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EFFECTS OF POPULATION DENSITY AND PACK SIZE ON THE FORAGING ECOLOGY OF GRAY WOLVES

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A decline in the gray wolf (*Canis lupus*) population in Isle Royale National Park prompted an intensive study of radiocollared individuals in 1988-1991, complementing an ongoing study begun in 1958. During winter, 1959-1991, the proportion of lone wolves was higher when the population was at low levels, whereas average size of packs declined with density of wolves. Sizes of territories (1971-1991) were not related to size of packs. In winter, food availability (kg wolf^{-1} day^{-1}) and kill interval (days/kill) varied inversely with size of packs. Social relationships of radiocollared lone wolves were flexible; they often formed temporary groups of two or three wolves. Small groups (less than four) and lone wolves roamed large areas of the island (300 km^2 and 540 km^2, respectively), frequently moving through territories of established packs. Solitary wolves and pairs readily killed adult moose, in contrast to a common belief that larger packs benefit from cooperative hunting.

Key words: *Alces alces, Canis lupus,* gray wolf, group size, Isle Royale, predation, population density, moose

Social relationships, movements, and feeding patterns of medium and large (more than four individuals) packs of gray wolves (*Canis lupus*) have been well documented (Allen, 1979; Fritts and Mech, 1981; Fuller and Keith, 1980; Peterson, 1977), but data are sparse for small groups (two or three animals) and lone wolves (Messier, 1985a; Rothman and Mech 1979). Traditionally, lone wolves were believed to be old individuals that had lost their mate (Young and Goldman, 1944), or dispersing individuals in search of a breeding territory and mate (Fritts and Mech, 1981; Peterson et al., 1984; Rothman and Mech, 1979). These solitary wolves reportedly inhabited the periphery of pack territories (Fritts and Mech, 1981; Peterson et al., 1984), feeding on small prey and scavenging kills left by large packs (Jordan et al., 1967; Mech, 1966; Nudds, 1978), although pairs of wolves were known to kill moose (*Alces alces*—Ballard et al., 1987; Peterson et al., 1984).

Wolves in Isle Royale National Park have been monitored annually since 1959 by snow-tracking from aircraft in winter. With this method, detailed information on predation and movements was obtained primarily for large groups that were readily located; data on small groups and lone wolves were fragmentary. The wolf population declined to 14 animals in 1982 after reaching an all-time high of 50 in 1980 (Peterson and Page, 1988). After a brief rebound, the population again declined to an all-time low of 12 wolves in 1991.

As part of a study of this population decline, wolves were live-captured and radiocollared for the first time during 1988–1991. Herein, we provide new data on the social relationships, movements, and food supply of lone and small groups of wolves. We test the null hypotheses that the proportion of lone wolves is the same at all population levels, that territory size, available food, and kill interval do not vary by

size of packs, and that size of packs is unrelated to density of wolves. Our aim is a better understanding of behavioral strategies of wolves in relation to group size and factors influencing group size.

METHODS

Study area. —Isle Royale National Park, Michigan, located in northern Lake Superior (47°55'N, 89°W), is an archipelago composed of one large island (544 km²) and several small islands. The archipelago was formed by interbedded volcanic lavas and sedimentary deposits that gradually subsided, creating the basin of Lake Superior with uplifted edges that form Isle Royale on the north and the Keweenaw Peninsula of Michigan to the south (Huber, 1975). Vegetation includes both boreal (*Picea glauca-Abies balsamea*) and northern hardwood forests (*Acer saccharum-Betula allegheniensis*). The prey base available for wolves includes moose, beaver (*Castor canadensis*), and snowshoe hare (*Lepus americanus*). The park is open to visitors from mid-April through October.

Capture and sampling of wolves. —Newhouse No. 14 leg-hold traps (modified as described by Kuehn et al., 1986) were used to trap 10 wolves from April 1988 to May 1991. Wolves were immobilized with a mixture of 4 mg ketamine hydrochloride and either 1 mg xylazine (1988) or 1 mg promazine hydrochloride (1989–1991). All animals were radiocollared, ear-tagged, weighed, measured, and blood was sampled for genetics and disease studies (Lehman et al., 1991; Wayne et al., 1991). Subsequent locations were made from aircraft once or twice daily in winter (mid-January–early March, weather permitting), and once every 2–4 weeks the rest of each year. All wolves were observed and censused in winter from aircraft and back-tracked when possible to previous locations, which provided information on group size, travel, and kills. Snowtracking without the aid of telemetry occurred from 1959 through 1987. Territories were determined for groups from all known locations during winter (minimum-area convex polygon—Mohr, 1947).

Moose and beaver carcasses used by the wolves were located from aircraft in winter (1971–1991). Dead moose were examined to determine sex, age, condition, and cause of death. Cause of death was assumed to be wolves if any of the following were present: signs of a struggle (chase marks, broken branches, blood on trees, aspirated blood,

blood stains on the hind legs); carcass disarticulated and heavily chewed; rumen usually separate from the carcass; carcass parts usually pulled away from the hair mat where the moose died. Cause of death was assumed to be malnutrition (and thus scavenged) if the moose was usually articulated, had died under conifer cover on its sternum or side, usually with intact rumen, no signs of struggle were present, and bone marrow was fat-depleted (Peterson, 1977). If the evidence was ambiguous, cause of death was recorded as unknown.

Available biomass (kg) of food wolf^{-1} day^{-1} was calculated, assuming average edible weights of 330, 261, 114, and 13 kg for adult male, adult female, young-of-the-year, and beaver, respectively (Peterson, 1977). If only portions of a carcass were used by a group or individual, estimates were made on the proportion consumed. We did not correct for food loss to scavengers such as ravens (*Corvus corax*) and red foxes (*Vulpes vulpes*). Although the amounts taken by these scavengers may be considerable from an unprotected carcass, wolves are dominant to ravens and foxes, and the latter may not feed when wolves are present (Magoun, 1976).

Diet. —In summer, wolf feces observed by researchers (1975–1990) were analyzed macroscopically for prey content, then removed from the trail or site to avoid double-counting. Data on contents of feces were averaged at 2-year intervals for comparison with data on beaver colonies (aerially censused in even years by P. C. Shelton) and young-of-the-year and adult moose populations (aerially censused every winter). Percent occurrence of prey, percent biomass of prey (Floyd et al., 1978) and number of prey (relative to moose) were calculated.

Statistical analyses. —Simple linear regression was used to determine if territory size, kill interval, and food wolf^{-1} day^{-1} were related to group size. Log transformations were used where necessary to assure the variance was homogenous. The Mann-Whitney test and one-way analysis of variance (ANOVA) were used to test differences among means. Chi-square analysis was used to determine if the proportion of each major component of wolf feces differed among years (feces with more than one type of prey were rare), and the Spearman rank correlation was used to determine if percent biomass in diet of wolves was related to the respective size of prey populations, averaged at 2-year intervals.

RESULTS

Group size.—During 1959–1991, the proportion of single wolves in the population ranged from 0.02 to 0.33 ($\bar{X}$ = 0.10, SD = 0.07), with the highest percent of singles occurring when numbers of wolves were low (Fig. 1). Mean size of packs (1971–1991) decreased with density of the wolves. The average size of packs in 1959–1985 ($\bar{X}$ = 9.8 ± 3.7SD) was significantly greater than that of 1986–1991 ($\bar{X}$ = 4.6 ± 2.1SD, Mann-Whitney test, P = 0.003). The number of packs on the island remained quite constant at two to four with the exception of 1976 and 1980, when numbers of wolves were high and additional packs were observed.

Social relationships.—Relationships of most small groups and lone wolves monitored in 1988–1991 were transient (group affiliation changed from year to year), with the exception of a pack on the west end of the island, which had the same alpha pair from 1987 to 1991. From the 1989 breeding season to early summer, one male was associated with two females, but in the previous 6 months he traveled with another wolf on only one known occasion. This same male was paired with a new female during the 1990 breeding season (parting in early March) and the same female through part of the 1991 breeding season (she disappeared in mid-February 1991), but they were together only occasionally during the intervening summer and autumn. Two females were associated from the time they were radiocollared in 1988 (including the 1989 breeding season with the male just mentioned) until one became established as the alpha female of an east-end pack in 1990. Thereafter, the other female of this pair usually was alone, but occasionally was with another lone female (this wolf sometimes followed the east-end pack, but disappeared in December 1990), or the same male as above. One radiocollared male was alone almost continuously; he was located visually with other wolves only three times in 2.5 years of monitoring (>55 observations). Two wolves were each the alpha males of
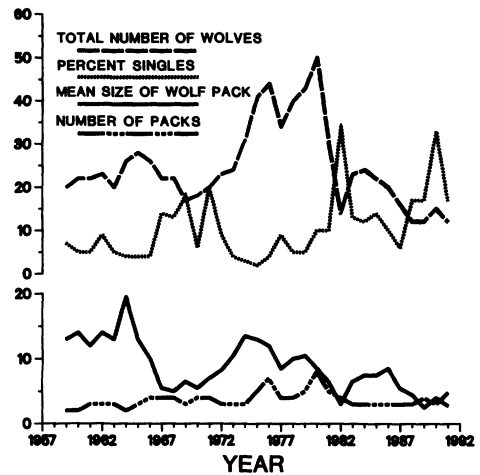

FIG. 1.—Total numbers, average size of packs, percent singles, and numbers of packs of gray wolves in Isle Royale National Park, 1959–1991.

two-member packs (one male was the offspring of the other). Another male, radiocollared as a 2-year-old in May 1991, remained with his natal pack (in the east end) at least through August 1991, when pups were known to be present.

Territory size was not correlated with group size (1971–1991; r^2 = 0.01, $d.f.$ = 52, P = 0.22), and movements of transient groups overlapped those of more established packs (Fig. 2). In 1989, a group of three wolves overlapped the north portion of the territory of a pair of wolves to the southwest, but different associations were formed the following year. A nonbreeding male and female pair overlapped an established west-end territory almost completely in 1990 and were totally within that territory in 1991. Based on ground observations at winter kills of moose (and ca. 7 h/year aerial observation) where identity of wolves was known, this pair did not scentmark (n = 7 moose in 2 years), as did other established and transient pairs, and neither extensive courtship behavior nor sign of estrous was observed.

Lone wolves traveled through territories of established packs much more than expected (Fig. 2), but not with total impunity. One radiocollared female was killed by the
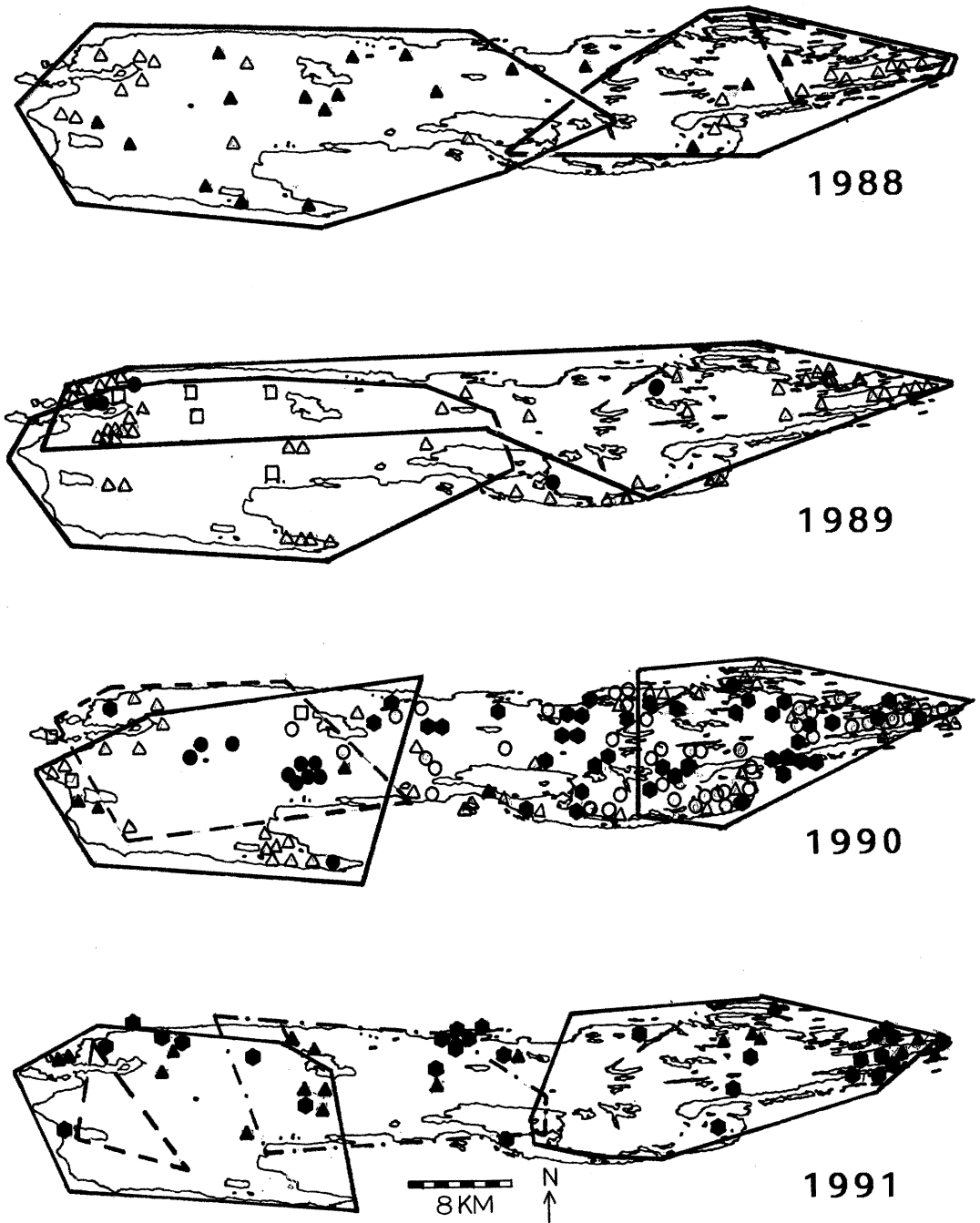
FIG. 2.—Locations of lone wolves in all seasons, overlain by areas used by packs in winter (dashed and solid lines), Isle Royale National Park, 1988–1991. Each symbol type represents a different lone wolf.

west-end pack near a moose she had killed in their territory. Some lone wolves were harassed, but not killed, by residents. One solitary male was observed on several oc-

casions near the west-end pack and kills that either he or they had made. On at least two occasions he was chased by the west-end pack, but he either evaded them or was al-
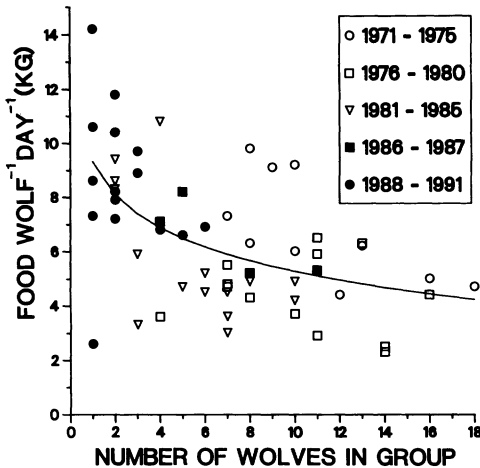
FIG. 3.—Food availability (kg wolf^{-1} day^{-1}) for different group sizes of gray wolves in Isle Royale National Park during winter, 1971–1991 ($\hat{Y} = 9.31 - 1.76 \log_{10}\bar{X}$).

FIG. 4.—Kill interval (days kill^{-1}) for different group sizes of gray wolves in Isle Royale National Park in winter, excluding two outlying points, 1971–1991 ($\log_{10}Y = 2.58 - 0.09\bar{X}$).

lowed to escape. A solitary female also seemed to be tolerated as close as 50 m by the east-end pack. A second lone female was chased and caught by this pack, then released, in January 1991.

Food supply.—Daily food per wolf in winter (1971–1991) was inversely related to the $\log_{10}$ of size of wolf groups ($r^2 = 0.30$, d.f. = 56, $P = 0.001$), with greater variance for small groups (Fig. 3). Mean food supply ($\pm SD$) at 5–6-year intervals was as follows: 1971–1975 (6.8 $\pm$ 2.0); 1976–1980 (4.4 $\pm$ 1.4); 1981–1985 (5.8 $\pm$ 2.5); 1986–1991 (7.8 $\pm$ 2.6 kg wolf^{-1} day^{-1}). All wolves had high availability of food in winter during 1986–1991 with the exception of one female (2.6 kg wolf^{-1} day^{-1}), that seemed to exist entirely by scavenging.

The $\log_{10}$ of kill interval (Fig. 4; range = 2.5–43.0 days/kill) also varied inversely with size of packs, $r^2 = 0.47$, d.f. = 56, $P < 0.001$). Ignoring two outliers (a lone wolf with 43 days/kill, and a group of three with 33 days/kill), the kill interval dropped ca. 33% as pack-size doubled.

Analysis of feces provided the only data regarding diet in summer (Table 1). Numerically, beavers and snowshoe hares were the most important prey for wolves, but in terms of biomass, adult moose consistently
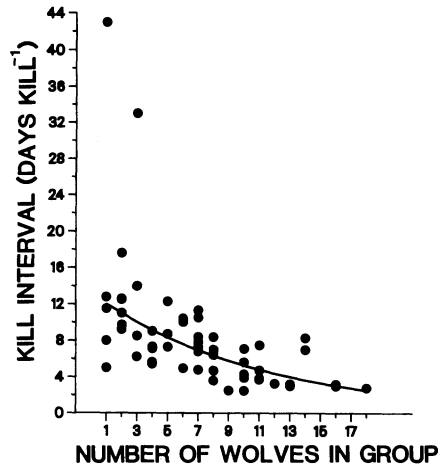
outweighed all other types of prey. Mean percent biomass ($\pm SD$) for all years (1975–1991) was as follows: adult moose, 63 $\pm$ 27%; young-of-the-year moose, 22 $\pm$ 21%; beaver, 14 $\pm$ 10%; snowshoe hare, 1 $\pm$ 1%. The proportions of these remains differed among the 2-year intervals (adult moose, χ^2 = 207.1, d.f. = 7, $P < 0.001$; young-of-the-year moose, $\chi^2 = 648.2$, d.f. = 7, $P < 0.001$; beaver, $\chi^2 = 157.8$, d.f. = 7, $P < 0.001$; snowshoe hare, $\chi^2 = 126.0$, d.f. = 7, $P < 0.001$). Percent biomass of beaver was less variable over time than percent biomass of either remains of young-of-the-year or adult moose, which varied inversely (Fig. 5). Percent biomass of beaver, young-of-the-year, and adult moose was unrelated to the number of beaver colonies ($r_s = 0.09$, d.f. = 7, $P = 0.77$), average population of young-of-the-year ($r_s = -0.02$, d.f. = 6, $P = 0.92$), and average population of adult moose ($r_s = 0.60$, d.f. = 10, $P = 0.29$), respectively, for the 2-year intervals (Table 1).

Patterns in winter feeding for small and large packs did not differ, but lone wolves tended to have a more variable diet. Lone wolves were capable of killing moose on a fairly regular basis. Five lone wolves that were radiocollared killed moose in winter and one of those wolves killed at least five

TABLE 1. — *Prey use by wolves during summer (June–August) in Isle Royale National Park, 1975–1990 (2-year intervals), as indicated by prey remains in wolf feces.*

Years[b]	n[c]	Percent occurrence				Percent biomass[a]				Relative number of prey				Number of beaver colonies[c]	Number of young[d]	Number of moose[e]
		Adult	Young	Beaver	Hare	Adult	Young	Beaver	Hare	Adult	Young	Beaver	Hare			
1975	1,291	46.7	2.0	44.4	0.1	90.0	0.9	9.4	0.0	1.00	0.06	2.29	0.02	—	126	1,153
1977	256	30.1	14.4	50.8	0.0	77.2	8.4	14.4	0.0	1.00	0.60	4.06	0.00	129	51	929
1979	1,002	36.9	22.6	30.9	2.2	80.9	11.2	7.5	0.3	1.00	0.81	1.02	0.92	83	98	757
1981	212	18.9	46.7	23.6	8.0	57.8	32.5	7.9	1.7	1.00	3.27	3.00	6.63	125	142	758
1983	307	10.7	44.0	33.9	3.9	43.4	40.4	15.1	1.1	1.00	5.41	7.56	5.63	151	183	970
1985	257	22.6	45.5	17.5	8.9	63.6	29.2	5.4	1.8	1.00	2.77	1.92	6.42	204	156	1,043
1987	101	40.6	10.9	46.5	2.0	84.0	5.1	10.6	0.3	1.00	0.35	2.72	0.76	199	240	1,516
1989	211	29.8	8.0	55.0	6.2	78.2	4.8	15.9	1.1	1.00	0.34	4.28	3.07	176	185	1,306

[a] Assumed consumed prey weights (kg), based on Fuller and Keith (1980) and Franzmann et al. (1978), and prey weight (kg) represented by each occurrence in feces (as calculated by Floyd et al., 1978) were as follows: adult moose (262.5, 5.63); young moose (45.0, 1.28); beaver (12.0, 0.62); snowshoe hare (1.2, 0.4).

[b] Year 1975 refers to 2-year interval, e.g., 1975–1976.

[c] The number of occurrences represented by all scats examined.

[d] From P. C. Shelton and Isle Royale National Park files.

[e] From R. O. Peterson, pers. comm.

moose (three adults and two young-of-the-year) during the winters of 1989 and 1990. This same wolf scavenged fish remains at campgrounds during summer 1990, but observations suggested that chronic physical decline prompted this unusual behavior. The wolf died of old age (>8 years) and malnutrition in January 1991. As a lone wolf, one female actively hunted beavers during mid-winter thaws in winter 1990, often sleeping beside beaver runways in daylight before making a kill. She also killed three moose (two adults and one unknown age) while alone and scavenged at least four additional moose carcasses in 1990 and 1991. Two female wolves killed at least one adult moose each, while a male killed at least one adult and one young-of-the-year as a lone wolf. Another female relied almost entirely upon scavenging kills made by the east-end pack in winter 1990, but also occasionally killed beavers during thaws.

DISCUSSION

Group size.—Variation in the proportion of lone wolves in a population has not been reported, and data are rare on the prevalence of lone wolves. The mean (10%) of single wolves in winter in the population at Isle Royale National Park was similar to other reports, but variability (range = 2–33%) was high. Estimates in other areas ranged from 8% in northeastern Minnesota (Mech et al., 1971) to 18% in Quebec (Messier, 1985*b*). In addition to changing over time or with density of wolves as reported here, the proportion of singles also may vary seasonally (Fuller, 1989).

When the population of wolves on Isle Royale declined during the 1980s, there was a concurrent decline in average size of packs and an increase in the proportion of single wolves. Two hypotheses explaining high proportions of singles or small size of packs have been proposed. First, if density of wolves is high relative to resources, more individuals may disperse due to intrapack strife or to find new food resources (Boutin et al., 1985; Keith, 1974; Messier, 1985*a*;
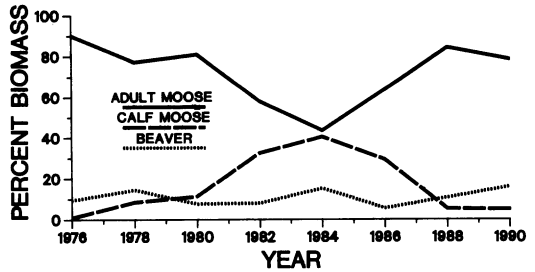

FIG. 5.—Comparison of prey content (percent biomass) of major components of wolf feces from Isle Royale National Park in summer, 1976–1990 (data averaged at 2-year intervals).

Packard and Mech, 1980). Packard et al. (1983), however, reported that some juvenile wolves (<22 months) stayed in their natal packs when densities were high, thus keeping reproduction at a minimum.

Alternatively, when density of wolves is low relative to resources, individuals may disperse to form several small reproducing groups, resulting in a population increase (Fritts and Mech, 1981; Keith, 1974; Mech, 1970; Packard and Mech, 1980; Zimen, 1976). Contrary to the first hypothesis, when densities of wolves were high on Isle Royale (1974–1981), the proportion of single animals was low and size of packs remained moderate, while the number of packs increased. A high proportion of singles and fewer packs would have been expected, because insularity prevents complete dispersal (Crowell, 1981). The social organization of wolves on the island in 1988–1991 is most consistent with the second hypothesis. When density of wolves was low, the preponderance of small packs, a high proportion of singles (possibly seeking mates), and high availability of food in winter would allow individuals to maximize reproductive opportunities. Although a population increase would have been expected, this had not occurred by 1991.

Social relationships.—Transient relationships between wolves have been reported elsewhere, usually involving young animals making forays to and from their natal pack before establishing their own packs and in-

dependent territories (Mech, 1987; Messier, 1985*a*; Peterson et al., 1984). All wolves radiocollared on Isle Royale have been fully-grown adults according to visual inspection of tooth wear, with the exception of two 2-year-old males. One of these males gradually dispersed and established a territory with a mate, while the other stayed with his natal pack. The changing affiliations of older adults may be due to attempts at pair bonding and breeding that have failed. One pack composed of a male and two adult females divided in mid-summer after a period of restricted movements in spring, suggesting failed reproduction. The observed lack of scentmarking (and thus of an exclusive territory) by a paired male and female during two winters may reflect a physiological inability to breed (Rothman and Mech, 1979).

Lone wolves were not restricted to marginal areas between packs as reported in other studies (Fritts and Mech, 1981; Mech et al., 1971; Packard and Mech, 1980; Peterson et al., 1984; Rothman and Mech, 1979; Van Ballenberghe et al., 1975), but rather they ranged throughout the island among established pack territories as noted by Messier (1985*b*). Movements of small transient groups also overlapped with those of established packs. Food stress often has been invoked as a reason for overlap of packs (Bekoff and Wells, 1980; Mech, 1977; Packard and Mech, 1980), although Messier (1985*b*) reported less overlap of packs in areas with low density of moose. In 1989, a year of extensive overlap of packs on Isle Royale, mortality of moose was high from malnutrition associated with a heavy infestation of ticks; other indices of food did not indicate a deficient food supply. Because of the comparatively low density of wolves during 1988–1991, and the limitations of insularity on movement of wolves, perhaps the small established packs could not adequately maintain their territorial borders to exclude other wolves.

Size of territory was not correlated with size of packs, in contrast to other studies

(Ballard et al., 1987; Messier, 1985*b*; Peterson et al., 1984). Fuller (1989) demonstrated only a weak correlation between these two variables, and Peterson et al. (1984) noted that one potentially breeding pair maintained a territory comparable to those of much larger packs. We hypothesize that size of territory on Isle Royale may be more a function of whether reproduction was attempted, even if unsuccessful.

Food supply. — Food availability in winter (1971–1991, range of 5-year means = 4.4–7.8 kg wolf^{-1} day^{-1}), was comparable to or higher than that reported elsewhere. Wolves feeding largely on moose were reported as having 4.5–14.9 (Ballard et al., 1987), 4.4–6.3 (Mech, 1966), and 1.6–2.8 (Messier and Crête, 1985) kg wolf^{-1} day^{-1} of available food. Wolves feeding on deer (*Odocoileus*) had 0.5–7.0 (Fritts and Mech, 1981), 2.0 (Fuller, 1989), 2.9 (Kolenosky, 1972), and 2.5 (Mech et al., 1971) kg wolf^{-1} day^{-1} of available food. The lowest calculated availability of food in winter for wolves in this study (2.3 kg wolf^{-1} day^{-1}) was within the ranges reported. Mech (1970, 1977) noted that 1.7 kg wolf^{-1} day^{-1} of consumed prey probably was required for maintenance of wolves in the wild, whereas 3.2 (Mech, 1977) to 4.5 (Nudds, 1978) kg wolf^{-1} day^{-1} may be needed for reproduction. Messier (1987) noted smaller size of packs and more deaths of wolves from malnutrition in areas of low density of moose (0.2 moose km^{-2}), where wolves had 1.7 kg wolf^{-1} day^{-1} of available food. In his study, food availability for wolves in areas of higher density of moose (0.4 moose km^{-2}) was 2.8 kg wolf^{-1} day^{-1}, still below the minimum level in this study. Starvation and other indicators of severe nutritional distress have been noted only on Isle Royale, an area of high density of moose (1.9 moose km^{-2}), when food availability has fallen below 4 kg wolf^{-1} day^{-1} (Peterson and Page, 1988).

Predation rate, indicated by kill interval (1971–1991, range 2.5–43.0 days kill^{-1} pack^{-1}), was related to size of packs, and was similar to other studies. Kill intervals

(days kill^{-1}) where moose were the main prey were 4.9–10.8 (Ballard et al., 1987), 3.2–14.3 (Peterson et al., 1984), 4.5–12.5 (Fuller and Keith, 1980) and 10.4–45.0 (Messier and Crête, 1985) with generally (but not always) higher intervals for small groups. Although large packs apparently can exist only with a short kill interval (high kill rate), small packs in this study also attained high kill rates. Proportionately higher kill rates for small groups may exist because of more loss to scavengers, whereas larger groups use more of a kill before there is loss to scavengers. Also, kill rates may not reflect size of packs because of the predominant influence of alpha wolves, which probably eat more than do subordinate wolves.

Our understanding of summer food economy of wolves on Isle Royale came only from analyses of their feces. Adult moose provided the greatest biomass of summer food for wolves on Isle Royale, as also reported in Alberta (Fuller and Keith, 1980) and Alaska (Peterson et al., 1984). Beavers were nearly as important as young-of-the-year moose in terms of percent biomass utilized, yet annual variation in these three dietary components remains unexplained by density of moose, abundance of young-of-the-year, or number of beaver colonies. These data, however, suggest an inverse relationship between adult and young-of-the-year moose in diet of wolves, while beavers remained secondary.

Information on feeding strategies used by lone wolves and pairs is scarce. It has been assumed that they exist by scavenging and preying upon beavers opportunistically (Jordan et al., 1967; Mech, 1966; Nudds, 1978). Although pairs of wolves have been shown to kill moose in other areas (Ballard et al., 1987; Mech, 1970; Peterson et al., 1984), documentation of lone wolves killing moose is rare (Cowan, 1947); however, lone wolves in our study were capable predators of moose.

Wolves and other social carnivores are thought to exist in large groups primarily to take large prey (Bekoff and Wells, 1980;

Nudds, 1978; Pulliam and Caraco, 1978; Zimen, 1976). If small groups and individual wolves can regularly kill moose, other reasons must exist for group living. Caraco and Wolf (1975) hypothesized that group size would be optimized in response to environmental variables that maximized individual fitness, but these were still related to foraging success. Packard et al. (1983) theorized that juveniles remained in packs to maximize individual fitness by delaying reproduction until they could either take over an alpha position in their natal pack or form their own pack with a different territory when resources permitted. Others have demonstrated that group sizes of predators were not optimal for maximizing food intake (Packer and Ruttan, 1988; Packer et al., 1990), although larger groups tend to decrease variance of food intake (Packer, 1986; this study) and there may be gains in inclusive fitness by allowing relatives to join the group (Packer and Ruttan, 1988; Rodman, 1981). Packer et al. (1990) suggested that grouping behavior among female lions (*Panthera leo*) evolved to facilitate protection of young and territory maintenance, another aspect of inclusive fitness.

The ability to prey upon moose and alter feeding patterns opportunistically allows lone wolves to survive until mates and territories can be acquired. On Isle Royale, the existence of several small groups instead of one or two large groups when the density of wolves was low suggests that wolves were attempting to maximize food intake and immediate reproductive possibilities, rather than future reproductive potential.

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