THE RISE AND FALL OF ISLE ROYALE WOLVES, 1975–1986

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Abstract.—The wolf (*Canis lupus*) population in Isle Royale National Park, Michigan, increased steadily in the 1970s, reaching a peak of 50 wolves (91 wolves/1,000 km²) in 1980. A population crash followed in 1980–1982, then wolf numbers stabilized at 20–24, the same level as during the 1960s. After a lag of 2–3 years, wolf density followed trends in moose (*Alces alces*) mortality rate, which was correlated with wolf-pack food supply. The increase in numbers of wolves resulted from proliferation of reproducing packs when food became more abundant in the early to mid-1970s. During the increase phase, pack size averaged 9.5 wolves, with annual survival of 84–87%, but during the crash, pack size dropped to 4.7 and survival was only 49%. Equilibrium was reached in 1983–1986, with average pack size of 6.5 and annual survival of 66–67%, coupled with annual recruitment of two pups/pack. For 2 years before the 1980–1982 crash, dispersal of individuals from packs was high, resulting in smaller pack size. Known mortality during the decline took the form of starvation and intraspecific killing, direct and indirect manifestations of reduced food supply.

The wolves isolated and protected in Isle Royale National Park in Lake Superior have continued to provide a rare opportunity to clarify predator-prey relationships between moose (*Alces alces*) and wolves (*Canis lupus*; Peterson et al., 1984b). The history of the wolf population since its beginnings in the late 1940s to 1974 was chronicled by Allen (1979), Jordan et al. (1967), Peterson (1977), Mech (1966), and Wolfe and Allen (1973). This study revealed population characteristics and regulatory mechanisms during 1975–1986, a period of unprecedented growth and decline.

STUDY AREA

Isle Royale is a 544-km² island in Lake Superior, located approximately 24 km from the Canadian north shore. The island is almost completely covered by northern hardwood (*Acer saccharum-Betula alleghreniensis*) or boreal forests (*Picea glauca-Abies balsamea*), but inland lakes and shoreline ice are extensively traveled by wolves. Details of Isle Royale physiography, climate, and vegetation were presented by Peterson (1977). To ensure a complete sanctuary for the wolf population, since 1979 Isle Royale National Park has been closed to visitors from November to mid-April. During the remainder of the year, most human activity is restricted to hiking trails. Areas with a history of wolf homesite-use in summer are closed to overnight camping. No mammalian pets are allowed on the island.

Isle Royale wolves feed almost exclusively on moose and beaver (*Castor canadensis*). Prey reached peak levels of 2.5 moose/km² and 0.6 beaver colonies/km² in 1969 and 1974, respectively; by the late 1970s prey declined to 1 moose/km² and 0.2 beaver colonies/km² (Peterson et al., 1984b; Shelton and Peterson, 1983).

Wolf ingress and egress were possible via occasional ice bridges to the mainland. However, except for a brief excursion of one wolf to the mainland in 1977 (Peterson, 1979), we were unaware of wolf movements to or from the island during the current study.

METHODS

Wolf surveys and observations were made from aircraft from mid-January to early March each year. Snow-tracking from light aircraft (e.g., Piper PA-18) proved to be an excellent technique for daily monitoring of wolf packs (Mech, 1966). Wolves were back-tracked to their previous location, providing complete coverage of travels and kills for 40–60 days each winter. Food availability for each pack was calculated given assumed prey weight and average utilization for the available sex and age classes of moose consumed (Peterson, 1977).

During 1975–1986, wolf social units (packs or singles) were observed 1,278 times in about 1,400 h of flight time. We tracked wolves a total distance of 8,787 km. Pack territories were defined each year by all known movements, usually by minimum-area polygons covering all pack locations.

Wolf packs were distinguished by size, location, and distinctive wolves (usually alpha, or dominant individuals), sufficient to identify all major packs in successive years, except when noted. Wolves were observed from aircraft with 7× wide-field binoculars or, in 1984–1986, a gyro-stabilized 15× monocular
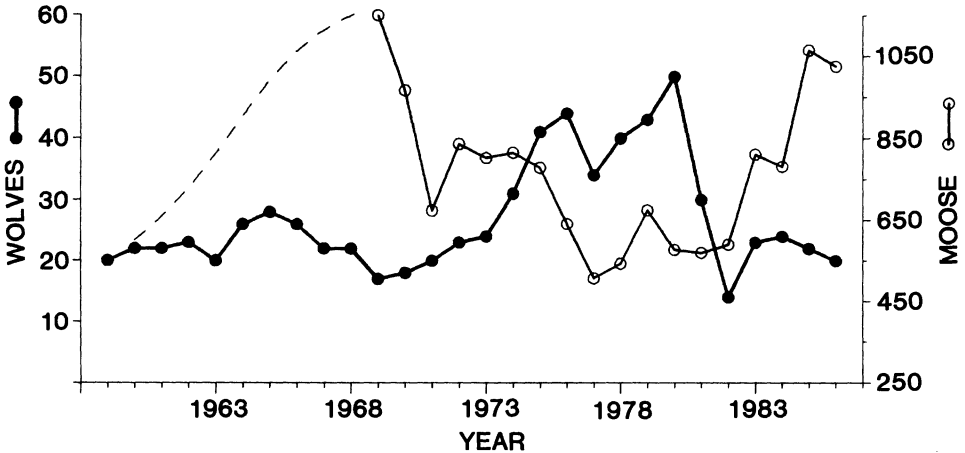
FIG. 1.—Fluctuations of wolves and moose numbers in Isle Royale National Park, 1959–86.

viewing device (Fraser-Volpe, Inc., Warrington, PA). On a day-to-day basis, individual wolves often were recognized by body conformation, pelage appearance, and tail characteristics. Social status of individual wolves was inferred from behavioral interactions among pack members (Peterson, 1977; Schenkel, 1947).

Pups were identified in winter by size, pelage, and behavior (Jordan et al., 1967; Peterson, 1977). In some years pups could be distinguished readily by small size, but usually such differences were slight or nonexistent, so behavioral observations were critical. The basic premises underlying our interpretations of behavior were that wolf play, hunting, social, and sexual behavior are all age-dependent (Fox, 1971; Scott and Fuller, 1965), and that 8-month-old wolves have not yet been incorporated into the social hierarchy that governs all behavior of older packmates (Zimen, 1975, 1981). In accordance with these ideas, the following specific behaviors were most helpful in classifying pups:

1) Pups exhibited a high frequency of social play behavior, relative to older wolves in the same pack (Bekoff, 1978, 1981b; Fagen, 1978).

2) Pups sometimes engaged in social play behavior at inappropriate times (e.g., while hunting).

3) Pups participated little in hunting and killing of moose, and at times displayed distinct fear of these large prey.

4) Pups showed a "freedom of behavior" (Zimen, 1975:340) not found in older wolves, probably reflecting social tolerance by older wolves (Bekoff, 1981a:172) and permissiveness of wolf parents (Fox, 1971:168).

5) Pups exhibited frequent reversals in evident social rank during social play (Fox, 1971:169).

6) There was no expression of sexual behavior in pups, yet they often exhibited intense interest in sexual behavior of alpha wolves without reproach.

7) Friendly behavior dominated pup interactions with other pups and alpha wolves, and only submissive expressions were directed toward older wolves (Zimen, 1975).

8) Pups usually traveled near the rear of the pack when hunting.

Aside from major packs, single wolves and temporary associations numbering up to five wolves were tracked and observed opportunistically. A total count of the population was made at least twice during each annual study, more commonly several times.

During summer, ground personnel hiked an average of 800 km each year to gather data on wolf food habits and reproduction. Traditional dens and homesites were examined each year and, if occupied, spontaneous and induced howling provided data on the number of pups present. Litter-size determination from howling was most feasible when the number of pups was <five (Harrington, 1987). Abandoned sites were searched thoroughly for prey remains and feces, and additional feces were examined throughout the island.

RESULTS

During the 16 years (1959–1974) before the study phase reported here, the wolf population numbered 17–31 wolves and contained one or two reproducing packs (Jordan et al., 1967; Mech, 1966; Peterson, 1977; Wolfe and Allen, 1973). However, the apparent equilibrium exhibited during this period was illusory, the result of a relatively brief study of a long-lived species (Fig. 1).

TABLE 1.—*Isle Royale wolf numbers and organization, 1975–1986.*

Year	Packs					Sum of core[a] packs	Size of other groups					Total
	East	West	Middle	South-west	Harvey Lake		5	4	3	2	1	
1975	18	10	7	—	—	35	—	—	1	1	1	41
1976	17	9	4, 3	3	—	36	—	1	—	1	2	44
1977	13	7	7	4	—	31	—	—	—	—	3	34
1978	12	8	11	7	—	38	—	—	—	—	2	40
1979	11	—	14	9	—	34	1	—	—	1	2	43
1980	10	—	14	7	4	35	—	1	—	3	5	50
1981	9	—	7	6	3	25	—	—	—	1	3	30
	East II	West II										
1982	2	4	—	—	2	8	—	—	—	1	4	14
1983	7	7	—	—	6	20	—	—	—	—	3	23
1984	5	10	—	—	6	21	—	—	—	—	3	24
1985	6	10	—	—	3	19	—	—	—	—	3	22
1986	5	11	—	—	2	18	—	—	—	—	2	20

[a] Core packs were those identified during more than 1 year.

Wolf Numbers and Organization

During 1975–1980, the wolf population increased each year except 1977 and fluctuated between 34 and 50 animals (Table 1). Additional packs became established, until five were present in 1980 (Fig. 2). New packs appearing during this period were Middle Pack (1975), Southwest
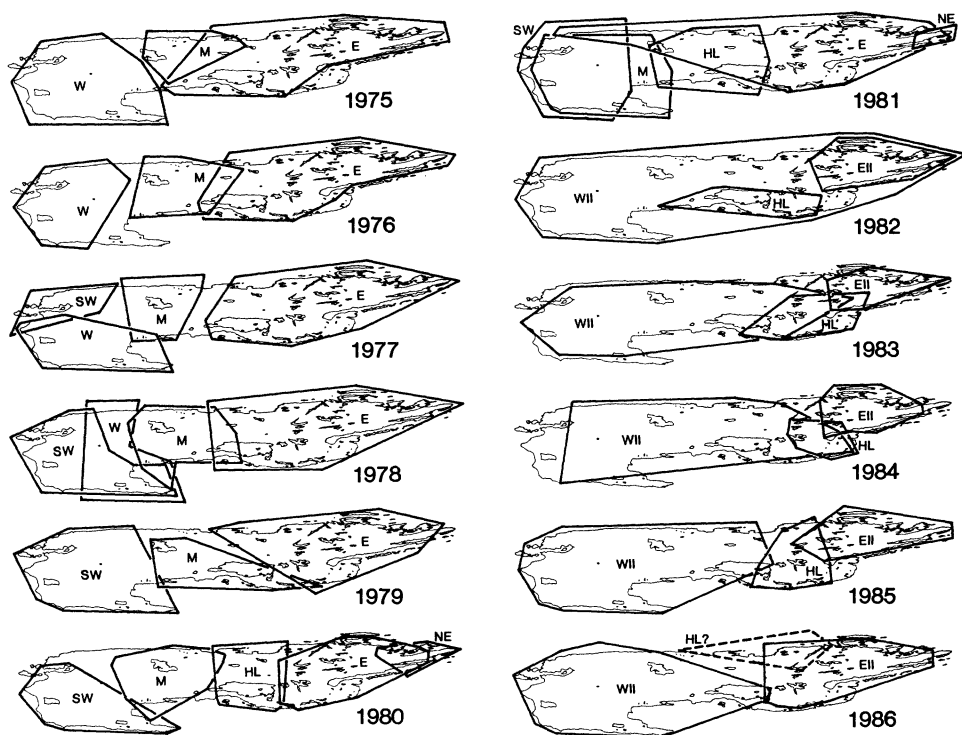

FIG. 2.—Isle Royale wolf pack territories as indicated by midwinter movements, 1975–1986. Pack abbreviations are as follows: W = West Pack, E = East Pack, M = Middle Pack, SW = Southwest Pack, HL = Harvey Lake Pack, WII = West Pack II, EII = East Pack II, NE = Northeast Pack.

TABLE 2.—*Comparative prey use by Isle Royale wolves in summer (May–August) during 1975–1983, determined by analysis of 2,648 fecal droppings.*[a]

Prey characteristic	Adult moose	Calf moose	Beaver	Snowshoe hare
% prey occurrence in feces	9	41	38	2
Relative no. of prey	1.00	5.96	9.78	2.54
% biomass of prey	44.8	38.1	16.6	0.4

[a] Only moose, beaver, and snowshoe hare (*Lepus americanus*) were considered, comprising 90% of all prey occurrences. 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 feces (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), showshoe 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).

Pack (1976), and Harvey Lake Pack (1980). Packs added during the increase phase resulted from growth of small packs or pairs that became established in areas not used by major packs.

In the late 1970s, emergence of Southwest and Middle packs offset simultaneous declines of West and East packs. West Pack, recognized since 1968, was not evident after 1978. Southwest Pack eventually replaced West Pack, but Middle Pack arose and thrived briefly in a portion of the island that had not been used heavily by other packs.

In 4 years (1976–1979), Southwest Pack displaced West Pack (Fig. 2). In 1978, the final year in which it was recognized, West Pack shifted into a portion of the island containing almost no moose in midwinter. In the following year this area was devoid of wolves, and West Pack apparently abandoned its traditional territory and fragmented. Seven wolves, probably derived from West Pack, initially were seen together in 1979 at the opposite end of the island, but later split into groups of three and two, plus two 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 northeast end of the island and traveled over areas not heavily used by the resident East Pack. Possibly some of these wolves became established at the northeast end, because a small group resided there in 1980 and 1981.

A dramatic wolf decline occurred in 1980–1982, when population size dropped from 50 to 14 wolves. One major pack, probably Southwest Pack, disappeared completely, and all packs were reduced greatly. The only pack traced with certainty from 1981 to 1982 was Harvey Lake Pack. During 1982–1986 the dominant West Pack II used a traditional Middle Pack homesite in summer, suggesting ties with this former pack. There were no other clues as to the origin of the packs present after 1981.

Four breeding females remained in the population in 1982, and three of these provided the nuclei of the three packs that partitioned the island during 1982–1986. During this period, Harvey Lake Pack, with little exclusive territory, clearly led a marginal existence. We documented attacks by neighboring packs each year except 1985; the Harvey Lake alpha female was killed by West Pack II in 1984. In 1986, East Pack II aggressively displaced Harvey Lake Pack, and thereafter the wolf population again was dominated by just two territorial packs.

With few exceptions, Isle Royale wolf packs claimed exclusive pack territories. Trespassing into other packs' territories was insignificant before 1981. In 1978, when West Pack and Southwest Pack exhibited strong overlap, areas of intensive use were still separate.

Territorial boundaries disintegrated in 1981, when East Pack traveled the entire north shore of the island, and Southwest and Middle packs overlapped extensively. In 1982, all previous territorial conventions seemed obsolete and spatial relationships were in flux. Thereafter, except for intrusions on Harvey Lake Pack, spatial order was restored.

Wolf Food Supply

From December to April, moose constituted virtually the only prey for Isle Royale wolves. During the open-water period, beavers were killed frequently, but more than 80% of prey biomass in summer was derived from moose (Table 2).

Moose mortality in winter (number deaths/day) was correlated with wolf pack food availability ($r^2 = 0.65$), calculated from data on kills of each pack, but not food per wolf ($r^2 = 0$). Wolf-pack
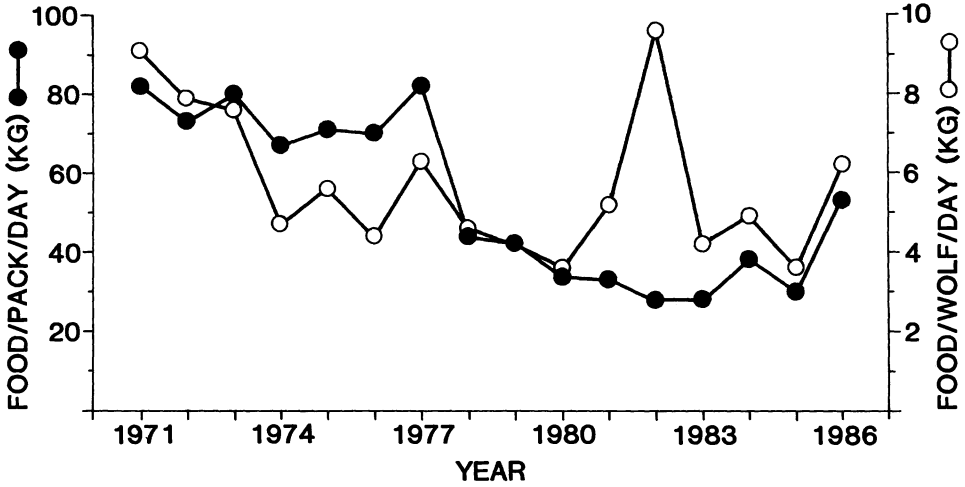
FIG. 3.—Daily food availability per pack and per wolf on Isle Royale, 1971–1986. Annual data represent an average value for all packs, weighted by pack size. Food availability was calculated on the basis of kills made by each pack.

food availability declined steadily during 1976–1981, producing progressively greater food stress for wolves in the late 1970s, then stabilized at a relatively low level in the early 1980s (Fig. 3). After a lag, wolf density followed trends in food supply (Fig. 4). Correlations between moose mortality and wolf density in the same and subsequent years suggest that the length of this lag was about 2–3 years (same year, $r^2 = 0.61$; 1-year lag, $r^2 = 0.74$; 2-year lag, $r^2 = 0.83$; 3-year lag, $r^2 = 0.81$; 4-year lag, $r^2 = 0.44$).

Reproduction and Survival

From 1974 to 1985 the number of litters of wolf pups born on Isle Royale each year ranged from two to four (Table 3). Initial litter size was unknown, but it was often possible to determine the number of surviving pups in midsummer or winter.

The number of reproducing females was greatest in 1977, 1978, and 1982, when there were four. One of the 1982 litters consisted of only one pup in June, born to a wolf pair isolated on
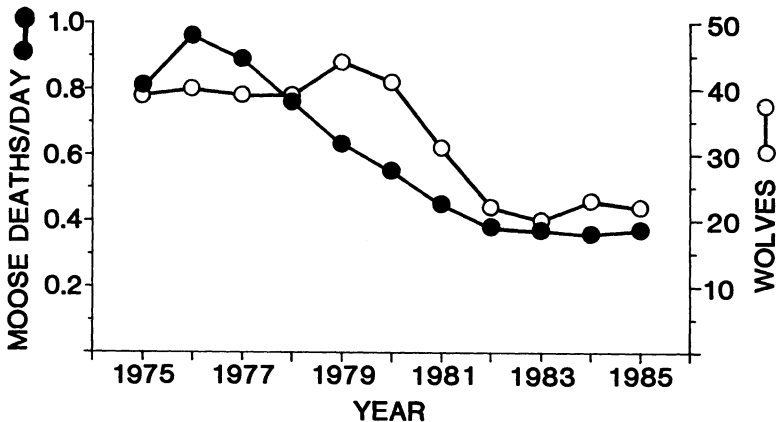

FIG. 4.—Trends in midwinter moose mortality and wolf numbers on Isle Royale, using 3-year moving averages (e.g., value for 1977 is the average of 1976, 1977, and 1978).

TABLE 3.—*Reproduction and mortality among Isle Royale wolves, 1974–1985.*

Year	Number of litters of pups	Pups present in summer (s) or winter (w)	Subsequent population change	Estimated annual mortality[a]
1974–1975	3	15 (s, w)[b]	31 to 41	18% (5.5/31)
1975–1976	3	10–12 (s)	41 to 44	21–26% (8.5–10.5/41)
1976–1977	3	8–9 (s)	44 to 34	44–47% (19.5–20.5/44)
1977–1978	4	n.a.	34 to 40	n.a.
1978–1979	4	n.a.	40 to 43	n.a.
1979–1980	3	9–12 (s)	43 to 50	8–15% (3.5–6.5/43)
1980–1981	3	7 (s)	50 to 30	57% (28.5/50)
1981–1982	3	9 (s), 0 (w)	30 to 14	53% (16/30)
1982–1983	4	13 (w)	14 to 23	29% (4/14)
1983–1984	3	10–11 (w)	23 to 24	39–43% (9–10/23)
1984–1985	2	7 (w)	24 to 22	38% (9/24)
1985–1986	2	4 (w)	22 to 20	27% (6/22)

[a] Mortality rates reflect change from 1 winter to the next. If only summer pup estimates were available, winter pup numbers were assumed equal to pup numbers the previous summer plus 0.5 pups/pack.
[b] Five pups estimated for East Pack in summer, and five each for West and Middle packs in winter.

a peninsula at the east end of the island, an area not used by wolves during the previous winter. Neither the pair nor their pup could be located during the next winter. Otherwise, all known reproduction occurred within established territorial packs.

If the number of pups present in winter and the change in population size since the previous winter were known, survival rate could be calculated for the animals present the previous year. This was possible beginning in 1982, after which the population was relatively small or all individuals were observed with a 15× gyro-monocular. Before 1982, estimates of pup numbers were derived primarily during summer. These summer-pup estimates were used to provide an indication of pup abundance the following winter, after considering the influence of two offsetting biases. Pup mortality in the intervening 5 months would lead to overestimation of pup abundance in winter, but if pups were underestimated during howling sessions in summer, this would lead to a comparable underestimate of pups in winter. For five packs with adequate data, summer pup counts averaged 0.5 (*SE*) = 0.6) pups/pack lower than winter counts. This was used as a correction factor for all summer pup counts.

Average annual wolf survival from 1 winter to the next thus was determined to be 84–87% during 4 years between 1974–1975 and 1979–1980, when wolf numbers were increasing or stable at a high level (Table 4). During the wolf crash of 1980–1982, average annual survival dropped to a comparable underestimate of pups in winter. For five packs with adequate data, summer pup counts averaged 0.5 (*SE* = 0.6) pups/pack lower than winter counts. This was used as a correction factor for all summer pup counts.

Mortality Factors

Before this study, only three fresh carcasses of Isle Royale wolves had been examined in 16 years; two were wolves killed by other wolves in winter, and one was a malnourished young pup that died in summer (Jordan et al., 1967; Peterson, 1977; Wolfe and Allen, 1973). In this study, cause of death was determined for nine additional wolves, including seven that were killed by other wolves and two that succumbed to malnutrition. Five of these wolves were recovered during the wolf crash of 1980–1982. Both wolves dying of malnutrition were males with heavily worn teeth; their respective whole weights were 25 and 26 kg (expected weight 35–50 kg), and femur marrow from one contained only 16% fat. Both exhibited infections associated with recently fractured ribs, probably inflicted by moose (numerous old rib fractures were evident in both). One was recovered in 1980 near a moose carcass in winter, where tracks revealed that the wolf was unable to fully lift its feet off the ground. The other was found in midsummer 1981 in a shallow, water-filled pit, from which it was unable to extricate itself.

TABLE 4.—*Observed activity of Isle Royale wolves, 1972–1986.*

Year	n^a	Frequency of observed activity (%)						
		Traveling	Sleeping	Hunting	Resting	Feeding	Playing	Courtship
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
1984	90	17	47	7	4	7	5	3
1985	73	22	33	2	8	5	1	2
1986	95	25	43	1	11	8	5	2
Total	1,626	28	38	5	10	10	3	4

[a] Number of cases when initial activity was noted at the beginning of the observation.

Behavior

Both the magnitude and pace of the natural wolf decline on Isle Royale in 1980–1982 were unprecedented for the species. Observations during this study revealed many details of interpack and intrapack behavior that reflected demographic changes.

Scent-marking.—During 1978–1986, the frequency of scent-marking (raised-leg urination, squat urination, or scratching; Peters and Mech, 1975) was recorded whenever wolf packs were traveling and not in direct pursuit of prey. In this period, we observed 201 scent-marks in 31 h, yielding an average of 3.5 marks/h when all years received equal weight. Scent-marking was performed solely by the alpha male and female, as documented in captivity by Peters and Mech (1975). Scent-marking frequency was especially high in 1982 and 1986, when it was linked to territorial adjustments or intrapack expression of dominance. In 1982, West Pack II averaged 14 marks/h as it traveled widely throughout the island, often tracking other wolves in the aftermath of an almost complete disruption of established territories. Likewise, in 1986, East Pack II exhibited 22 marks/h during initial movements in newly claimed territory that had belonged to Harvey Lake Pack. Also in 1986, the alpha female in West Pack II marked at a rate of 18/h while tracking, then encountering and dominating, a female pack-mate that had left the pack briefly to follow other single wolves (perhaps potential mates).

Intraspecific aggression.—The relative rarity of direct conflicts between packs reflects the mutual avoidance typical among adjacent wolf packs (Peters and Mech, 1975). From this we conclude that most direct conflicts represent purposeful attacks by an established pack, either to maintain its territory free of foreign wolves or, more rarely, to expand its territory. Interpack aggression was prominent during the spatial reorganization of the early 1980s. During 1981–1986, we recovered six wolves that were killed by other wolves, compared to five similar cases in the previous 21 years. The context of such fatal attacks included single wolves and packs caught while trespassing and also aggressive attacks by packs on neighboring groups. Between 1981 and 1986, for example, Harvey Lake Pack was attacked within their own territory (delineated by travels and scent-marks) at least four times by West Pack II and East Pack II.

The most unusual behavior exhibited by any pack was the extensive movement of West Pack II in 1982, when it covered the entire island. Its 19 km/day travel rate was the maximum recorded in 16 years, almost twice the long-term average. Extensive travel was not necessary to locate suitable prey, as the kill rate of this pack was exceptionally high. In 1982, it was common for this pack to leave a carcass after a single feeding, then continue tracking other wolves.
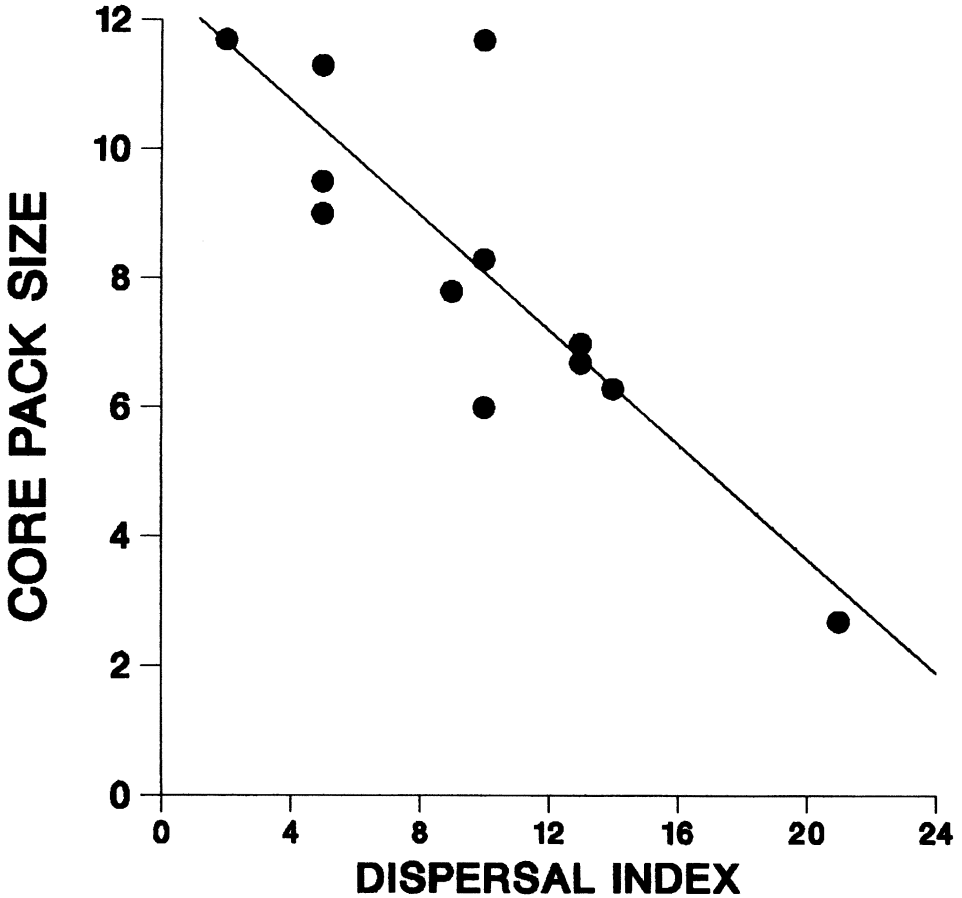
FIG. 5.—Relationship between dispersal (proportion of single wolves in the population) and average core pack size on Isle Royale ($Y = 12.5 - 0.44X$, $r^2 = 0.70$).

Two nonfatal attacks were witnessed, in 1981 and 1983. In the first, East Pack ran down and attacked a single wolf of unknown origin on a frozen lake, but then ceased their attack and bedded nearby while the single wolf lay immobile on its side. When it arose, the pack renewed its attack, yet allowed the wolf to retreat submissively to cover and to escape. In the second, West Pack II, led by the alpha pair, tracked Harvey Lake Pack to a kill within Harvey Lake Pack territory. After finding Harvey Lake Pack at the kill, West Pack II chased these wolves for almost 2 km, still led by alpha pair. After passing by a Harvey Lake Pack pup, West Pack II brought down the alpha female. Lying on her back, she snapped defensively while being bitten and threatened continuously for about 2 min. West Pack II then allowed her to crawl off submissively into cover and to escape without further pursuit.

Dispersal.—Zimen (1976) proposed that food shortage increased aggression within packs, prompting subordinate wolves to leave the pack. Among wild wolves, such departures often are temporary and are especially frequent during the February breeding season (Messier, 1985; Peterson et al., 1984a; Van Ballenberghe, 1983), when most of our observations were made. As food stress for Isle Royale wolves increased in the late 1970s, pack size declined until, by 1981, all packs contained fewer than 10 wolves. From 1975–1980 to 1981–1982, average core-pack size dropped from 9.5 ($SE = 0.77$) to 4.7 ($SE = 1.02$). This decline was correlated with increased dispersal, evidenced by a growing proportion of single wolves in the population (Fig. 5). In 1980,

with both wolf density and food stress at a maximum, 30% of the population existed as single wolves or in small, temporary associations (Table 1). Survival of these wolves was evidently poor, because the proportion of wolves outside "core" packs declined to 13% in 1981. Simultaneously, all core packs declined in size for the first time. In 1983–1986, with wolf density adjusted more closely to food supply, average pack size increased to 6.5 ($SE = 0.79$).

Activity pattern.—Mech and Karns (1977) documented a decrease in activity in one Minnesota wolf pack that underwent food shortage in winter. In spite of a large reduction in wolf food supply at Isle Royale, there was no clear relationship to the proportion of time spent sleeping or resting ($r^2 = 0.09$, $P > 0.25$, Table 4). In this study, many factors could have masked such a relationship.

DISCUSSION

The increase of Isle Royale wolves in the 1970s was the first major perturbation in the wolf population since its establishment in about 1949. Throughout the late 1970s, wolf density exceeded 80 wolves/1,000 km², and the 1980 peak of 92 wolves/1,000 km² represents the highest density recorded for wild wolves. This tends to refute the notion that wolf social behavior intrinsically limits wolf density to a maximum of 38/1,000 km² (Pimlott, 1967; Woolpy, 1968).

It is clear that the only natural limits to wolf density are those ultimately imposed by food supply. Social behavior, however, responsive to variation in food supply, was the key proximate regulator of wolf density (Keith, 1983; Messier, 1985; Packard and Mech, 1980; Zimen, 1976). As food supply expanded in the early 1970s, wolf-pack territories shrank and dispersal was low, leading to a proliferation of large wolf packs. By the early 1980s, declining food supply, resulting from progressive culling of a reduced moose population, resulted in territorial trespassing, interpack violence, and increased dispersal, ultimately producing fewer packs of smaller size, as also found in Minnesota (Mech, 1977*b*, 1986; Mech and Karns, 1977).

The behavioral responses of wolves to increased then decreased food supply were not symmetrical. The increase phase was accommodated gradually, but responses to the food decline, especially territory enlargement, were abrupt. Extreme responses to food shortage, exemplified by trespassing and interpack violence, seemed to be delayed as long as possible. Violent confrontations between packs are, of course, unlikely to uniformly enhance reproductive fitness of alpha wolves, the primary participants in such conflicts (Mech, 1977*b*:573). Such delays in response to food declines are ecologically significant, in that high wolf density can be maintained for several years in spite of a declining prey base. Prey populations thus may be held at low levels by predation for many years (Mech and Karns, 1977; Nelson and Mech, 1981). Where man also hunts the same prey, this may exacerbate management conflicts brought on by low prey density (Gasaway et al., 1983). In theoretical models, such lags in population responses also may produce cyclicity in predator-prey systems (May, 1981; Peterson et al., 1984*b*).

A striking development was the stabilization of the wolf population in the early 1980s at a level identical to that of the early 1960s. By 1986, even the spatial organization of the population was similar, with a large, dominant pack inhabiting the southwestern two-thirds of the island and a smaller pack resident on the remainder. We interpret this as a response to similar levels of food availability, as the moose population numbered 600–1,000 and was increasing during both periods.

Food availability measured for less than 2 months in midwinter proved adequate for understanding general wolf population responses at Isle Royale. This could indicate that midwinter (just before and during the breeding season) is a critical period of the year, perhaps influencing ovulation in the alpha female (Mech, 1977*a*). However, it is also possible that midwinter kill rates are correlated with food availability during the remainder of the year in this largely single-prey system.

High dispersal and conspicuous mortality were associated with the wolf decline of 1980–1982, at a time when average daily food availability approached 3 kg/wolf (30–40 kg/pack). This is about 10% of body weight for 30 kg adults, but ravens (*Corvus corax*), foxes (*Vulpes vulpes*), and other scavengers removed an unknown proportion. Subordinate wolves could readily have

faced daily food availability lower than the 6% of body weight postulated by Mech (1970) as a minimum maintenance level. Of course, it is the subdominant wolves with least access to food that are most likely to disperse, and the dispersers that are subject to highest mortality rates (Mech, 1977*b*; Messier, 1985; Peterson et al., 1984*a*).

A "fence effect," or elevated population density, is often characteristic of insular small-mammal populations, where density-regulating dispersal is prevented (Crowell, 1981). Could restricted wolf dispersal explain the high level of conflict and killings of the early 1980s? We argue that two separate conditions can explain the existence of elevated animal density on islands: 1) island area too small in relation to normal home range; 2) lack of a dispersal sink, for a species in which dispersal contributes to population regulation. For the Isle Royale wolf population as a whole, neither condition appears to be fully met. It is clear that the entire island is rarely used by a single pack. If food supply is high, wolf-pack territories may be considerably less than 50% of the island area. Furthermore, although we believe dispersal contributes significantly to regulation of pack size and, therefore, population density, an adequate natural dispersal sink (mortality from malnutrition and intraspecific aggression) exists on Isle Royale. Yet, because it is almost certain that the area covered by movements of most dispersing wolves would exceed that of Isle Royale (Fritts, 1983; Fritts and Mech, 1981; Mech and Frenzel, 1971; Peterson et al., 1984*a*; Van Ballenberghe, 1983), our first condition appears met in the case of dispersing wolves. We conclude that the unusual level of observed violence resulted from both extraordinarily high wolf density arising from abundant food, and from restricted opportunities for dispersers to leave the island. On Isle Royale, it is likely that dispersing wolves are killed more often by other wolves than on the mainland, where wolf density is usually lower and vacant areas more readily located. Although we acknowledge the restricted dispersal movements, we attribute the long-term high wolf density on Isle Royale to an abundant food supply (Van Ballenberghe et al., 1975), not to a classical "fence effect."

We hypothesized that wolves and moose on Isle Royale have the potential for continued cycling with a period of oscillation on the order of 3–4 decades (Peterson et al., 1984*b*). The immediate future for Isle Royale wolves will depend on abundance of moose in vulnerable age groups. Accordingly, wolf food supply should remain stable or decline until abundant moose cohorts born after 1980 begin to enter the age of senescence in the late 1980s. If our hypothesis is correct, wolf numbers should remain near present levels through the close of the decade.

ACKNOWLEDGMENTS

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