (1983) has carried this type of analysis further, developing a model which provides moose:wolf ratios that should not be exceeded in order to achieve a stable moose population in which hunting removes a given proportion of annual recruitment.

How reliable are these guidelines, which are being implemented on a fairly large scale in Canada and Alaska? Will use of wolf:prey ratios provide an improved basis for management, or is it simply a facade of quantification with little improvement in real understanding? A partial answer to these questions will be possible after examining more recent data on Isle Royale wolves and moose, which have consistently played a dominant role in past discussions of the impact of wolf predation on prey population dynamics.

PREDATION DYNAMICS

During 1971-84 Isle Royale wolves were tracked during 995 pack-days, covering 9,770 km (Table 10). A total of 278 kills (28% calves) were recorded during 1,489 pack-days. The average pack of 8.7 wolves traveled 9.6 km/day and killed a moose every 6.9 days.

During the study period the moose population declined, stabilized, then began to increase (Ch. 2). During the same period the wolf population increased, stabilized, then declined (Ch. 2). As expected, there were obvious trends in pack size, kill rates, and travel rates during these fluctuations.

Travel rate per carcass in relation to food availability suggests that the pack is the proper unit for analysis of predation and travel patterns. There is a significant inverse relationship between travel/carcass and daily food supply when

Table 10. Travel and kill rates of Isle Royale wolf packs, 1971-84.

Parameter	Mean	SD	N or mean N/year
Pack size	8.7	4.0	35 packs over 14 yrs
Travel (km)/day/pack	9.6	3.6	35.5 days/pack/year
Distance traveled(km)/carcass	49.1	26.3	7.9 carcasses/pack/yr
Kill interval (days)	6.9	3.8	42.5 days/pack/year
Food(kg) availability/wolf/day	5.7	2.1	42.5 days/pack/year
Food(kg) availability/pack/day	46.4	23.5	42.5 days/pack/year

calculated on a per pack basis, but there is no significant relationship when food supply is calculated on a per wolf basis (Figs. 13 and 14).

Daily travel rate was positively correlated with food/pack/day (Fig. 15) and also pack size (Fig. 16). Large packs exist only with high food supply (Ch. 2), and these packs travel further each day and tend to have the shortest kill interval (Fig. 17).

During the study wolf food supply dwindled as kill rates declined in a linear fashion (Figs. 18 and 19). Since moose constitute wolf food supply, we examined the relationship between wolf food levels and moose population size and found no significant relationship (Fig. 20).

Furthermore, we have found considerable variation in wolf kill rates. Wolf kill rates, though variable, were positively correlated ($\underline{P}(0.10)$ with pack size (Fig. 21). Generally, large and small packs killed moose at high and low rates, respectively, and medium-sized packs exhibited a 3-fold variation in kill rates.

At low kill rates, many packs were supported by only a marginal food supply of 3 kg/wolf/day; below that level mortality to starvation was documented. If pack kill rates failed to provide at least 3 kg food/wolf/day pack size declined, likely because of dispersal. Maximum observed kill rate increased with pack size up to a group of 10 wolves, thereafter leveling off at 0.4 moose/day or 1 kill every 2.5 days. Observed kill rates for Isle Royale wolves bracket all other values for wolves killing moose (Peterson et al. 1984b; Ballard, final report).

The island-wide kill of moose was not significantly related to wolf density (Fig. 21). Rather, kill rate declined directly with time (Fig. 22).

Since moose:wolf ratios are a common tool for managers in assessing wolf:prey relationships, we next examined the relationship between the rate of increase in the moose population and the moose/wolf ratio. There was no significant relationship (Fig. 23). Moose exhibited positive rates of increase over a range of moose/wolf ratios from 14:1 to 42:1, and declined over a ratio range from 12:1 to 68:1.

Wolf predation on moose has repeatedly been shown to be non-random, with strong selection for calves and moose older than 8 years of age (Peterson et al. 1984). At Isle Royale there has been substantial temporal variation in the age distribution of moose killed by wolves (primarily in winter). Calves consistently composed over 40% of the kill from the

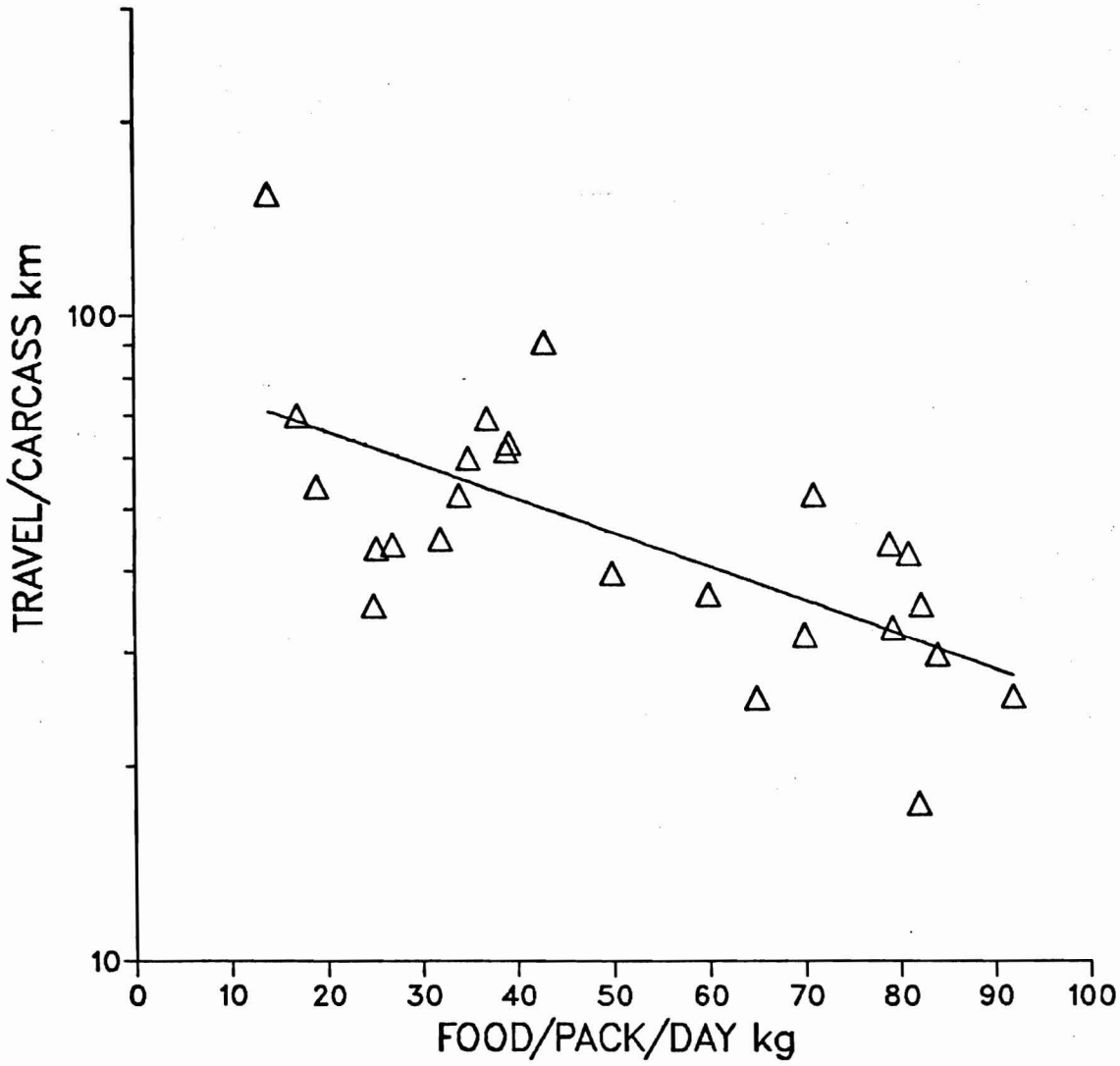


Fig. 13. Wolf pack per carcass travel rates in relation to per pack food availability, 1971-84. Straight-line regression $Y = 83.3-0.642X$, $P<0.005$, $r^2 = 0.32$.

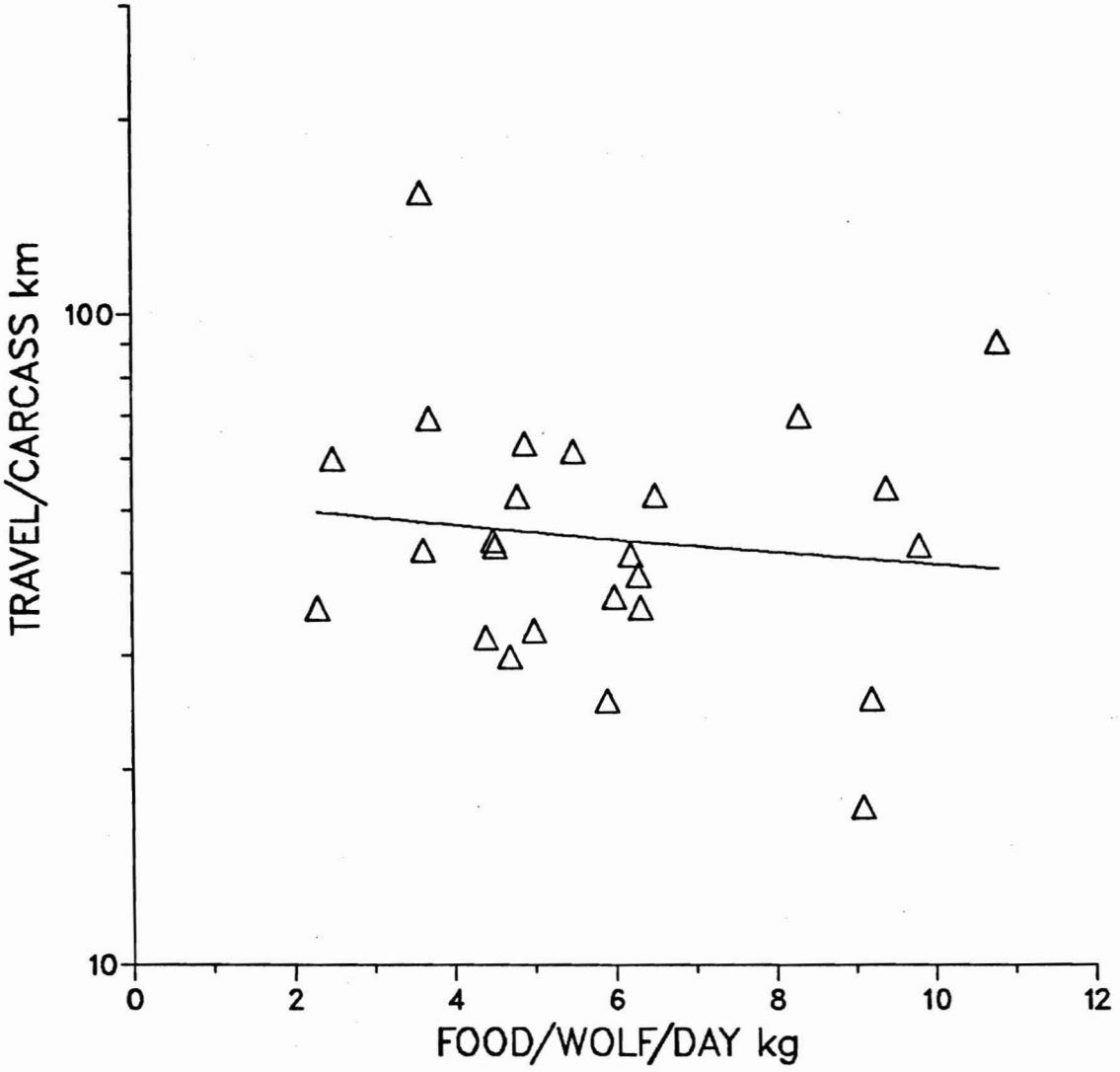


Fig. 14. Wolf pack per carcass travel rates in relation to per wolf food availability, 1971-84. Straight-line regression $Y = 57-1.12X$, $P<0.75$, $r^2 = -0.03$.

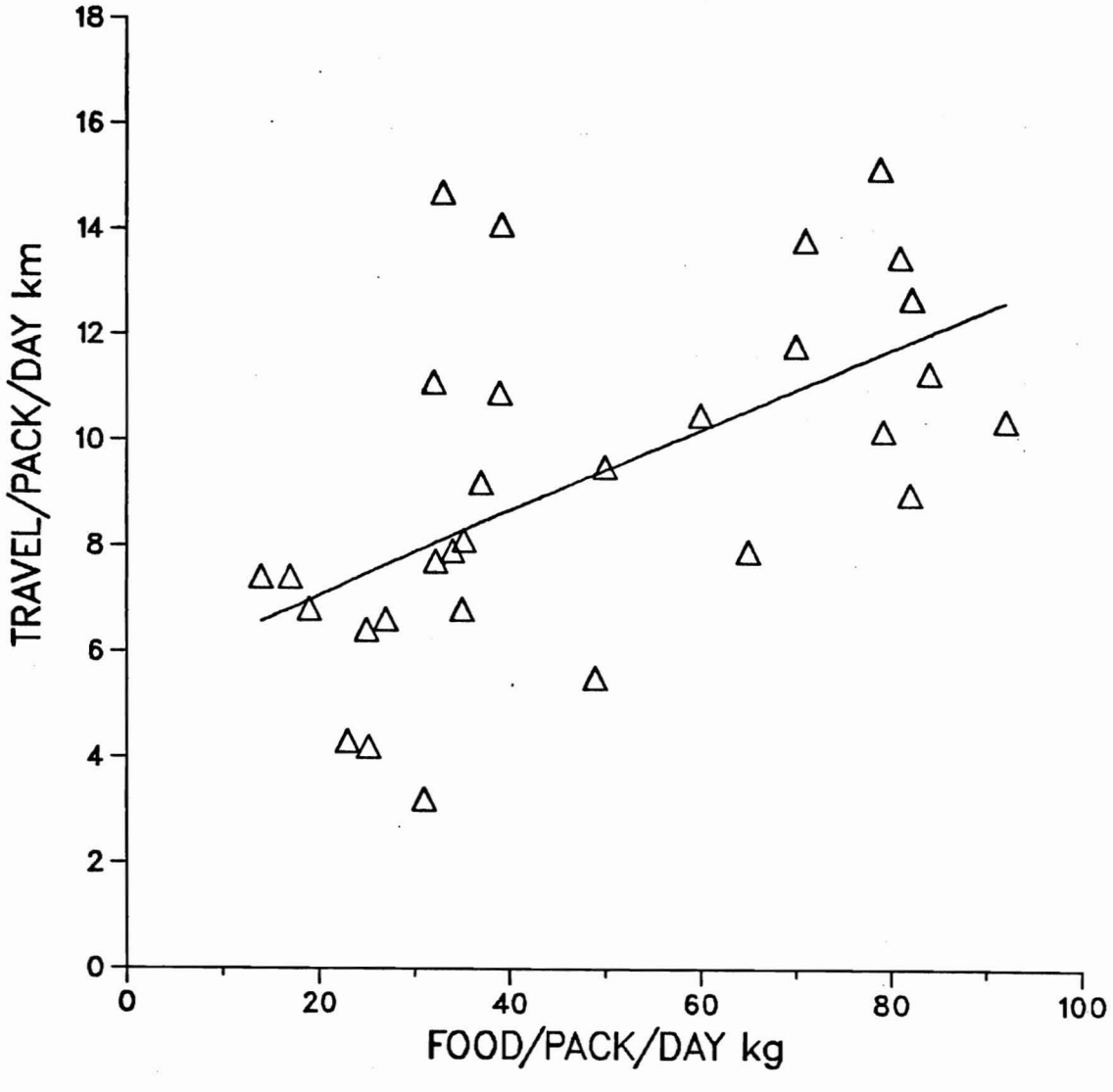


Fig. 15. Wolf pack daily travel rates in relation to per pack food availability, 1971-84. Straight-line regression $Y = 5.54+0.78X$, $P<0.001$, $r^2 = 0.31$.

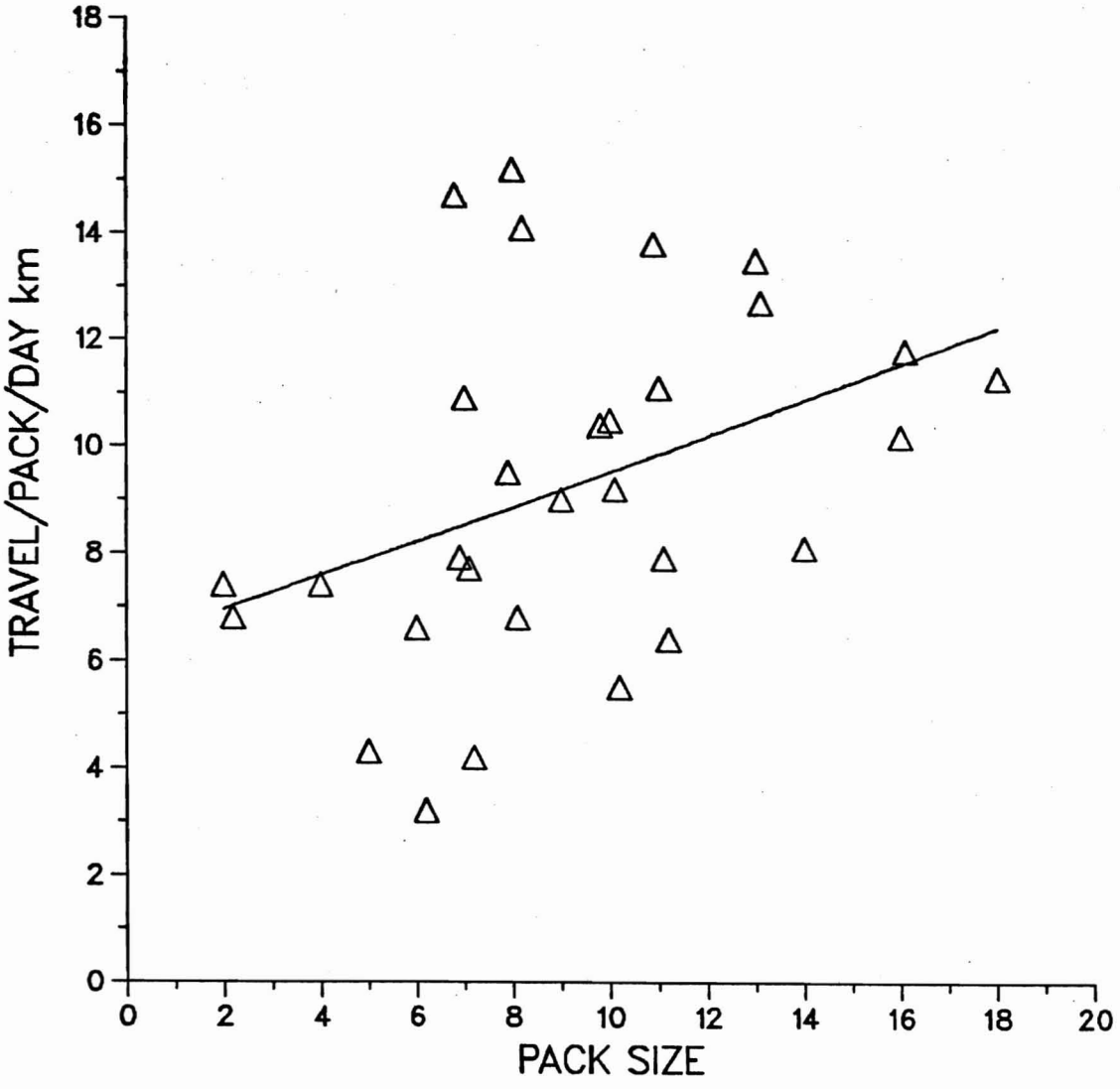


Fig. 16. Wolf pack daily travel rates in relation to pack size, 1971-84. Straight-line regression $Y = 6.21+0.33X$, $P<0.05$, $r^2 = 0.13$.

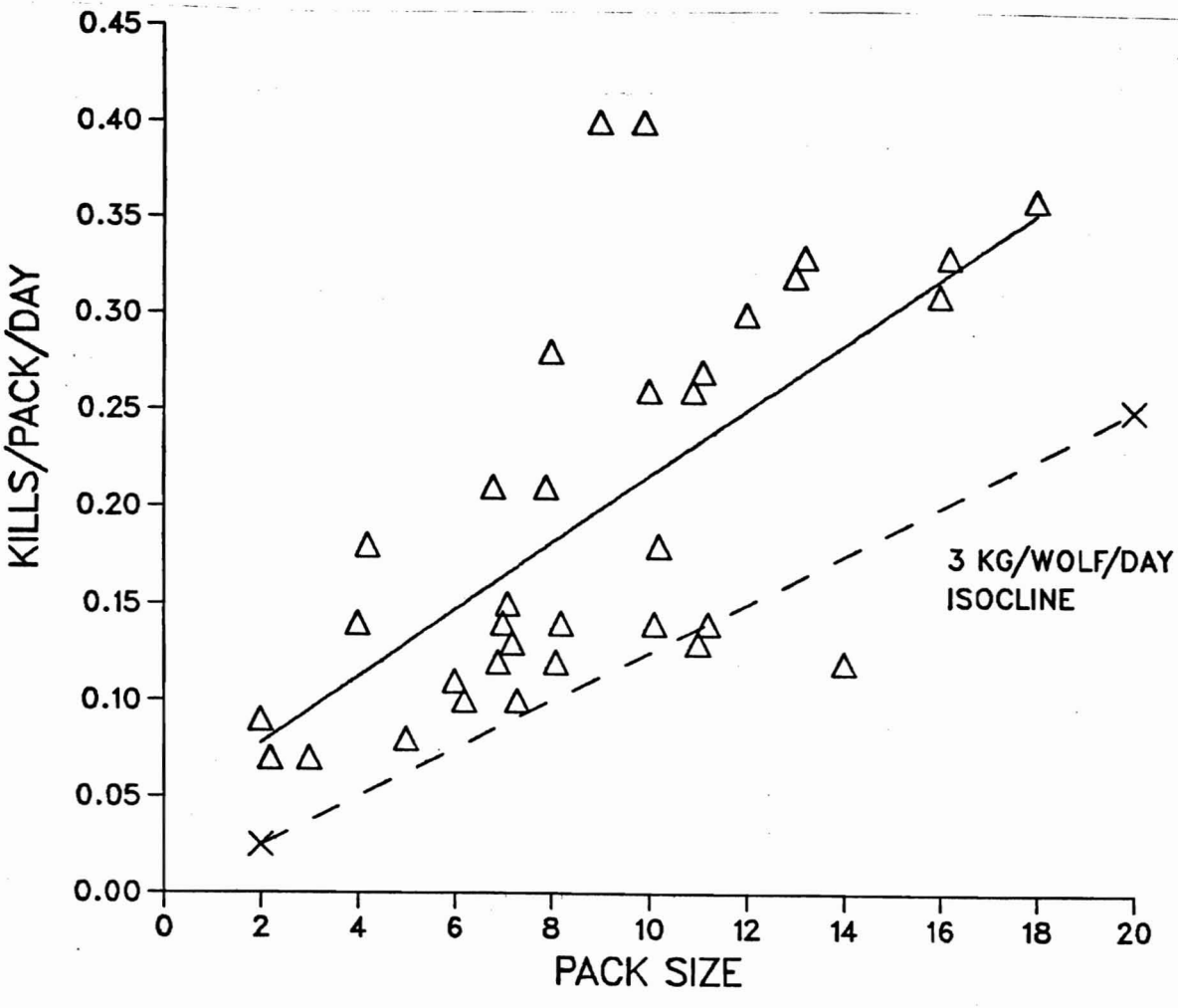


Fig. 17. Wolf pack kill rate in relation to pack size, 1971–84. Straight-line regression $Y = 0.044+0.017X$, $P<0.001$, $r^2 = 0.43$. The 3 kg/wolf/day isocline indicates maintenance-level food supply.

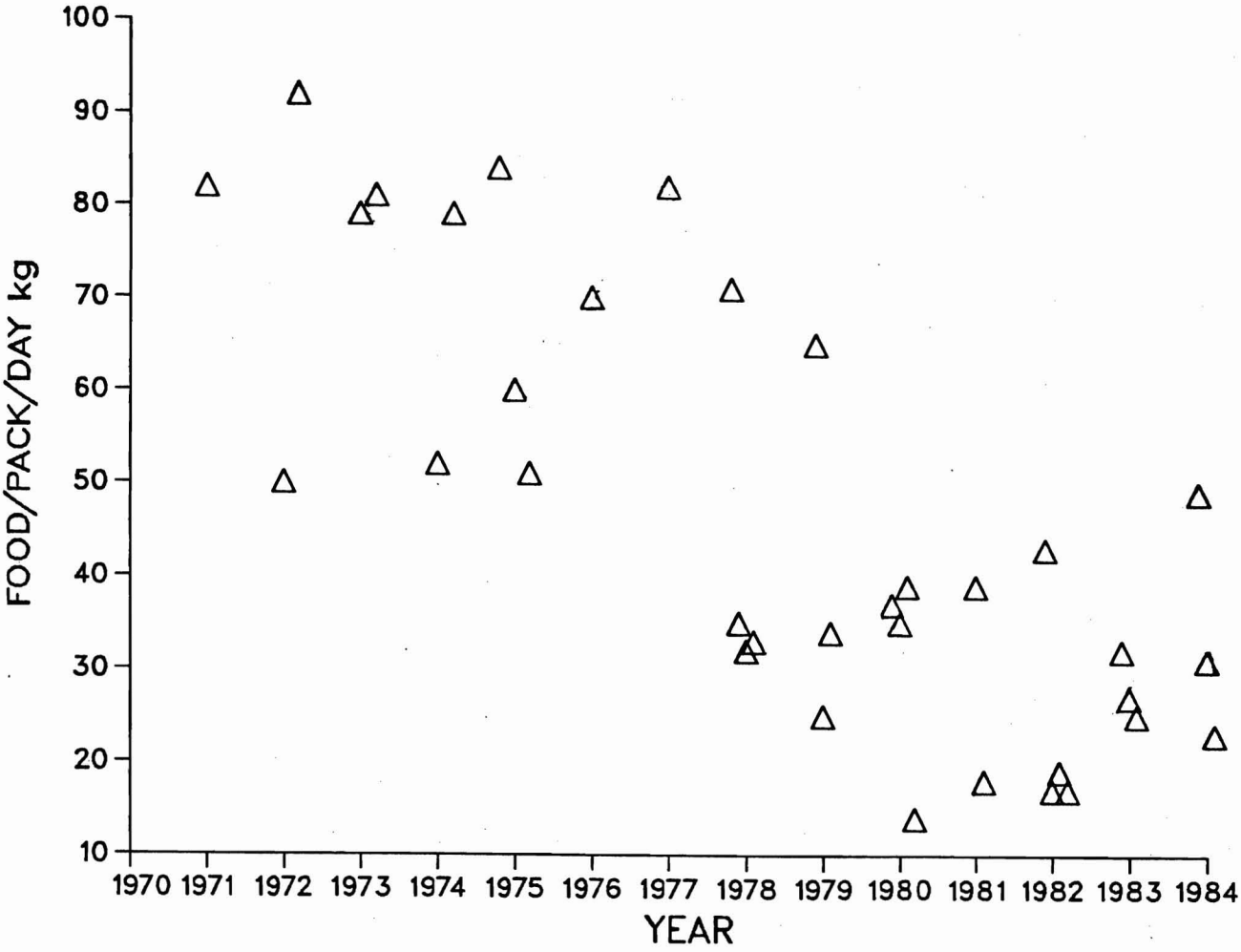


Fig. 18. Trend in per pack daily food availability on Isle Royale, 1971-84.

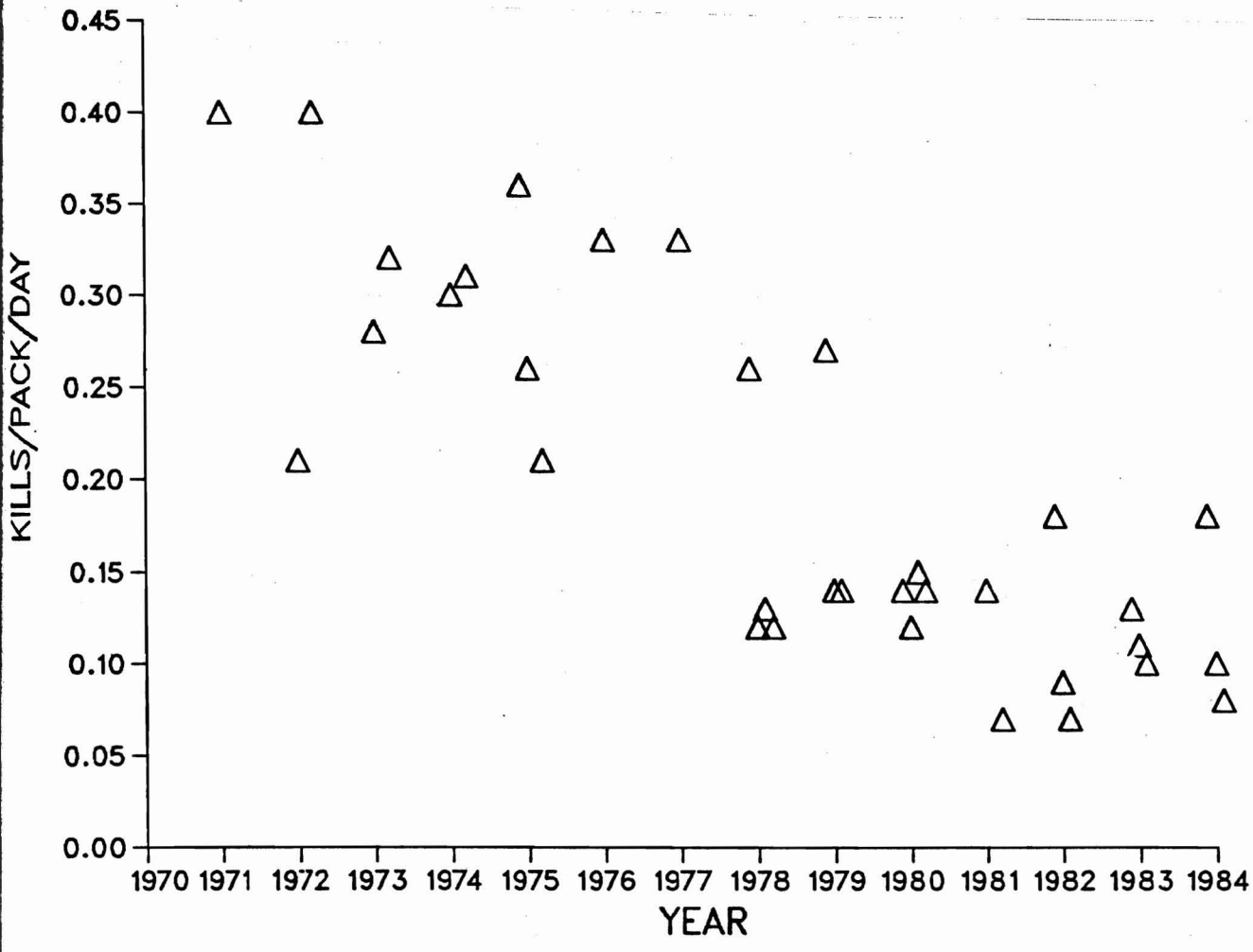


Fig. 19. Trend in pack moose kill rates on Isle Royale, 1971-84.

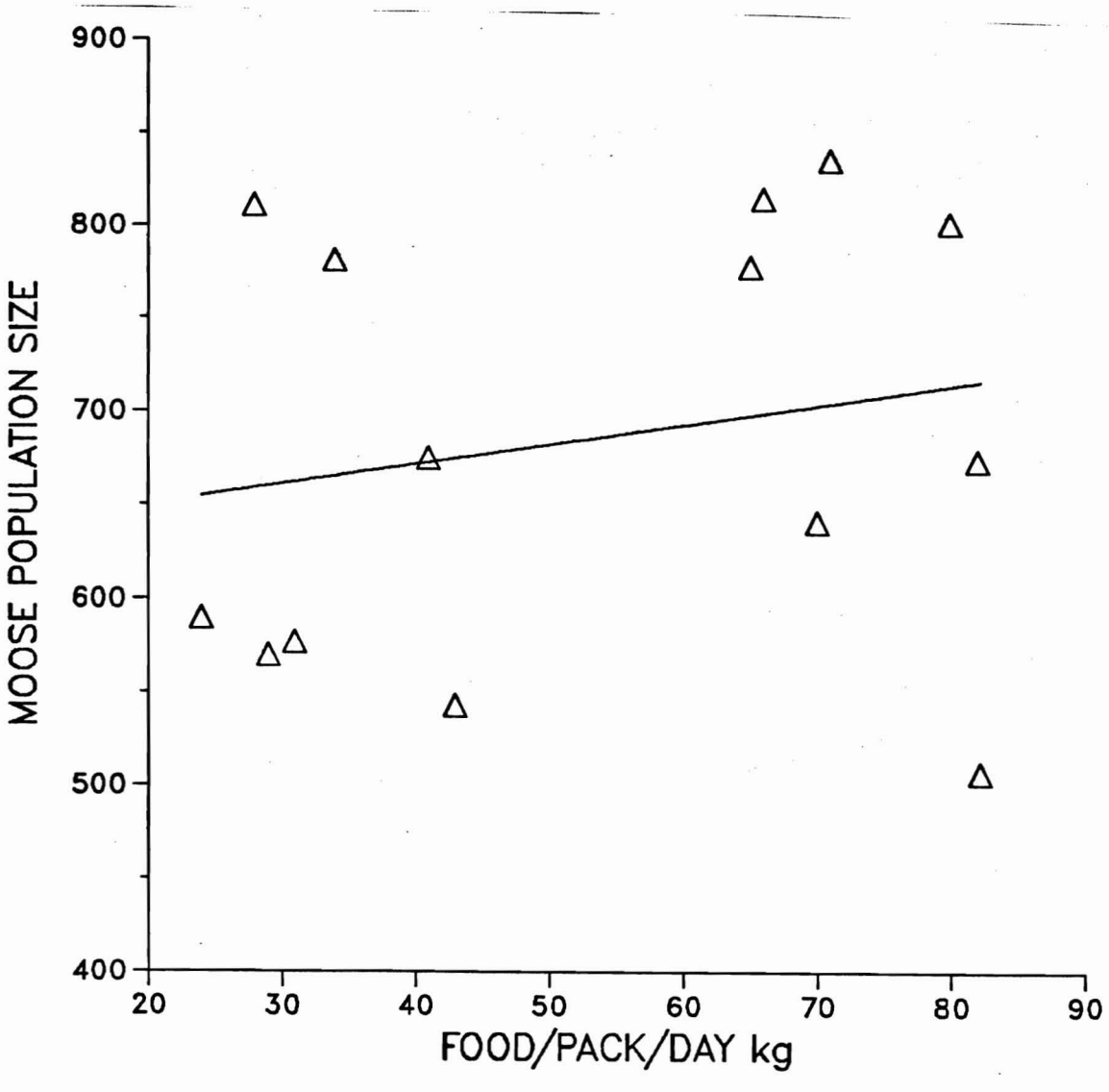


Fig. 20. Isle Royale moose population size in relation to per pack food availability, 1971-84. Straight-line regression $Y = 629+1.06X$, $P<0.50$, $r^2 = 0.04$.

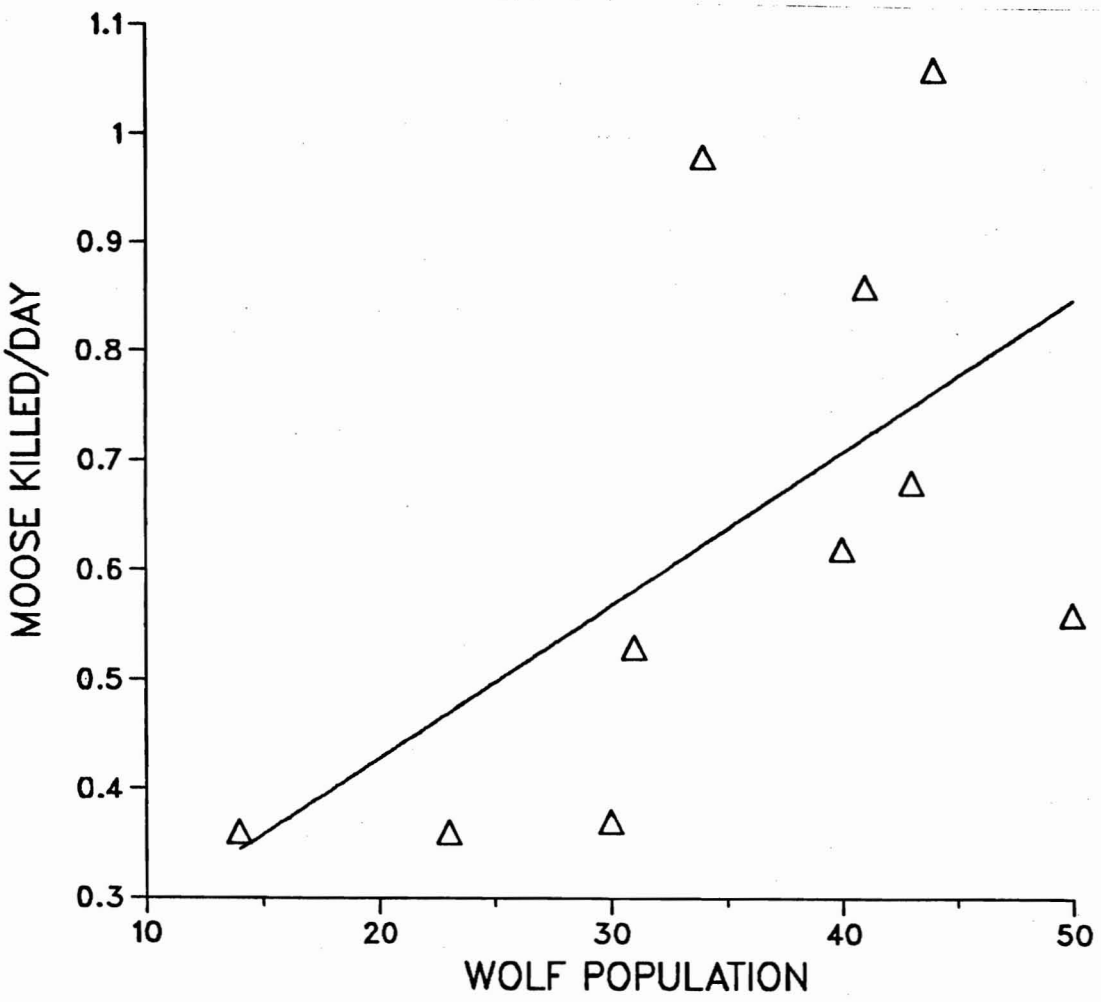


Fig. 21. Total predation loss for Isle Royale moose in relation to wolf density. Straight-line regression $Y = 0.148+0.01X$, $P<0.10$, $r^2 = 0.27$.

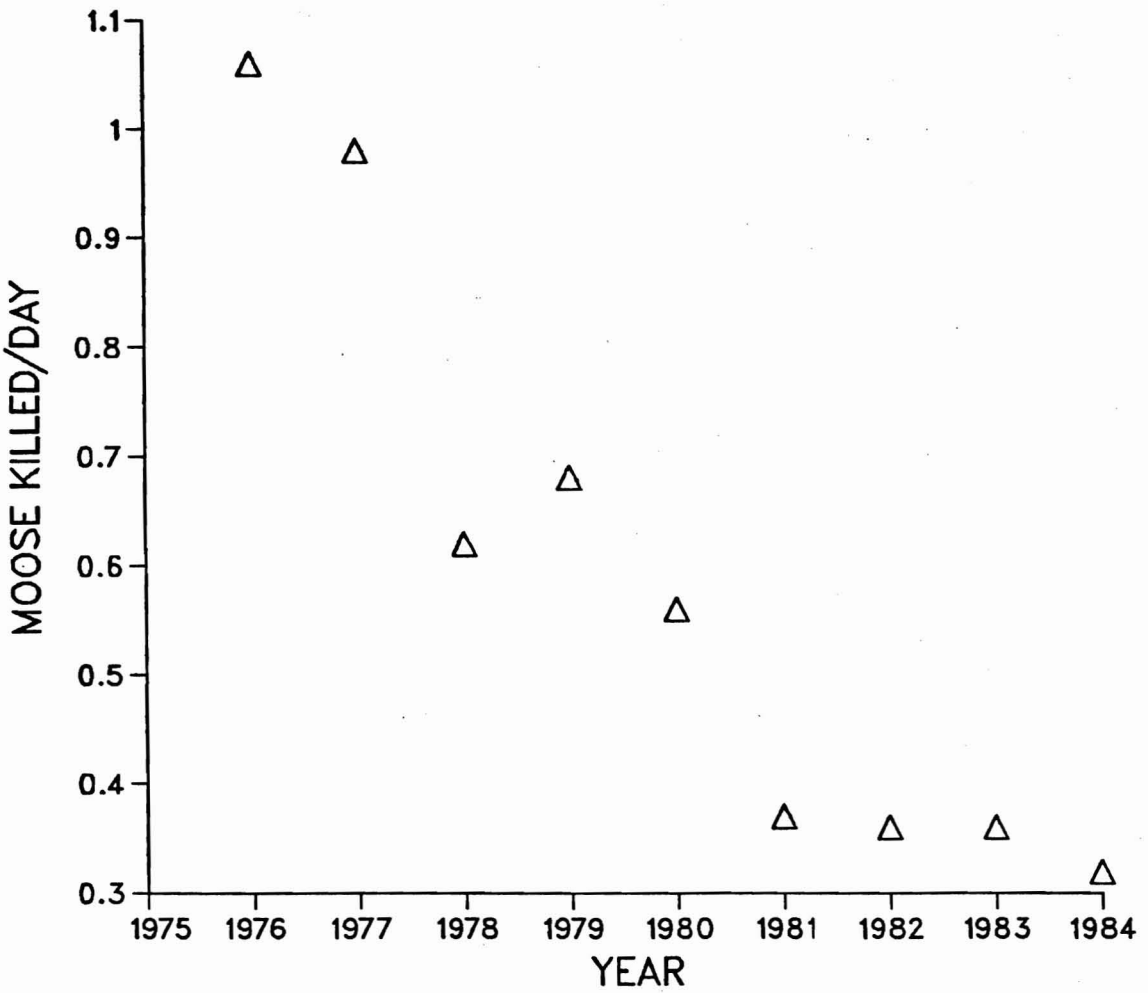


Fig. 22. Trend in total predation loss in midwinter for Isle Royale moose.

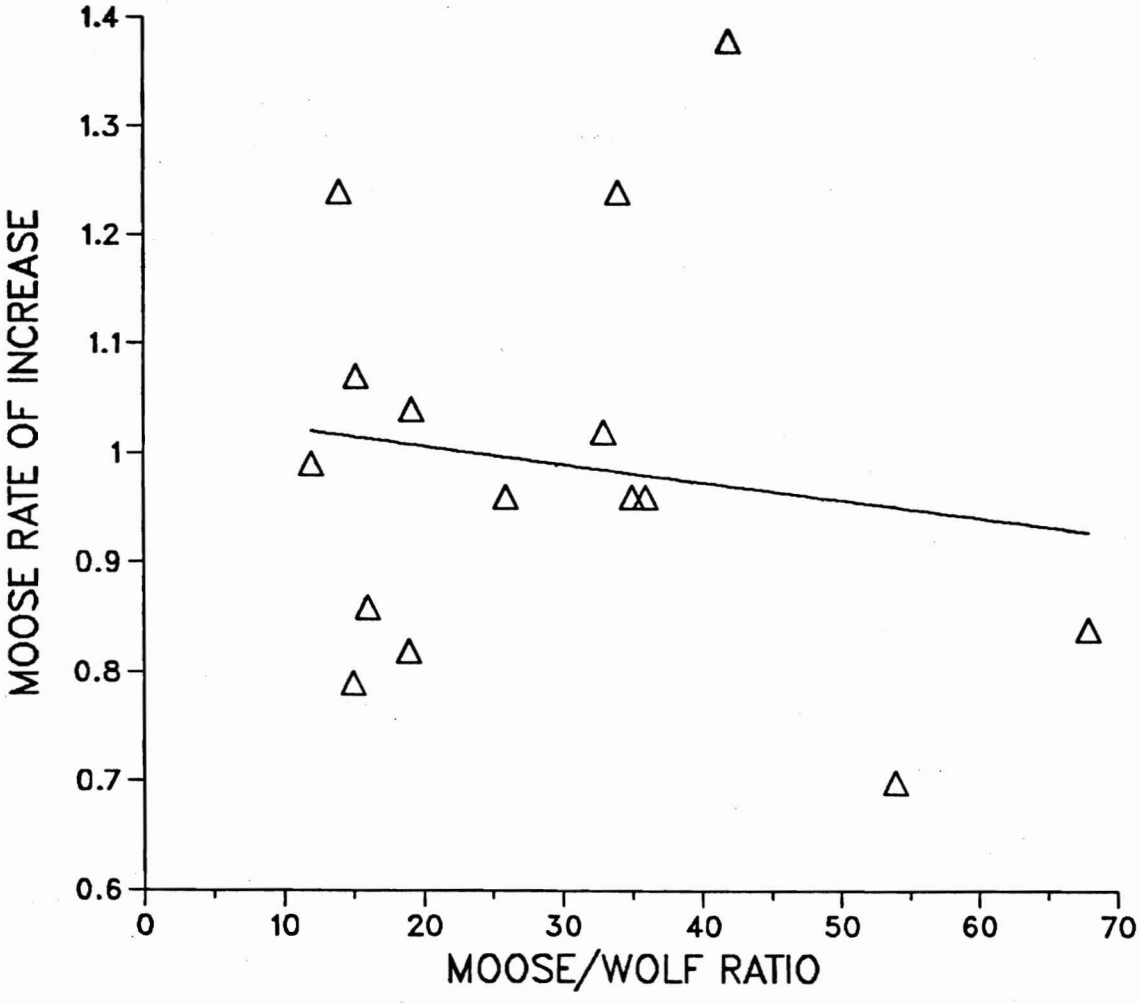


Fig. 23. Relation between finite rate of population increase for Isle Royale moose in relation to moose/wolf ratio. Straight-line regression $Y = 1.04-0.0016X$, $P<0.75$, $r^2 = -0.05$.

late 1950's until the mid-1970's, but in the late 1970's calves became less prominent in the wolf diet, dropping to only 8% of the kill in the early 1980's. Since 1970, wolf predation on calves has been unrelated to calf abundance. While calf composition in the kill was 43%, 18%, and 8% in 1970-74, 1975-79, and 1980-84, respectively, calf proportion in the living population (assuming an even sex ratio) was 30%, 20%, and 37%, respectively. During 1981-83, calf percentage in the herd averaged 44%, yet wolves took relatively few animals in this age group. Earlier data from Isle Royale (Peterson 1977) indicated that wolves typically killed calves about twice as often as they occurred in the population. Similar patterns were evident in other, more limited studies of wolf-moose relationships (e.g. Peterson et al. 1984b).

There have also been significant temporal shifts in the age distribution of moose older than 1 year in the wolf-killed sample. Moose between the ages of 1 and 5 years were killed at peak frequency during 1970-74 and declined in importance both before and after this period. Moose older than 9 years consistently composed 1/4 to 1/3 of the kill prior to 1975, but have increased to 72% since 1980.

The most significant change in the composition of the kill that may help explain the above fluctuations is the incidence of arthritis among adult moose. There has been a clear increase in the incidence of arthritis both among moose aged 7-12 years and those over 12 years (Table 11). Neither a change in relative predation on different age groups nor sex ratio of the kill is responsible for these trends, and we are left to conclude that there has been a significant increase in the frequency of arthritis in the moose population.

ON WOLF:MOOSE RATIOS

Recent discussions of wolf:prey relationships have suggested that consideration of wolf:prey ratios will lead to an improved understanding of the role of predation in specific cases where management of these populations is a practical necessity (Gasaway et al. 1983, Keith 1983, Bergerud et al. 1983). Keith's analysis relied heavily on calculations based upon an assumed <u>per wolf kill rate</u>. All of the above studies assumed that wolf-moose relationships were, for practical purposes, adequately represented by simply the numerical relationship between predator and prey.

While development of these ideas was partially based on Isle Royale data, consideration of the entire record from Isle Royale suggests that serious errors of interpretation may be possible if management is based on such a simplistic approach. In fact, moose:wolf ratios were an entirely inadequate predictor of subsequent change in the moose population. The

Table 11. Age-specific incidence of arthritis among moose dying on Isle Royale.

Time period	Age 7-12 years		Age over 12 years	
	%	N	%	N
Pre-1964	11	124	16	32
1965-69	23	52	22	46
1970-74	21	89	31	35
1975-79	39	111	57	77
1980-83	37	27	62	53

reason for this is simple: wolf kill rates were almost unrelated to wolf numbers.

Elsewhere we have hypothesized that wolves and moose at Isle Royale are fluctuating on a long-term cycle, with instability caused by lags in this predator-prey system (Peterson et al. 1984a). A most prominent lag is caused by the long life span of moose, fundamentally a result of its large body size. If food supply for wolves consists primarily of moose older than 7-8 years of age (which is true even if calves are prominent in the kill because of the difference in prey biomass), then wolf predation can be expected to be responsive to factors which affect moose abundance and vulnerability in these older age classes. Survival of these cohorts during the first year of life is highly variable, and this has certain impacts on wolves 8-10 years later.

Further, we hypothesize that the increase in arthritis may reflect long-term influence of an altered developmental pattern early in life, perhaps caused by pre- or post-natal malnutrition. The cause of cartilage degeneration leading to primary degenerative joint disease is not understood for any species, and such an understanding in the case of moose is non-existent. Our hypothesis is based primarily on the fact that moose dying with a high incidence of arthritis in 1980-84 were born during a period of peak population density and demonstrated malnutrition in the late 1960's and early 1970's. During this period, mortality from malnutrition was demographically significant, wolf predation on cohorts born during this period has been consistently high ever since, and calves born during this period were significantly smaller than the obviously viable cohorts born a decade later (Peterson et al. 1984a).

We believe that the highly variable nature of moose vulnerability should not be ignored when assessing the impact of wolf predation in any specific case. Keith's model incorporating hunting and wolf predation is based on <u>average</u> recruitment, <u>average</u> wolf predation rates, and presumably <u>average</u> moose vulnerability, as reflected in assumed per wolf kill rates. It provides for no temporal variation in wolf-moose relationships which, as this study demonstrates, can be of over-riding importance. Moose age distribution and population dynamics in any specific case will rarely result from the interaction of average parameter values.

While variation in wolf predation on calf moose is clear, its cause cannot at this time be isolated. Lack of predation on calves in the early 1980's could have resulted from lower calf vulnerability (attributable to higher calf viability or better defense provided by dams) or exceptionally high vulnerability among the old age classes, possibly caused by an

increase in arthritis. In either case, the demographic influence of wolf predation has been lessened by the shift in predation pressure toward older age groups. Most important, this shift can clearly be attributed to vulnerability factors inherent in the moose population. This is not to suggest that wolf density had no bearing on overall calf survival; the increase in calf survival after the wolf decline is ample evidence of wolf density effects. Consideration of only wolf density and moose:wolf ratios cannot, based on our data, be considered an adequate basis for managing wolf and prey populations.

CHAPTER FOUR

WOLF-AVOIDANCE STRATEGIES OF MOOSE

Coevolution of predators and prey has produced an impressive array of morphological and behavioral characteristics that enhance survival and reproductive success (Bertram 1978, Harvey and Greenwood 1978, Pianka 1978, Gosling and Petrie 1981). Coloration, specialized anatomy, social organization, patterns of habitat selection, and defensive behaviors of large mammalian prey have thus been shaped to a considerable degree by natural selection in the form of predation by large carnivores (e.g. Geist 1980, Bergerud 1974, Jarman 1974, Jarman and Jarman 1979, Sinclair and Griffiths 1979). However, behavioral adaptations of prey are "often very subtle and exceedingly complex" (Eisenberg 1981: 420), and our ability to sort out such complexity has been limited by lack of detailed knowledge of prey life history and behavior, the low frequency at which predation is actually observed, and, in the case of large carnivores, reduction or elimination of key species even in remnant natural habitats. Thus, while the white-tailed deer Odocoileus virginianus Zimm. has received an enormous amount of scientific attention in North America, possible anti-predator strategies associated with patterns of social organization and habitat selection have only recently been postulated (Hirth 1977, Mech 1977, Nelson and Mech 1981).

In Isle Royale National Park, unhunted wolf Canis lupus L. and moose Alces alces L. populations have co-existed since the late 1940's (Mech 1966). During continuing studies of these species at Isle Royale in the 1970's, two anti-predator strategies were suggested by the distribution of moose, especially cows with calves, relative to small offshore islets and human camps.

In January and February of 1972, 1974, 1979-81, stratified samples of plots were counted from light aircraft to estimate moose numbers on the main island, while complete counts were made of moose on major surrounding islets (Stephens and Peterson, in preparation). After leaf-fall in late October, 1972-81, sex and age composition counts were conducted from light aircraft (Peterson 1977).

Annual counts of relative summer moose abundance utilized the number of moose observed per distance hiked by researchers as they searched for wolf packs and moose carcasses from 1970 to 1980. From early June through late August research teams hiked an average of 960 km yr^{-1}, of which a third was off-trail. Routes were well-distributed throughout the island, traversing all major habitats, including swamps, bogs, ridges, forests, stream and pond banks, lake shores, and human camps.

Only land-based observations of moose initially seen from outside of buildings were included in the summer ground count. Each observation was classed as an unlikely, possible or probable repeat of moose previously counted, based on its location, sex, age, and other distinguishing characteristics, such as bell shape and size, hock sores, and abnormal growths. Probable repeats were excluded from the count.

Sex, age, time, and general location were noted for all moose observations; hiking routes were drawn on 1:62500 topographic maps. During 1976-1980, observation locations were also plotted on similar maps, and relative visibility (poor, moderate, or good) and observation duration were recorded with other variables on a prepared form.

Two to eight percent of the total winter moose population was on islets (Table 12). Winter moose densities on islets averaged 7.1 moose km^{-2}, 415% greater (range 162-700%) than on the main island (Paired t-test, $t = 4.04$, $P<0.01$). Densities on islets tended to be greater than in localized heavy-use areas within 2 km of shorelines (7 vs. 5 moose km^{-2}; Paired t-test, $t = 1.46$, $P=0.22$). In addition, the population on islets possessed a greater proportion of calves than did the sample from the main island (20 vs. 11%; Paired t-test, $t = 4.06$, $P<0.05$). In 1981, when most of the islet areas were examined, 8.3% of the total estimated moose population was found on islets. Similarly, during the October 1979 aerial count (the only year when islets were extensively sampled in autumn), the proportion of cows observed with calves was greater on islets than on the main island (62 vs 21%, $x^2 = 4.75$; $P<0.05$).

Distribution of moose twins in winter indicates further the significance of islets and shoreline habitats for calves. During aerial surveys in October (1959-1973) only 11% of cow moose with calves had twins (Peterson 1977). In winter, twin calves are exceedingly rare - only 8 sets were recorded among 3800 aerial moose observations at Isle Royale during 1973-82. Four sets of twins were observed on islets, and 3 of the remaining 4 sets were less than 100 m from the shoreline on the main island.

To assess the demographic significance of islets as a refuge from wolf predation, data on cow density on islets at the time for birth is desirable. Available data are only from winter, but these can be used to estimate the proportion of calves present on islets at least at this time of year; it is likely that cow/calf density on islets would be much greater near the time of birth.

The proportions of midwinter adult and calf populations which inhabited islets can be estimated for the years 1979-1981 if several assumptions are made (Table 13). We estimated that 11% and 3% of the calf and adult populations,

Table 12. Comparisons between winter moose populations on the main island, in stratum 3 (i.e., areas of greatest moose concentrations on the main island), and on islets. All populations figures were derived from quadrat counts and corrected for sightability. Islets comprised less than 2% of the area of the archipelago.

Parameter	Year					Overall
	1972	1974	1979	1980	1981	
Moose km^{-2}						
Main island. . . .	1.6	1.5	1.6	1.0	0.8	1.3
Stratum 3.	4.6	5.5	6.2	5.5	3.3	5.0
Islets[a]	5.9	12.3	4.2	7.9	5.1	7.1
% calves						
Main island. . . .	b	11.6	7.8	12.2	14.4	11.3
(N of moose) . . .		(69)	(115)	(98)	(97)	(379)
Stratum 3.	b	18.6	10.7	7.5	25.0	13.3
(N of moose) . . .		(51)	(56)	(67)	(36)	(210)
Islets[a].	b	20.4	14.3	25.9	17.6	20.2
(N of moose) . . .		(44)	(14)	(27)	(34)	(119)

a. The proportion of islet area counted was 48% in 1972, 1974, 1977 and 1980 and 87% in 1981.

b. Calves were not distinguished from other.

Table 13. Proportions of calf and adult moose populations located on islets in midwinter, based on winter quadrat counts, autumn aerial composition counts, and wolf-kill data.

Parameter	Year			Overall
	1979	1980	1981	
Total winter population[a] . . .	888	585	481	---
Proportion of calves from previous autumn count	0.09	0.11	0.07	---
Wolf-kills/day[b]	0.7	0.6	0.4	---
Winter calf population				
Total	64	52	24	140
On islets	2	7	6	15
(%)	(3)	(14)	(25)	(11)
Winter adult population				
Total	824	533	457	1814
On islets	12	20	28	60
(%)	(2)	(4)	(6)	(3)

a. In 1981, for example, if a midwinter population of 481 is assumed (based on the quadrant count), and a total of 36 moose killed by wolves from 1 Nov-31 Jan (if 0.4 moose/day were killed during that time: from Peterson unpubl. data) an autumn population of 517 can be calculated. Furthermore, 7% of these moose were calves (based on the autumn aerial survey) and 12 calves were killed by wolves (if 34% of the moose killed were calves: from Peterson 1977:151) during November-January, then the midwinter moose population would have consisted of 24 calves and 457 adults.
b. Kill period assumed to be 90 days between the autumn composition counts and the winter quadrat counts.

respectively, existed on islets in winter during this three year period, though islets comprise less than 2% of the area of the archipelago.

Moose on islets were exposed to predation pressure in winter when ice bridges typically formed to all islets. We have examined remains of 98 moose that died on islets, primarily killed by wolves in winter. This sample comprised 44% calves, 27% adult (yearling and older) males, and 29% adult females. Moose dying on the main island (N=1270) comprised 32% calves, 35% adult males, and 33% adult females ($x^2 = 7.03$, $P = 0.03$).

During summers, we found that cows and calves were likewise not distributed randomly with respect to human camps; cows and calves appeared there more often than bulls. Cows comprised 84% (N=100) of the yearling and adult moose in camps, and only 45% (N=183) of the population located further than 1 km from these areas ($x^2 = 39.36$, $p<0.01$, Fig. 1). Moreover, cows in camps were seen more commonly with calves than those more than 1 km away from camps (34 vs 23%; Wilcoxon paired T-test, $T = 0.00$, $P = 0.05$; Fig. 2). The proportion of moose observed within 1 km of human camps was essentially the same during 1976-1980 ($x^2 = 1.03$, $P > 0.90$).

The above differences were not due to observational bias. Relative visibility values assigned to calves were no different for those in camps than for those in the back-country ($x^2 = 0.01$, $P > 0.90$). Furthermore, we did not watch cows in camps much longer than those in the backcountry (median: 5.0 vs. 2.5 min.; Mann-Whitney; $U = 5987.0$, $P = 0.05$), nor did we observe those with calves for a longer time than those without calves (Mann-Whitney, $U = 8320.5$, $P = 0.35$).

We propose that the preference shown by Isle Royale moose for islets is largely attributable to the survival advantage that accrues for very young calves. We suggest further that the well known preference of moose for conifer in winter may reflect anti-predator behavior, not simply moose selection of habitats with a moderate winter microclimate and less snow, as commonly suggested (Van Ballenberghe and Peek 1971, Phillips et al. 1973, Coady 1974, Peterson and Allen 1974, Peek et al. 1976, Peterson 1977). Peterson (1977) suggested that conifers may be preferred by cows with calves because of the protection provided from wolf attack. It is clear from Mech's (1966:174-189) observations that moose commonly seek conifer cover and windfalls during encounters with wolves. One of us (ROP) has often seen moose use structural features of the habitat to reduce exposure to wolf attack. Winter microclimate appears similar on both islets and the adjacent shoreline of the main island. Therefore microclimate differences do not adequately explain the heavier use of islets by moose.

Moose have coevolved with capable predators; wolves prey on moose year-round (Mech 1966), Peterson (1977) and bears (Ursus arctos and Ursus americanus) kill primarily calf moose less than 2 months old (Franzmann et al. 1980, Ballard et al. 1981). Mortality rates for calves are highest early in life and predators may claim the majority of calves at this time (Franzmann et al. 1980, Ballard et al. 1981). Strong selection pressure thus exists for behavior that reduces the frequency of predator encounters for young calves. Moose inhabiting small islands probably experience reduced contacts with predators and also are able to escape into nearby water during actual encounters. Water provides a highly effective defense for moose that is widely used during moose-wolf encounters (Peterson, unpubl. data).

Peterson (1955:63-64) and Edwards (1978:50) have commented on the tendency of cows to seek islands and insular areas immediately prior to birthing. The disproportionately great number of cows with calves on islets during our 1979 October aerial count, as well as during the winter, suggests an abnormally high year-round usage of islets.

Island occupancy is most advantageous early in the life of a calf (first summer), when there are no ice bridges to the mainland that facilitate wolf travel, and when calves participate only minimally in their own defense. It is not clear that island occupancy is similarly advantageous in winter, at least at Isle Royale. Islets there are distributed around the periphery of the main island, along primary wolf travel routes, and many islets harboring moose are repeatedly visited by wolves in the course of a single winter. The high proportion of calves among moose dying of wolf predation on small islands in winter is evidence of the abundance and vulnerability of calves on islets during that season. The proportion of both calf and adult moose on islets increased as wolf predation declined (Table 13), suggesting that predation pressure influenced the proportion of moose using islets, particularly cows with calves.

Why then, do some cows with calves remain on islets for much of the year? First, it may be quite advantageous for moose to be thoroughly familiar with local escape terrain (Pulliainen 1974), especially if spatial orientation of cow and calf relative to protective cover is critical to survival. Secondly, the moose we observed on islets in winter are probably only a remnant of the cow/calf pairs present at the time of birth. Calf concentrations on islets in winter may result from strong selection for islet occupancy in summer and continued preference in winter for familiar sites that provide maximal protection against wolves whenever they appear.

Calves comprise a high proportion of the kills made by wolves on small islets, and the sex ratio of the other moose

killed there was about equal. This suggests that calves are indeed vulnerable in these sites in winter and that cows do not select islets in winter to the point where males are excluded. These data, together with the inverse relationship between predation pressure and islet occupancy in winter, suggest that the winter preponderance of calf moose on islets results from a higher calf survival rate there in summer and fall.

How significant are the islets to the Isle Royale moose population as a whole? We estimated that 11% (Table 13) of the midwinter calf population was found on islets, and presented data which suggested that survival of calves on islets was higher than on the main island. Very likely the calves found on islets in winter were also born there, since the selective advantage of inhabiting islets would be greatest for very young calves. It is also likely that many calves born on islets are moved back to the mainland before winter; the islets on which Edwards (1978) found cows and calves in summer are usually not used by moose in winter. We conclude that the proportion of calves born on islands is greater than 11% and is probably of demographic significance.

On Isle Royale, cows with calves comprise a larger proportion of the population around human camps than bulls or cows without calves. Wolves rarely traveled within 1 km of these settlements during the summer months. We propose that human camps provided a refuge from wolf predation for cows with calves. Geist (1980) has suggested that deer (Odocoileus hemionus) also find refuge from predators around human settlements. Other authors have suggested that, in some circumstances, moose that are hunted tend to avoid areas of human concentration (Hancock 1976, Rolley and Keith 1980).

The disproportionate number of observations of cows with calves in camps is attributed to an actual difference in moose distribution by sex and age, rather than observational bias. A reasonable explanation is that the use of camp areas by cows benefited calves. Since visibility values for calves in camps were no different from those in the backcountry it appears that any habituation to humans which they or their mothers might have acquired in camps did not affect their visibility. Furthermore, the slight difference in median observation times for camp and backcountry cows seemed too small to substantially increase the probability of sighting calves that might have been present.

We found that Isle Royale moose occurred at higher density on offshore islets and a higher proportion of calves existed both on islets and near camps. Peterson (1977) earlier found evidence that calves may be more common along the shoreline of Isle Royale. While a more favorable winter microclimate may exist on islets and along shorelines, this would not explain the preponderance of cows and calves

relative to camps in summer, nor the winter concentrations of moose on islets. We suggest that predator avoidance is the primary factor responsible for the observed distribution patterns relative to both islets and camps. Cow moose may deliberately choose islands and camps as relatively predator-free birth sites, but calf abundance on islets in winter seems to result largely from higher early survival of calves. In any case, coevolution of wolves and moose has apparently resulted in subtle patterns of habitat selection which confer a survival advantage that seems especially clear for moose calves, the age group most vulnerable to wolves.

CHAPTER FIVE

DO WOLVES ALONE LIMIT MOOSE POPULATIONS?

A number of conceptual issues in wolf-prey ecology were recently raised by Bergerud et al. (1983), who presented results of a 5-year study of wolf and moose populations in Pukaskwa National Park, Ontario. They drew a number of interesting comparisons between their study area and Isle Royale, and came to somewhat different conclusions regarding population regulation of moose than those contained herein.

Bergerud et al. (1983) proposed that Isle Royale moose are limited by wolf predation in summer on moose calves. They use Leopold's (1948:39) definition of a "limiting factor" as "one factor (which) often far outweighs all the others in the extent to which it pulls down the unimpeded rate of increase." They asserted that weather-food interaction is not the limiting factor for Isle Royale moose, as Peterson (1977) proposed, since "availability of food has no impact on altering the vulnerability of new cohorts to predation" (p. 984). They argue that different wolf-moose systems reach equilibrium at different levels due to variation in the quality of space (habitats) in which to interact with wolves. "Space" refers primarily to escape habitats such as shorelines and small islands, since water is the ultimate escape habitat for moose (cf. Peterson et al. 1984b). In summary, Bergerud et al. (1983) attempt to explain all salient features of wolf-moose dynamics by 1) relative numbers of wolves and moose and 2) physical characteristics of habitat which relate directly to moose escape from wolves. We regard this "predation hypothesis" as an admirably simple yet inadequate explanation of wolf-moose dynamics.

We regard prey vulnerability as an important determinant of wolf predation effect. This is especially noteworthy for adult moose, for which data on age-selection patterns evident among hundreds of wolf-killed moose clearly demonstrate the strong selectivity of wolf predation (Peterson et al. 1984). While calf survival is a primary determinant of population trajectory, the other half of any population model is clearly adult mortality, which we believe is conclusively linked to individual vulnerability. Furthermore, recent fluctuations in the vulnerability of Isle Royale moose calves to wolf predation in winter are probably attributable to changes in calf vigor or predatory release caused by unusually high vulnerability among old moose with a high incidence of arthritis (Peterson and Page, in prep.). It is not yet possible to project the demographic significance of this change in calf vulnerability.

In support of their hypothesis, Bergerud et al. (1983) undertook a reanalysis of data on Isle Royale calf frequency

among wolf-kills and a winter snow depth index based on monthly mean maximum snow depth from November through April. They found no correlation between percent calves among wolf-kills in winter and the snow index, nor between percent calves in the kill and the snow index from the previous winter (when calves were in utero), and thereby inferred that there is no evidence that snow depth affects calf vulnerability to wolves or cohort viability through an in utero effect. However, absence of evidence in a selected body of data is not evidence of absence of a general relationship. Some time ago Peterson and Allen (1974) pointed out that calf occurrence among wolf-kills increased during periods when snow conditions at the time of the kill exceed 76 cm, approximately chest-height for calves. A snow index based on snow depths through an entire winter does not necessarily reflect snow conditions at any single point in time.

Furthermore, there is a significant inverse relationship (though not without much variation) between calf size and winter severity prior to birth (Peterson et al. 1982). The link between calf vulnerability to wolves and calf size has not been established, but we think it is probably significant that occurrence of calves among wolf-kills in winter was very high when calves were relatively small, but quite low when calves were relatively large (Peterson and Page, in prep.).

The principal flaw in the predation hypothesis is that a single factor has been proposed as a sufficient explanation for population phenomena which in reality may result from a complex interaction of many factors. Multifactorial hypotheses may indeed be more difficult to test (cf. Lidicker 1978), but single-factor hypotheses may sacrifice accuracy for simplicity. Bishop and Rausch (1974) proposed (correctly, in our estimation), that effects of severe winters were largely density-dependent, but this relationship has never been quantified. Perhaps this is due in part to the complex problem of measuring the relevant characteristics of snow cover (Kelsall and Prescott 1971) and the resulting ungulate responses.

The comparisons drawn by Bergerud et al. (1983) between Pukaskwa and Isle Royale were the most stimulating. They point out that Isle Royale supports at least twice the moose density of Pukaskwa and purport to explain this difference on the basis of their predation hypothesis. Specifically, they suggest that wolf predation effects at Pukaskwa are greater due to: (1) the higher wolf:moose ratio and (2) the less frequent escape habitats (shorelines and islands). They indicate that the wolf:moose ratio at Pukaskwa was 1:25, while the ratio at Isle Royale was 1:30-80. The actual mean ratio at Isle Royale between 1969 and 1984 was 1:29, remarkably close to the Pukaskwa ratio, so we shall dismiss the first point raised.

While Isle Royale probably does have a greater frequency of shoreline and island habitat than Pukaskwa, a more detailed examination of moose distribution and density at Isle Royale suggests certain shortcomings of this explanation. The northeast half of Isle Royale has more shoreline and island habitat (on a per unit area basis) than does the southwestern half. The hypothesis predicts that moose density will thus be higher on the northeast half of Isle Royale, but this is not the case. In 1984 the northeast half of the island contained an estimated 270 moose, while the southwest half contained 491 moose.

Virtually all of the likely explanations for the different moose densities in the two halves of Isle Royale relate to the likely higher resource level for moose at the southwest end; this again suggests a strong link between the demographic influence of wolf predation and moose vulnerability, a link which is influenced in a complex way by the moose forage base.

The southwest end of Isle Royale has a thick layer of glacial till that is at least 70 feet deep in places. At higher elevations it supports a sugar maple-yellow birch forest that is clearly distinct from the boreal type which dominates the northeast half of the island and, apparently, Pukaskwa National Park. While comparative measurements of moose forage resources in both halves of Isle Royale have never been reported, we predict that the more developed soils of the southwest half will tend to support higher plant productivity than those of the northeast half. Also, almost all of the mineral licks known to be used by moose are in the southwest half of Isle Royale (Risenhoover and Peterson, unpublished data).

We provide the following alternate hypotheses for the difference in moose density at Pukaskwa and Isle Royale:

Hypothesis 1 -- Weather/food influence on moose dynamics is more favorable for moose at Isle Royale than at Pukaskwa.

Hypothesis 2 -- Lack of moose dispersal from Isle Royale has led to elevated moose density.

We cannot exclude either of the above two hypotheses. There is some evidence that both hypotheses may be correct, as detailed below.

We will refer to hypothesis 1 as the "food hypothesis", since there are probably no significant differences in weather (temperature and precipitation) that would directly affect moose in the two areas. While Bergerud et al. (1983) stated that "both populations inhabit similar boreal forest habitats" (p. 985), it seems clear that Isle Royale supports a transition forest, comprising elements of both boreal and northern hardwood types, while Pukaskwa is dominated by the boreal type alone. There are substantial differences in

forest composition in the two areas. For example, jack pine (Pinus banksiana) heads the list of Pukaskwa tree species, while it is important as a canopy tree species on less than 1% of Isle Royale. Jack pine characteristically occupies the open rock and lichen mat habitats common throughout the Canadian Shield, areas with poor soils and low nutrient availability. Sugar maple (Acer saccharum) and yellow birch (Betula allegheniensis), dominant tree species on the southwestern half of Isle Royale, are not even included in the tree species list for Pukaskwa. We cannot directly infer what these forest differences will mean in terms of moose forage availability; it may be significant that moose eat sugar maple and yellow birch, but not jack pine. There may be other, more subtle differences in vegetation growth patterns. For example, Bergerud et al. (1983) state that the 1/4 of Pukaskwa which burned in 1931 and 1936 is being heavily used by moose and beaver. Almost 20% of Isle Royale burned in 1936, but forest regrowth has now far exceeded the reach of moose. Perhaps this is due to faster tree growth at Isle Royale, again suggestive of basic differences in primary production. It is quite possible that unusually high moose density at Isle Royale has caused unique patterns of plant response which provide more forage than would be the case with less-impacted vegetation. For example, there is substantially more forage available outside 38-year-old exclosures established by Krefting (1974) than inside the exclosures (Risenhoover, unpubl. data). Snyder and Janke (1976) clearly demonstrated the very pronounced influence of moose foraging on plant survival and growth form. In summary, the "food hypothesis" is still viable, worthy of further investigation.

We have previously regarded the "dispersal hypothesis" as the best explanation for the elevated moose density at Isle Royale (Allen 1979). Density elevation is commonly observed on islands and has been variously termed the "Krebs effect", "fence effect", and "island effect" (Tamarin 1980; Crowell 1983). According to a conceptual model by Crowell (1983), density inflation for Isle Royale moose could be potentially attributable to: (1) fewer predators, (2) fewer competitors, and (3) restricted dispersal. While Isle Royale lacks bears (predators on moose calves), it supports one of the consistently highest densities of wolves ever recorded; reduced predation pressure is not applicable here. Aside from defoliating insects, major competitors with moose in boreal systems include white-tailed deer and snowshoe hare. Large size provides the moose with a major competitive edge, but the presence of Paraelaphostrongylus tenuis in deer (a brainworm often fatal to moose) enables deer to outcompete moose if deer are plentiful. The amount of actual competition from deer at low-density, the common situation in moose range, is likely small but has never been estimated. We speculate, then, that release from competition with deer does not contribute significantly to moose density elevation at Isle Royale.

Snowshoe hares, of course, are present at Isle Royale, but we believe this species is strongly out-competed by moose.

Excluding depauperization as a likely cause of density elevation for Isle Royale moose leaves only restricted dispersal as a possible cause. Dispersal is a prominant feature of mammalian population regulation, thought to be dominant in some species (Tamarin 1978). A common consequence of dispersal in mammals is a high mortality rate as dispersers are confronted with unfamiliar surroundings and new dangers. Comparative data of this type is not available for moose, but a necessary condition for population regulation via dispersal is the presence of a "dispersal sink", the place where dispersers vanish. Fencing and insularity restrict dispersal, leading to "frustrated" dispersal, then reassimilation of dispersers back into the population.

The presence of vacant habitat on Isle Royale (e.g., the 1936 and 1948 burns) would seem to suggest a potential dispersal sink. However, suboptimal habitat by itself is not necessarily a dispersal sink. "For suboptimal habitat to be a dispersal sink, the animals that enter it must in some way be prevented from reentering the core population. This can happen either of two ways. The dispersers can move on, or they can be killed in the suboptimal habitat." (Tamarin 1980:127-128). Isle Royale moose have nowhere else to go. There are very few moose killed in the 1936 and 1948 burns at Isle Royale, so dispersal by Isle Royale moose must inevitably be "frustrated".

Referring again to the Pukaskwa-Isle Royale comparison, we suggest on the basis of the above argument that the "egress (dispersal) hypothesis" has been prematurely dismissed by Bergerud et al. (1983) (p. 982). In order for restricted dispersal to account for the observed density difference between Pukaskwa and Isle Royale, a necessary assumption is that Pukaskwa and the surrounding area provides a dispersal sink that is not present at Isle Royale. Wolf predation undoubtedly functions as at least the equivalent of a dispersal sink, as evidenced by the high frequency of yearlings among wolf-kills. However, both areas have similar wolf:moose ratios. While we can provide no definitive conclusion, it is possible to suggest potential dispersal sinks that are unique to the Pukaskwa system. Animals are free to leave the Park in all but one direction. Areas outside the Park are more disturbed by fire and logging. The tendency for moose to disperse into burned areas (Peek et al. 1976) prompts us to speculate that egress into habitats outside the Park was of demographic significance to Pukaskwa moose. This is suggested further by the trends in moose distribution over a 4-year period in Pukaskwa. Early in the study the Park supported fewer moose than most of the surrounding areas. As the population declined, the Park was depopulated to a greater extent than the surrounding areas.

Human-caused mortality may serve as a dispersal sink at Pukaskwa; in the early years of the study by Bergerud et al. (1983), annual hunting mortality was estimated at about 5% of the population. All three moose killed by trains and 2 of the 3 moose reported dying of unknown causes were yearlings. This evidence is consistent with our suggestion that functional dispersal sinks exist at Pukaskwa that are absent at Isle Royale.

In conclusion, we agree that wolf predation has been the major mortality factor for moose calves on Isle Royale. Peterson and Page (1983) have already pointed out that the substantial increase in calf survival that accompanied the wolf crash in 1980-82 is ample evidence of the effect of predation on recruitment and rate of increase. However, we also believe that moose vulnerability is a key component of the demographic influence of wolf predation. Bergerud et al. (1983) ignored any forage effects more subtle than outright starvation, stating that in the absence of wolves, food availability has no impact on altering vulnerability to predation. But given no limitations by food or weather, will not the influence of predation be greatly different?

CHAPTER SIX

THE BOTTOM OF THE LADDER: MOOSE-VEGETATION INTERACTION ON ISLE ROYALE

The conclusions of Chapter 1 indicate that moose-forage relationships play a key role in moose population fluctuations. A review of the literature on Isle Royale moose reveals many studies that have focused on this topic. With a few notable recent exceptions, however, most studies have produced little more than an analysis of moose food habits. Most important, it is not evident which component(s) of moose-forage interaction underlies increased moose vulnerability to wolf predation at high population densities.

Initial studies of moose at Isle Royale focused on the relationship between moose and vegetation, for the effects of heavy moose browsing were obvious. A. Murie spent the summers of 1929 and 1930 studying moose at Isle Royale and predicted that a population crash was imminent (Murie 1934). Later studies by Hickie (1936), Kellum (1941), and Coburn (1934) documented the moose die-offs of the 1930s and summarized successful attempts to remove about 70 moose for re-stocking in the Upper Peninsula of Michigan.

L.W. Krefting, of the U.S. Fish and Wildlife Service, began studies of Isle Royale moose in about 1945. His focus was again the relationship between moose and forage. In 1948-52 Krefting established 4 exclosures measuring 50 feet square; these were sampled for stem density, size and species presence at intervals until 1972 (Krefting 1974). Characteristics of forest structure were summarized by Hansen et al. (1973). Browse transects provided trend information on availability and utilization of forage by moose in 1950-70 (Krefting 1974). During this time, Krefting documented a decline in availability of all major forage species except balsam fir. Simultaneously, counts of moose pellet groups increased consistently, from which Krefting (1974) inferred that the moose population increased steadily. However, the extent to which higher pellet density might have reflected reduced digestibility of browse is unknown.

Since 1970 there have been several moose-vegetation studies. These findings, together with aspects of Krefting's work will be reviewed below.

Food Habits. Food habits of moose on Isle Royale have been estimated indirectly using browse utilization transects (Krefting 1974, de Waal Malefyt 1974), from actual observations of feeding moose (Edwards 1978), or from a combination of these techniques (Belovsky and Jordan 1978, Miquelle 1979).

These studies have been confined to either the southwestern end of the island where a sugar maple - yellow birch forest predominates, or to the northeastern portion of the island where a paper birch - balsam fir - white spruce association is dominant. Because these areas differ in canopy and understory species, they provide moose with varying amounts of available browse, and, consequently, direct comparisons of results are difficult.

Summer food habits of moose were estimated by Krefting (1974) using browse utilization transects at 3 different areas on Isle Royale. Data for the maple - yellow birch climax forest (southwest) suggest that a shift in moose diets occurred from 1946 to 1971. In 1946, diets were composed primarily of sugar maple, mountain maple, mountain ash, paper birch and trembling aspen (Table 14). When Krefting sampled these areas again in 1971, 80% of the diet was composed of mountain ash and mountain maple.

Belovsky (1978) found similar diets for moose inhabiting the southwestern end of the island during 1972-74 (Table 14). Using browse utilization transects and direct feeding observations they calculated that 84% of moose diets consisted of mountain ash and mountain maple. Miquelle (1979), working in the same area in 1977-78, also found mountain maple and mountain ash to be the main components of summer moose diets. Miquelle suggested that the apparent shift in diet preference to primarily mountain ash and mountain maple may be a reflection of change in species composition or abundance resulting from years of heavy utilization by moose during all seasons of the year. His data also indicated that mountain ash and particularly mountain maple were more tolerant of utilization by moose than were other species.

Food preferences of moose inhabiting the northeastern portions of Isle Royale have been reported by Krefting (1974), who found that 78% of moose diets consisted of trembling aspen, mountain alder, juneberry, and beaked hazelnut (Table 14).

Winter food habits of moose on Isle Royale have been estimated only from browse utilization transects run in spring. Belovsky (1981) reported that mountain ash, yellow birch, and mountain maple comprised 83% of winter moose diets on the southwest end of Isle Royale (Table 15). Krefting (1974) also reported the importance of mountain ash along with trembling aspen, balsam fir, and paper birch (Table 15).

Krefting's (1974) data for the northeastern portion of the island indicate that balsam fir and trembling aspen are important winter foods (Table 15). De Waal Malefyt (1974) reported that 72% of all twigs removed were balsam fir (Table 15).

Table 14. Food preferences of Isle Royale moose in summer, expressed as percent of total diet, as revealed by several studies. Trace (t) indicates < 1.0%.

	Southwest maple & yellow birch type				Northeast spruce, fir & birch type
	Krefting (1974)		Belovsky	Miquelle	Krefting
Plant species	1948	1971	(1978)	(1979)	(1974)
Mt. ash (*Sorbus americana*)	12.5	57.4	49.4	18.8	4.7
Mt. maple (*Acer spicatum*)	15.5	22.6	34.3	57.1	--
Paper birch (*Betula papyrifera*)	11.8	9.1	4.1	3.6	4.9
Trembling aspen (*Populus tremuloides*)	9.1	t	--	1.3	25.1
Yellow birch (*Betula allegheniensis*)	2.7	t	7.1	8.3	--
Sugar maple (*Acer saccharum*)	18.4	1.8	1.8	t	--
Beaked hazel (*Corylus cornuta*)	2.3	2.7	1.0	1.6	13.7
Red osier dogwood (*Cornus stolonifera*)	3.9	--	--	1.2	1.1
Juneberry (*Amelanchier* spp)	2.1	t	--	t	16.5
Bush honeysuckle (*Diervilla lonicera*)	t	4.0	2.3	3.0	t
Canada honeysuckle (*Lonicera canadensis*)	t	--	--	t	--
Willow (*Salix* spp)	7.5	--	--	--	2.8
Mt. alder (*Alnus crispa*)	t	--	--	--	22.8

Table 15. Food preferences of Isle Royale moose in winter, expressed as percent of total diet, as revealed by several studies. Trace (t) indicates <1.0%.

	Southwest maple & yellow birch type		Northeast spruce, fir & birch type	
	Krefting	Belovsky	Krefting	deWaal Malefyt
Plant species	(1974)	(1978)	(1974)	(1974)
Mt. ash (*Sorbus americana*)	22.4	32.7	5.4	4.2
Mt. maple (*Acer spicatum*)	1.8	23.9	1.7	---
Paper birch (*Betula papyrifera*)	10.8	3.8	8.9	8.3
Trembling aspen (*Populus tremuloides*)	12.8	---	14.1	3.0
Yellow birch (*Betula allegheniensis*)	0.9	27.8	---	---
Beaked hazel (*Corylus cornuta*)	7.8	1.1	9.3	3.2
Red osier dogwood (*Cornus stolonifera*)	8.7	---	7.4	3.0
Juneberry (*Amelanchier* spp)	3.9	1.4	8.8	---
Willow (*Salix* spp)	6.3	---	8.2	---
Mt. alder (*Alnus crispa*)	t	---	3.3	---
Highbush cranberry (*Viburnum* spp)	t	---	3.9	---
White cedar (*Thuja occidentalis*)	t	2.8	---	---
Balsam fir (*Abies balsamea*)	11.6	6.6	22.4	72.0

The usefulness of browse utilization transects in estimating available biomass, biomass consumed, diet preferences, and the status of a population in relation to "carrying capacity" is very limited. To produce even reasonable results requires large numbers of randomly placed transects, and statistically adequate sampling intensity is usually around 50%, because of variability. Certain areas are overutilized every year due to heavy concentrations of animals (i.e., winter range), while other areas receive little or no use because they are avoided for other reasons (i.e., predator evasion).

For this reason, data presented by Krefting (1974), de Waal Malefyt (1974), and, to some extent, Belovsky and Jordan (1978) are of limited value. For example, using Krefting's figures, his winter sampling intensity was 0.0032% in 1945 and 0.0046% in 1971 in the spruce-fir-birch type (1.42 acres divided by 44,000 acres). Belovsky's data on winter diet selection was based on a total of 2,000 twigs. Although Miquelle (1979) provided good estimates of summer dietary preferences (at least in the Windigo area), no reliable data exists on winter diets of moose on Isle Royale.

Several recent studies have attempted to examine various aspects of the feeding strategies of moose on Isle Royale. Edwards (1978), working in the northeastern end of the park, compared diet selection of different sex-age classes of moose. She concluded that summer habitat selection and diet of lactating and barren (non-lactating) cow moose differed as a result of their different metabolic and energy requirements. Cows with calves limited their activities to areas in close proximity to water and commonly frequented islets as an anti-predator strategy against wolves. Barren cows were able to utilize areas farther away from water and could therefore be more selective in their diet.

Belovsky and Jordan (1978a) attempted to quantify a number of parameters associated with time-energy budgets of moose, including daily intake rates, diet preferences, and the availability of different forage items. These data were then used to construct constraint equations for optimization models that were used to predict optimal diets, habitat selection and activity patterns (Belovsky 1978, 1981, Belovsky and Jordan 1978, 1981).

Miquelle (1979) also measured intake rates and diet selection of moose in summer. He concluded that although sufficient biomass existed for moose to meet their quantitative intake requirements by feeding on a monotypic diet of a preferred species, they chose a diverse diet of several preferred species.

Although many of the ideas presented by Edwards (1978) have interesting implications and make "biological sense", her

conclusions are only weakly supported by data. When data were presented, sample sizes were generally small, and confidence intervals were ignored in analysis.

The limited work of Belovsky and Jordan (1978), which has given rise to subsequent publications (Belovsky 1978, 1981, Belovsky and Jordan 1981), is unfortunately flawed by numerous poor and inaccurate assumptions and is based largely on weak data that lacks statistical significance. Belovsky's assumption that maintenance and reproductive requirements for bulls and barren cows were equal is contrary to data available in the literature. He also overestimated the metabolic requirements of moose by approximately 30%. In addition, several of his constraint equations (concerning sodium requirements and ruminant digestion) are not supported by data. In summary, because the initial collection of data was very unorthodox and partially based on unmeasureable assumptions, the subsequent models produced are of doubtful biological value. Miquelle (1979), who attempted to duplicate some of Belovsky's methods, discovered that at least 3 of Belovsky's assumptions were either invalid or could not be duplicated.

Although Miquelle (1979) provides data on summer feeding strategies of moose in terms of diet selection, we still know relatively little about use patterns and nothing about home range size and the importance of optimal diet and its role in seasonal energy balance. Significant aspects of moose abundance and distribution remain poorly understood.

Sodium Dynamics of Moose. As a result of recent attention concerning the lower relative amounts of sodium in terrestrial versus aquatic plants, Botkin et al. (1973) hypothesized that moose on Isle Royale are obligated to feed on aquatic vegetation in order to meet their sodium requirements. This idea was further developed by Belovsky (1978). Belovsky estimated the sodium requirements of moose by accounting for the loss of sodium through defecation, urination, body growth, fat deposition, reproduction, and lactation; he assumed that this amount must be replaced if moose are to remain in sodium balance. Results from diet optimization modeling, which was constrained by estimated sodium requirements, suggested that 15% of a moose's diet should come from aquatic plants in order to meet these needs.

Aho and Jordan (1979) measured the production of aquatic biomass and its utilization by moose at Isle Royale. In addition, he collected samples of aquatic plant species and analyzed them to determine sodium concentrations. Results indicated that sodium concentrations varied among and between species and among sites. Also, he found that production of aquatic biomass was quite variable among ponds. Moose did not select feeding sites based on the availability of biomass,

suggesting that other factors were involved (i.e., sodium concentration, palatability, ease of movement).

Aho found, interestingly, that moose feeding on aquatics did not select for species with the highest sodium concentrations. Also, moose appeared to feed indiscriminantly within patches, suggesting that palatability was unimportant. Aho also could find no evidence suggesting that ease of movement was a problem for moose feeding on aquatics. Although sample sizes were small, Aho's data indicated that 74% of the total standing crop of aquatic vegetation was provided by lakes and that moose were removing an estimated 22% of aquatic plant production annually.

In view of Aho's (1978) findings, it appears that there are other factors influencing the use of aquatic vegetation beyond those presented by Belovsky (1978) or Jordan et al. (1973). Although there is no question that sodium is an important mineral for moose, there is no evidence that supports Belovsky's (1978) contention that sodium is the limiting factor for moose on Isle Royale.

Finally, Belovsky's claim that sodium requirements can be met only from aquatic vegetation are unfounded. Natural mineral licks are used extensively by most ungulates in North America and apparently provide the sodium needs for species which do not ingest aquatic plants. Peterson (unpubl. data) found that sodium was obtained in significant quantities from natural licks at Isle Royale.

Effects of Moose on Vegetation. Krefting (1974) examined the effects of moose browsing on Isle Royale vegetation based on data from 4 exclosures at various locations on the island. His data indicated that moose had a significant effect on the height growth and diameter of aspen, balsam fir, red osier dogwood, willow, paper birch, pincherry, Canada honeysuckle, mountain ash, and mountain maple. He also speculated that ground hemlock was nearly eradicated and that overuse of beaked hazelnut had resulted in total kill in certain areas. He felt reproduction for all of the above species was being controlled by moose browsing. A study of balsam fir found that many stems less than 3 feet tall were over 30 years old.

Snyder and Janke (1976) examined effects of moose browsing on the course of succession in the boreal forest type. Results indicated a reduction in tree density and shrub layer height, giving rise to more open, even-aged forests which are richer in low ground cover. American yew was nearly eliminated while balsam fir and mountain ash were significantly reduced on even moderately browsed sites; spruce density was increasing in areas of heavy browsing, apparently due to reduced competition.

CHAPTER SEVEN

MANAGEMENT IMPLICATIONS

Implications for Park management stemming from this research all relate to maintenance of the island with as little disturbance of its major wildlife populations as possible. Where this concerns wolves and moose, the rationale is obvious--there is no other location on the planet that provides a simple, large mammal predator-prey system that is totally protected and effectively isolated from ingress, egress, and human-caused disruption. Additional background on many of the following areas can be found in Peterson and Morehead (1980).

Park Closure

The current administrative policy of a winter closure of the Park by order of the Superintendent should be maintained indefinitely. This provides assurance that wolves and moose will continue to be undisturbed by humans during the winter, when wolf predation effects on adult moose survival are most pronounced. The presence of visitors in winter at Isle Royale could be expected to alter wolf travel routes, activity patterns, and probably distribution of hunting effort. It could lead to a deterioration of avoidance behavior toward humans now exhibited by wolves during the summer visitor season.

It is appropriate here to emphasize the unique opportunity provided to scientists by the undisturbed character of Isle Royale wolves. Most of our understanding of important aspects of how wolf behavior really works has been gained at Isle Royale, where wolves are unusually visible to aerial observers. In other areas of North America, even where wolves are tolerant of aircraft, it is rare to observe details of courtship and other social behaviors. The ongoing research/monitoring program at Isle Royale is uniquely dependent on actual observations (as opposed to radio-signals) of wolves to identify packs, document pack movements, etc. This is possible only because of the undisturbed character of this Park.

Area closures during summer

Throughout the early 1980's specified areas of the island have been routinely closed to overnight camping by visitors in order to provide security for denning wolves. In order to avoid spotlighting currently-used areas the same series of closures is instituted each year, including all zones with a tradition of wolf use. Also, since the NPS no longer supports monitoring of wolves in summer, such closures cannot be made on the basis of current use.

I am not aware of any significant contacts between wolves and humans at homesites during the past 5 years. The same degree of separation should be maintained in the future, since it probably underlies the avoidance behavior that wolves exhibit toward all humans. I believe such avoidance represents learned behavior that is assimilated by each generation of young wolves before they have had significant contact with humans. Social bonds are established in this species during the first 2 months of life, and it is critical that wolf pups do not experience contact with humans during this time. It is entirely possible that, should avoidance behavior deteriorate, wolves could become campground visitors just as foxes do throughout the island. Obviously, this would be highly undesirable. Such habituation of wolves toward humans has occurred in Katmai National Monument and along the Alaska pipeline (L. D. Mech and D. Klein, pers. commun.).

The current zone closure policy should be continued, since it appears to work. It might be argued that there is no evidence that the closures are even needed. It is true that there were no problems involving wolf-human contacts before institution of the zone closure policy. The closures, however, clearly indicate the intent of Park management policies and perhaps they sensitize visitors and the seasonal Park staff to the importance of protecting this resource. Should problems arise there is a mechanism already in place to effectively respond (e.g., closure to overnight camping could be enlarged to total closure).

Pet prohibition

Mammalian pets have been prohibited from the Park since approximately 1980, for reasons outlined by Peterson and Morehead (1980). This wolf population is very susceptible to introduced pathogens. Many pathogens are in a constant state of evolution, and routine immunization programs for pets cannot eliminate the possibility of inadvertent introduction of disease organisms. Since Isle Royale wolves are isolated and perhaps subject to problems associated with diminishing genetic stock, they may be sensitive to pathogens in unpredictable ways.

Some of the above claims are exemplified by the possible role that canine parvovirus may have played in the wolf population crash of 1980-82, when over 50 wolves died on the island and the entire cohort of pups disappeared in 1981. Parvovirus was virtually unknown prior to 1977, when a new strain rapidly spread around the world. Local outbreaks occurred in 1981 in Houghton (J. Pepper, D.V.M. and D. Aho, D.V.M., pers. comm.), and the pathogen could have readily reached Isle Royale on the soles of hiker's boots. As of 1985 it is still unclear if parvovirus reached Isle Royale (in which case it should still be present), and it will never be possible to demonstrate without doubt that disease played a contributing role in the wolf crash. Allowing pets on the

island would, among other impacts, reduce unnecessarily our confidence in the assertion that Isle Royale wolves indeed exhibit entirely natural population dynamics.

Trail and campground development

Here I will simply reiterate earlier recommendations (Peterson and Morehead 1980) to limit the extent of trail and campground development to the current system, with the overall objective being to maximize the proportion of the island that is devoid of people, especially at night.

Peterson and Morehead (1980) presented data indicating that wolves avoided establishing dens and summer homesites within 0.5 miles of Park trails, and most were 1.0 mile or more away from trails (Fig. 10). Only a few portions of the Park are sufficiently remote that wolves can indeed rear pups at these distances from campers.

I argue that avoidance behavior of wolves toward humans could readily break down if pups are exposed to humans at a younger age, as Isle Royale foxes are (Fentress 1967, Mech 1970, Zimen 1981, E. Klinghammer pers. commun.). It should be a priority management objective to maintain current wolf avoidance toward humans.

Separating wolves and humans at night provides additional security for wolves from individuals who would actively seek out summer homesites for the purposes of observation or photography. If the present campground system proves to be inadequate and additional camping capacity is needed, present campgrounds should be enlarged in preference to adding new campgrounds.

Fire management

Management policies currently allow for continuation of natural fire frequency on Isle Royale. An unresolved question is whether the large extent of man-caused fires during the past century has so altered forest composition that restoration of a natural fire regime will require use of prescribed burns.

The impact of controlled burns on moose habitat is considerable, as is the impact of moose herbivory on any newly-created habitat. For obvious reasons, such a program would have to be quite small in extent. However, it is likely that "recreation" of a more patchy forest through continual small prescribed burns would be difficult because of the intense browsing pressure that moose can bring to bear on small areas of favorable forage.

For the above reason, and because our present understanding of moose-habitat relationships on Isle Royale is

far from complete, prudent policy would be a "hands-off" approach to both natural fire prevention and introduction of prescribed fires. There is every reason to believe that natural fire frequency is very low at Isle Royale--witness the original state of the vegetation (McKaig 1978) and the fact that all significant fires in the last 100 years have been man-caused.

Conventional thinking would lead one to predict that the moose population will eventually decline because of forest succession. Certainly the ongoing invasion of the northeastern portion of Isle Royale by conifers will change moose habitats considerably from their present condition. We do not have a sufficient understanding of moose-habitat relationships to predict with confidence exactly how this will impact moose density.

Currently, highest moose density at Isle Royale can be found in the oldest forests at the southwestern end, where there are no historically recorded fires. We have tended to think of these forests as in a climax "steady state", but recent (1985) data on moose impact on balsam fir indicates that fir will largely disappear from upland forests at the southwest end after the current canopy trees decline and die.

Continuing forest succession at the northeastern end of Isle Royale will produce a canopy dominated by fir and spruce, with uncertain impacts on moose. It is clear that presently the least valuable portions of the island, from the standpoint of moose (and therefore wolves), are those that burned in 1936 and 1948. Burns do produce a flush of nutrients and early successional-stage shrubs and trees that provide optimum moose habitat for a short period of time (Krefting 1974, Peek et al. 1976), but thereafter many decades must pass before moose will again utilize such areas to a significant extent.

In conclusion, our present state of knowledge of moose-habitat relationships is not adequate to predict future trends in moose density that might result from continued forest succession. Without such knowledge it would be inadviseable to conduct prescribed burns for the purpose of manipulating moose numbers (e.g., in the event of wolf extinction). At the same time, wilderness management policies dictate that naturally-occurring fires be allowed to burn unimpeded.

Gene pool considerations

Determining critical population size for a multitude of endangered species throughout the world is an important and difficult management problem. It is a major issue of concern today for small highly endangered wolf populations (e.g., Scandinavia and Italy). Both wolf and moose populations on

Isle Royale probably resulted from a few colonizers, thus their genetic variability may be limited by the "founder effect." In addition, small wolf population size probably is resulting in a progressive reduction in genetic variability; simple models suggest that this loss may be 15% per generation (U. S. Seal, pers. commun.).

The Isle Royale wolf population provides an extremely valuable natural experiment which will, in time, reveal long-term genetic viability in a very small population of a large mammal. I can think of no other comparable small and isolated population of mammalian carnivores. At present, careful observation is probably adequate to detect change in gross morphological features. For example, the "rope-tailed" wolves that originated in the East Pack in the early 1970's (Peterson 1977) and eyes of different color in the West Pack II alpha male in 1986 represent unique morphology not seen in any of several hundred wolves studied in Minnesota in the last 20 years (L. D. Mech, pers. commun.).

The major unanswered questions that are pertinent to wolf gene pool considerations at Isle Royale are: (1) To what extent are deleterious genes represented in the wolf genome? Careful breeding records of a manipulated captive population might shed some light on this, but I am not aware of any such interpretation. However, an inbred population of wolves in the Stockholm Zoo has exhibited a high rate of premature blindness that is likely a result of small gene pool (A. Bjarvall, pers. commun.); (2) How long is generation time for Isle Royale wolves? This could be answered by radio-collaring alpha wolves, but I suspect that lifespan of breeding individuals at Isle Royale is quite long compared to wolves elsewhere, where human persecution is a dominant source of mortality. In two known cases that probably represent extremes, alpha females at Isle Royale have held this role for 5 and 11 years, respectively. In 37 years of existence, Isle Royale wolves may have passed through 5-6 generations.

The above discussion suggests that more than half of the original genetic variability may have been lost in Isle Royale wolves due to the small number of breeders. Because of the importance of this issue for endangered species management elsewhere, I recommend that there be no manipulation of wolf gene pool at Isle Royale. This will allow a determination of the results of a natural experiment in genetic recombination within a very small mammalian gene pool.

Research needs

A comprehensive assessment of research needs relating to wolves and moose can be found in the Resources Management Plan for Isle Royale National Park. I will only offer general

comments on additional research needs that would enhance our understanding of this important wolf-moose system.

Since the Resources Management Plan was written, it has become more clear that a long-term understanding of wolf-moose dynamics should include an assessment of moose-forage interaction. We need a fundamental understanding of the flexibility of moose forage requirements, plus an accurate assessment of island-wide trends in forest succession that impact moose forage. I consider Risenhoover's study of moose foraging behavior and Brandner's study of island-wide impact of moose on balsam fir demography to be logical starting points. A strategy for further studies remains to be worked out, since it will depend heavily on results of this initial work.

The radio-collared moose present on Isle Royale have furnished a wealth of basic material on moose movements and behavior. It is still too early to judge the full scope of understanding that will result from this effort. It is clear already, however, that it would be possible to monitor individual moose at Isle Royale through telemetry for their entire lives. This raises the possibility of assessing, for example, life-long reproductive performance of females belonging to different cohorts or existing in different portions of the island, or direct estimation of annual mortality rates for the moose population, key parameters that should fluctuate through the course of a moose "cycle". Thirdly, radio-collared moose can provide an accurate means to assess moose sightability during winter aerial censuses, an important variable that may greatly influence annual moose estimates. These objectives could be accomplished through relatively low-level efforts with approximately the current number of radio-collared individuals.

In 27 years researchers on Isle Royale have constantly refined their hypotheses in light of new data. The complexity of natural systems, especially those which include long-lived animals, requires close scrutiny over long periods of time in order to achieve proper understanding. The fact that this study continues attests to the general significance of its findings, the tenacity of researchers and the patience of the National Park Service and other supporters. The time scale for wolf and moose life cycles and the longitudinal natural experiment that continues on Isle Royale argues strongly for maintenance and enhancement of long-term research in this ecosystem.

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APPENDIX 1: REVISED LIFE TABLE FOR ISLE ROYALE MOOSE

Skeletal collections for Isle Royale moose represent the only data suitable for construction of a life table for this species. The value of these calculations lies in the fact that age-specific natural mortality rates can be derived. These statistics are an important parameter in any detailed population model.

Since the time of the last reported life table (Peterson 1977), the size of the collection has almost doubled. There were important changes in mortality patterns during this time, as wolf predation pressure shifted from young to old age classes. The data incorporated into the current life table are derived from a 25-year period, encompassing major shifts in population density and mortality patterns. For this reason the calculated mortality rates should be the most accurate gathered thus far for moose (Table 1).

As before (Peterson 1977), calves were excluded from life table calculations because their remains are highly perishable and often completely ingested by wolves. Average annual mortality for adult males and females was calculated to be 12% and 11%, respectively, slightly lower than that reported by Peterson (1977). Age-specific mortality was less than 10% for moose younger than 7 years, then rose rapidly until all males died out by age 18 and females by age 20 (Figs. 1-3).

Moose dwelling in forested areas have a mating system based on contact between single males and single females; body sizes for the sexes tend to be more similar than for tundra moose employing a harem mating system. Mortality calculations for Isle Royale moose confirm that there is only a slight differential mortality between the sexes (Fig. 3). Male mortality between the ages of 1 and 2 years is about 50% higher than for females, possibly attributable to greater dispersal of males. The slight sex differential arising from this early mortality is maintained until age 7-8, after which male and female survival diverges. This leads to a preponderance of females among older moose (Fig. 4).

Peterson (1977) concluded that the long-term sex ratio among adult Isle Royale moose was even. This conclusion was further supported by examination of additional skeletal remains over the last 10 years, resulting in a collection almost exactly split between males and females. This also validates the general approach to carcass examinations, which relies heavily on "random" ground coverage in summer to provide the most unbiased sampling of mortality.

Table 1. Life table for Isle Royale moose, based on all skeletons examined in 1958-83.

Age	Total					Females					Males				
(yrs)	# dead	d_x	l_x	q_x	L_x	# dead	d_x	l_x	q_x	L_x	#dead	d_x	l_x	q_x	L_x
1-2	86	91	1000	.091	955	28	65	1000	.065	968	38	88	1000	.088	956
2-3	38	40	909	.044	889	16	37	935	.040	917	17	39	912	.043	893
3-4	42	45	869	.052	847	20	47	898	.052	875	15	35	873	.040	856
4-5	38	40	824	.049	804	15	35	851	.041	834	21	49	838	.058	814
5-6	35	37	784	.047	766	12	28	816	.034	802	19	44	789	.056	767
6-7	51	54	747	.072	720	28	65	788	.082	756	21	49	745	.066	721
7-8	67	71	693	.102	658	27	63	723	.087	692	35	81	696	.116	656
8-9	85	90	622	.145	577	38	89	660	.135	616	41	95	615	.154	568
9-10	86	91	532	.171	487	42	98	571	.172	522	37	86	520	.165	477
10-11	88	94	441	.213	394	33	77	473	.163	435	45	104	434	.240	382
11-12	80	85	347	.245	305	31	72	396	.182	360	44	102	330	.309	279
12-13	89	95	262	.363	215	47	110	324	.340	269	41	95	228	.417	181
13-14	55	59	167	.353	138	29	68	214	.318	180	24	56	133	.421	105
14-15	43	46	108	.426	85	22	51	146	.349	121	19	44	77	.571	40
15-16	36	38	62	.613	43	26	61	95	.642	65	8	19	33	.576	24
16-17	10	11	24	.458	19	7	16	34	.471	26	3	7	14	.500	11
17-18	7	7	13	.574	10	4	9	18	.500	14	3	7	7	-	4
18-19	2	2	6	-	5	2	5	9	.556	7	-	-	-	-	-
19-20	2	2	4	-	2	2	5	4	-	2	-	-	-	-	-
TOTAL	940					429					431				

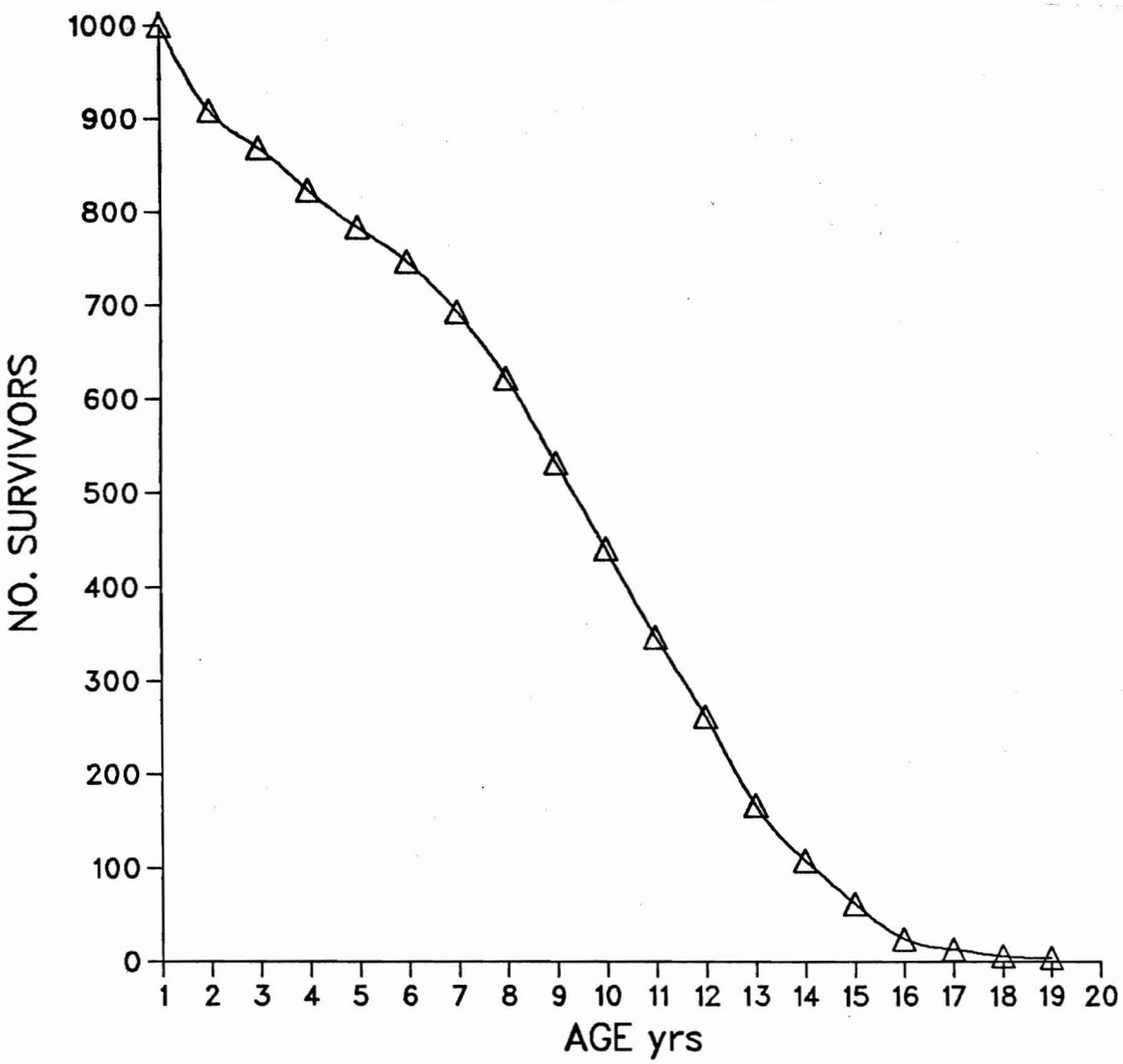


Fig. 1. Composite survivorship curve for moose older than 1 year of age at Isle Royale (sexes combined).

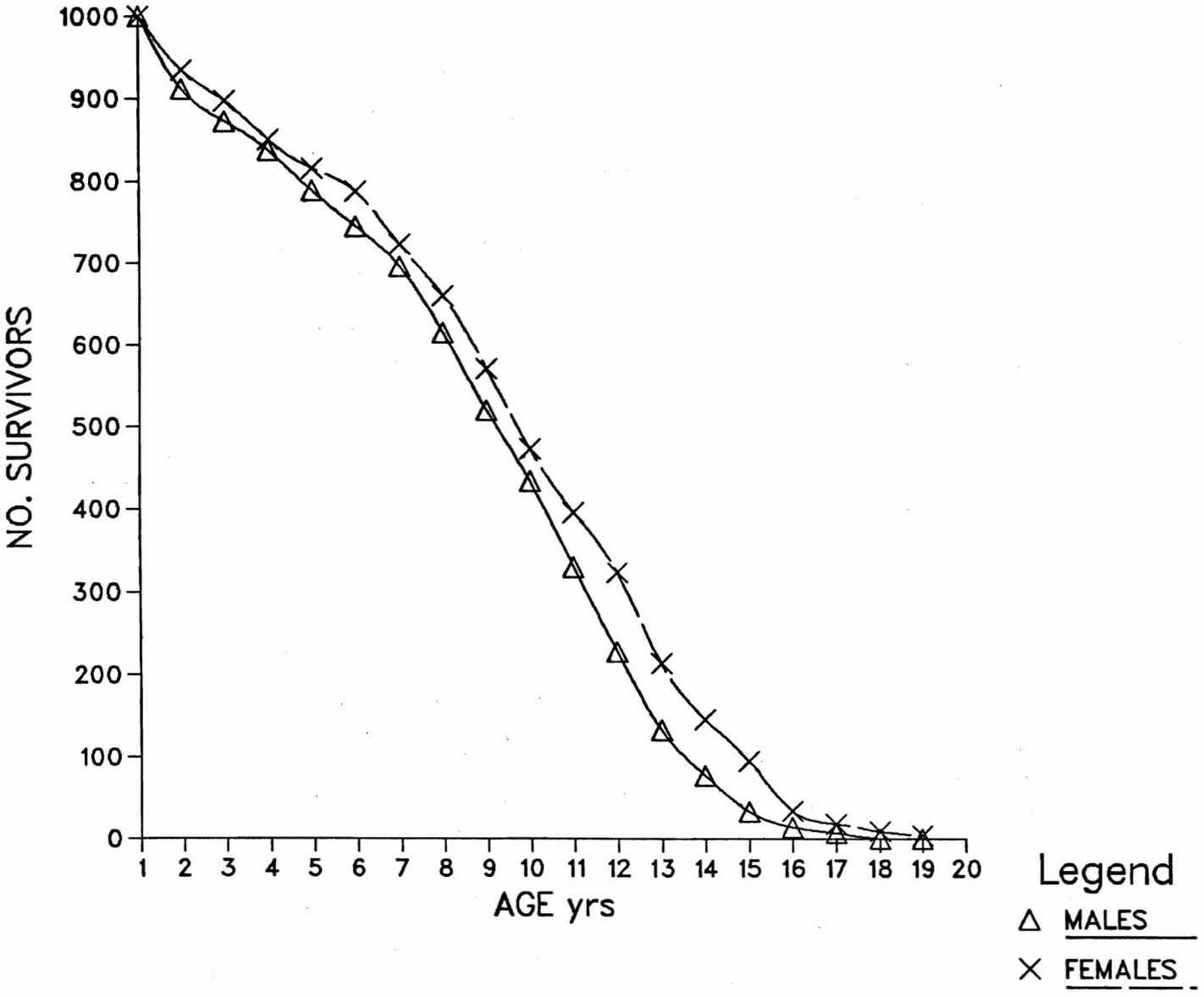


Fig. 2. Survivorship curves for male and female moose at Isle Royale, beginning at 1 year of age.

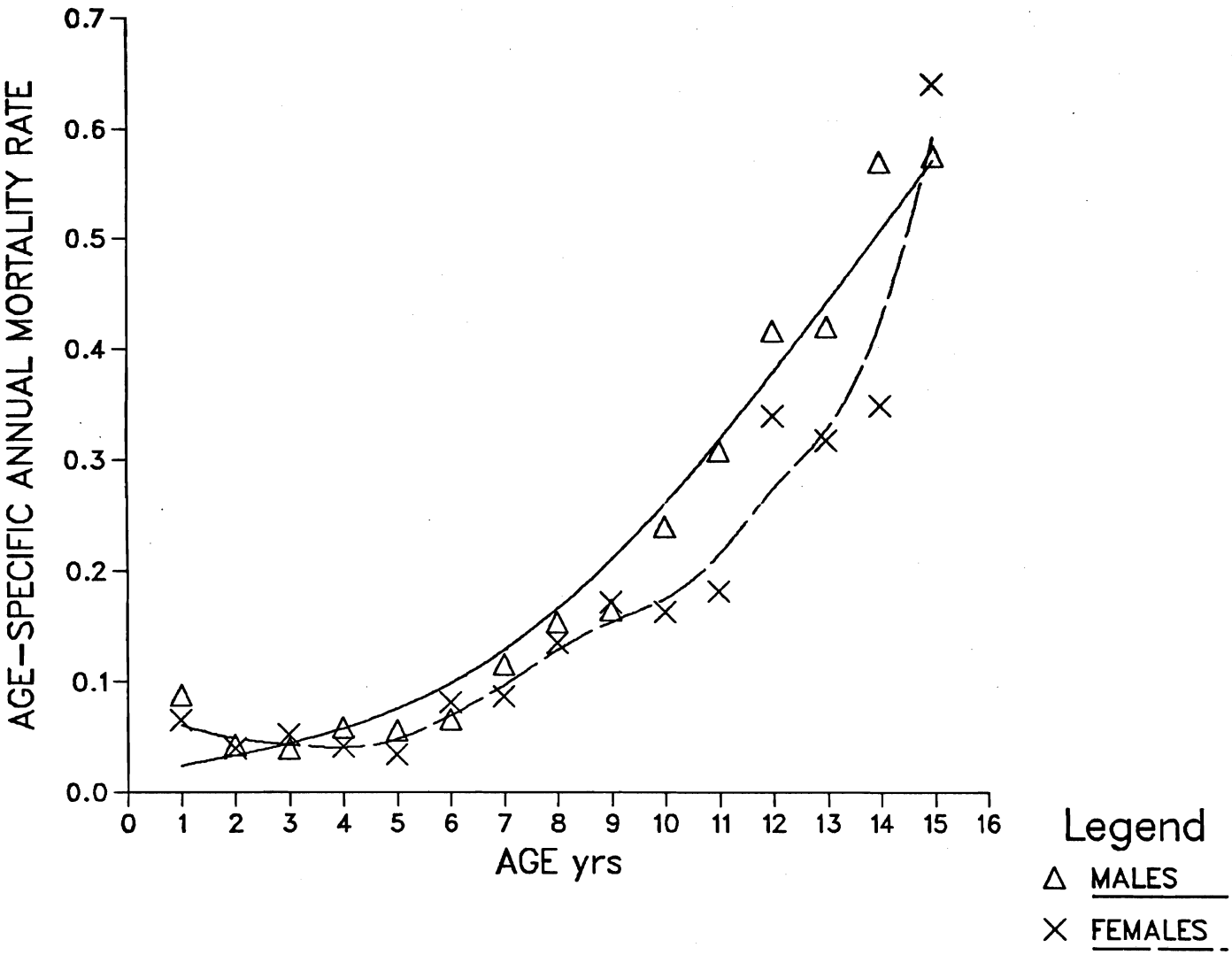


Fig. 3. Age-specific mortality rate for male and female moose at Isle Royale, beginning at 1 year of age.

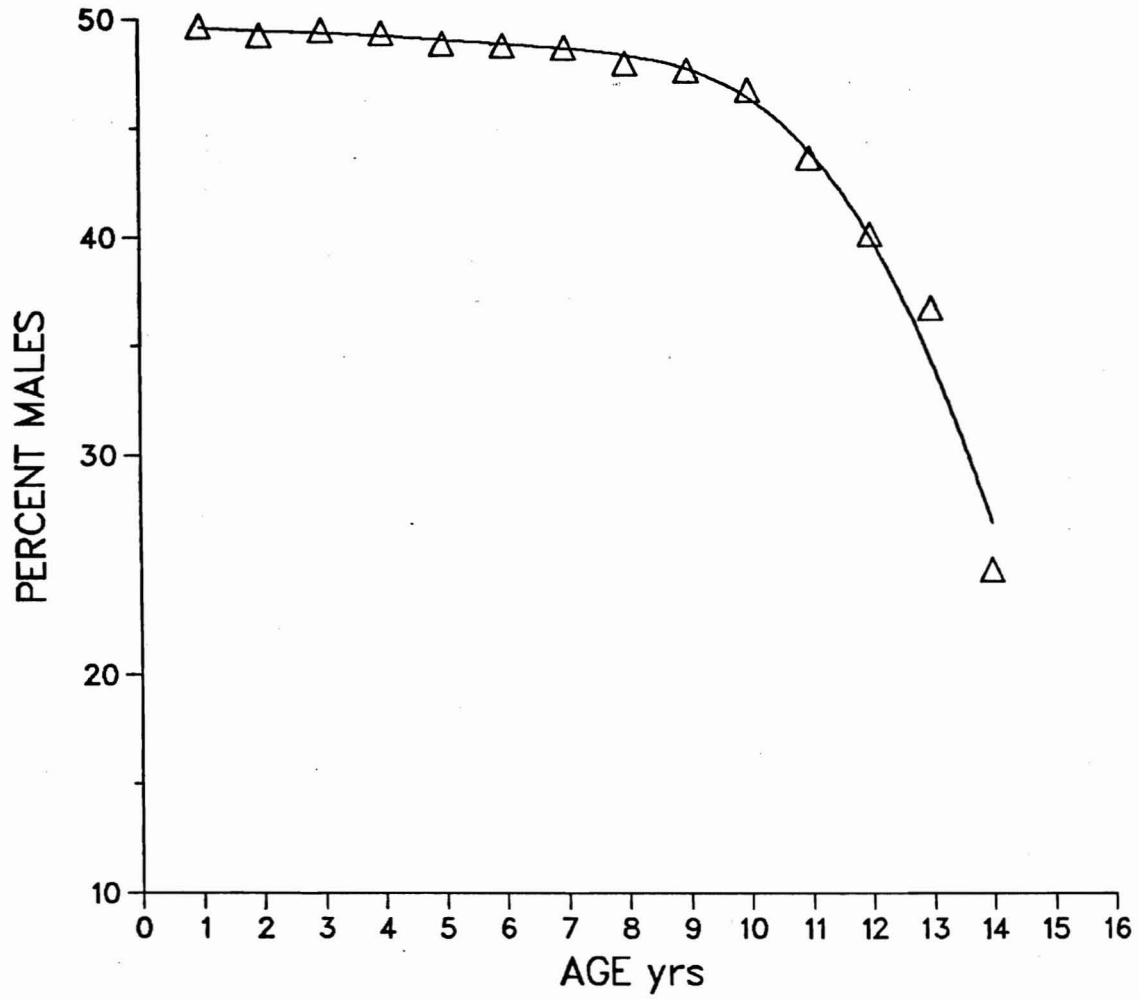


Fig. 4. Age-specific sex ratio for Isle Royale moose older than 1 year of age.

APPENDIX 2: LIST OF RAW DATA FILES KEPT BY R. O. PETERSON AT MICHIGAN TECHNOLOGICAL UNIVERSITY

1) All field notes of project personnel, 1970-84, with some prior to 1970.

2) Autumn aerial survey data, 1972-83. Sex and age frequency of moose observed plus areas sampled.

3) Summer field data, 1970-83:

- maps of routes hiked
- maps of locations of moose observed
- data on moose observed - sex, age, group size, frequency observation (moose/mi)
- scat contents of wolves
- howling frequency of wolves
- wolf sign

4) Winter field data, 1971-84:

- wolf population size, organization
- wolf pack territorie
- wolf travel and predation rates
- moose population estimates based on stratified sampling
- snow and weather conditions

5) Moose autopsy file, 1958-84.

6) All skeletal specimens collected, 1958-84, primarily from moose.

APPENDIX 3: MAP OF ISLE ROYALE, SHOWING LOCATIONS REFERRED TO IN TEXT.

