Dispersal of wolves (*Canis lupus*) in northeastern Minnesota, 1969–1989

ERIC M. GESE[1]

Department of Fisheries and Wildlife, University of Minnesota, St. Paul, MN 55108, U.S.A.

AND

L. DAVID MECH[2]

U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, MD 20708, U.S.A.

Received February 1, 1991

GESE, E. M., and MECH, L. D. 1991. Dispersal of wolves (*Canis lupus*) in northeastern Minnesota, 1969–1989. Can. J. Zool. **69**: 2946–2955.

We examined the dispersal patterns of radio-collared wolves (*Canis lupus*) from 21 packs in the Superior National Forest, Minnesota, from 1969 to 1989. A total of 316 wolves (542 wolf-years) were captured, radio-collared, and followed during 21 years of radio-tracking; 75 were identified as dispersers. Both sexes dispersed equally. Of the adults, yearlings, and pups, 8, 75, and 16%, respectively, dispersed. Most dispersers left when they were 11–12 months old, only a few wolves dispersing as adults. Dispersal occurred mainly in February–April and October–November. Adults dispersed short distances into nearby territories, but yearlings and pups dispersed both short and long distances. Yearling and pup dispersal rates were highest when the wolf population was increasing or decreasing and low when the population was stable. Adults had the highest pairing and denning success, yearlings had moderate pairing and low denning success, and pups had low pairing and denning success. Yearlings and pups that dispersed a short distance had a higher success of settling in a new territory, likely reflecting available vacancies in nearby territories. Thirty-five percent of the known-age wolves remained in their natal territory for >2 years; two wolves were known to have remained for >7 years. The relative weight of pups at capture apparently did not affect their age or success of dispersal or the tendency to disperse.

GESE, E. M., et MECH, L. D. 1991. Dispersal of wolves (*Canis lupus*) in northeastern Minnesota, 1969–1989. Can. J. Zool. **69** : 2946–2955.

Nous avons examiné les routes de dispersion de Loups gris (*Canis lupus*) munis d'émetteurs-radio au sein de 21 meutes de la forêt nationale Superior, au Minnesota, de 1969 à 1989. Au total, 316 loups (542 loups-années) ont été capturés, munis d'un émetteur et suivis durant 21 ans par radio; 75 ont été identifiés comme des disperseurs, des mâles autant que des femelles. Huit pourcent des adultes, 75% des jeunes de 1 an et 16% des louveteaux se sont dispersés. La plupart des loups quittaient la meute à l'âge de 11–12 mois pour se disperser et quelques-uns le faisaient à l'âge adulte. C'est surtout en février–avril et en octobre–novembre que se faisait la dispersion. Les adultes parcouraient des courtes distances pour se rendre dans des territoires voisins, alors que les loups plus jeunes et les louveteaux parcouraient de courtes ou de longues distances. Les taux de dispersion des jeunes et des petits étaient plus élevés lorsque la population augmentait ou déclinait et ils étaient faibles lorsque la population était stable. C'est chez les adultes qu'on enregistrait le plus haut taux de succès des accouplements et des élevages, alors que les jeunes de 1 an avaient un taux moyen de succès à l'accouplement et peu de succès à l'élevage et ces taux étaient tous deux faibles chez les louveteaux. Les jeunes de l'année et les louveteaux qui parcouraient de courtes distances avaient plus de chance de se trouver un nouveau territoire, ce qui reflète probablement la disponibilité d'endroits libres dans les territoires avoisinants. Trente-cinq pourcent des loups d'âge connu sont restés dans leur territoire d'origine pour plus de 2 ans; deux loups y sont restés plus de 7 ans. L'âge au moment de la dispersion, le succès de la dispersion ou la tendance à partir ne semblent pas reliés à la masse relative des louveteaux au moment de la capture.

[Traduit par la rédaction]

Introduction

Dispersal, or natal dispersal (Greenwood 1980; Shields 1987), has been defined as the movement of an animal from its point of origin to where it reproduces or would have reproduced if it had survived and found a mate (Howard 1960). Breeding dispersal is the movement of an adult between consecutive breeding sites or groups (Greenwood et al. 1979; Shields 1982). Dispersal plays a major role in genetic structure, regulation, spatial distribution, size, longevity, composition, and social organization of many animal populations (Hamilton 1972; Lidicker 1975; Taylor and Taylor 1977). Various evolutionary hypotheses, including inbreeding avoidance, mate competition, and resource competition, have been proposed as ultimate explanations for dispersal patterns in mammals (Greenwood 1980; Moore and Ali 1984; Waser 1985). Proximate causes of dispersal include physiological changes (Burt 1949; Blair 1953; Holekamp 1984), aggression from conspecifics (Wynne-Edwards 1962; Christian 1970), increased social pressure or limited food associated with increased density (Snyder 1961; Van Vleck 1968; Christian 1971), lack of breeding opportunities, and ectoparasite load.

Much has been published about wolf dispersal (e.g., Van Ballenberghe 1983; Messier 1985*a*; Ballard et al. 1987; Mech 1987; Fuller 1989), yet most of the information is anecdotal or based on small samples. To adequately assess wolf dispersal and its role in wolf colonization, population maintenance, and biology, long-term information in necessary. Mech (1987) examined the dispersal patterns of 18 offspring of the Perch Lake pack in northeastern Minnesota from 1973 through 1984, but that assessment involved only one pack of wolves. This paper examines the dispersal patterns of radio-collared wolves from 21 packs in northeastern Minnesota from 1969 to 1989.

Study area

The study was conducted in the Superior National Forest (SNF) in St. Louis, Lake, and Cook counties of northeastern Minnesota (latitude 48°N, longitude 92°W). The climate is cool temperate, with snow cover

---

[1]Present address: Department of Wildlife Ecology, University of Wisconsin, Madison, WI 53706, U.S.A.

[2]Mailing address: U.S. Fish and Wildlife Service, North Central Forest Experiment Station, 1992 Folwell Avenue, St. Paul, MN 55108, U.S.A.

averaging >1 m during 5 months of winter beginning in mid-November. The area is relatively flat, with many rocky ridges, hills, swamps, lakes, and rivers. Altitude ranges from 325 to 700 m. The vegetation is mixed coniferous and deciduous forests. Dominant conifers include jack pine (*Pinus banksiana*), white pine (*Pinus strobus*), red pine (*Pinus resinosa*), black spruce (*Picea mariana*), and balsam fir (*Abies balsamea*). White birch (*Betula papyrifera*) and aspen (*Populus tremuloides*) dominate the deciduous component of the forest (Ohmann and Ream 1969; Nelson and Mech 1981).

The wolf population in the SNF has been studied since 1966 (Mech 1977*a*, 1979). The wolf population began declining about 1970 (Mech 1986) because of a decline in numbers of white-tailed deer (*Odocoileus virginianus*) beginning in 1968 (Mech 1977*a*, 1977*b*; Mech and Karns 1977; Nelson and Mech 1986), but it appears to be recovering and slowly increasing as the deer population increases. Wolf hunting and trapping in the study area has been illegal since 1970. Illegal killing of wolves still occurs, usually during hunting and trapping seasons in fall and winter. Several of the radio-collared wolves were legally harvested in adjacent Canada.

Methods

Wolves were captured in the SNF with steel leg-hold traps (Mech 1974; Kuehn et al. 1986). Animals were immobilized via a syringe and drugs on the end of a jabstick. Drugs were injected as needed to maintain immobilization. We aged, weighed, sexed, and blood sampled each wolf, assessed its general physical condition, and radio-collared it. Age was estimated by tooth replacement (Van Ballenberghe and Mech 1975), incisor wear, first-molar wear, and testis or teat size. Based on known-age wolves (19 males, 13 females) captured as pups, then recaptured as yearlings or adults, wolves were divided into three age categories: pup (<12 months old), yearling (12–24 months old), and adult (>24 months old). Wolf pups were identified by small size, light weight, and the presence of deciduous (i.e., milk) teeth (Van Ballenberghe and Mech 1975). Yearling females were identified as having inconspicuous teats, yearling males had testes <2.5 cm long, and both sexes had permanent teeth showing little or no wear (Van Ballenberghe et al. 1975). Adult females had either inconspicuous or conspicuous teats, adult males had testes >3.8 cm long, and the teeth of adults generally exhibited moderate to heavy wear. If teat or testis size was ambiguous, then tooth wear was used to estimate age. Yearlings may have been mistakenly aged as adults, but would have been young, nonreproductive adults. The age of the wolf was updated as it grew older.

We attempted to recapture wolves to replace their radio collar as frequently as necessary to maintain contact with the animal. However, recapture success was low owing to the wariness of trap-experienced animals (Mech 1987). Each wolf was monitored via radiotelemetry (Mech 1983) to determine dispersal time, direction, and distance. Wolves were aerially located every 3–5 days. Wolves were followed until they settled in a new territory or moved too far from the study area, or their signal was lost. Information from some dispersers was obtained by returns of collars from hunters and trappers.

We identified known dispersers as wolves for which the natal or breeding territory was known and the dispersal movement (time, direction, and distance) was well documented, or their radio signals disappeared while they were still in the territory but the animal was recovered from outside the territory. We distinguished between natal (i.e., the animal was caught in its known natal territory) and breeding dispersal (i.e., the animal was captured as an adult, but it was not known whether it was captured in its natal territory). Breeding dispersal was emigration from a territory that may not have been the animal's natal territory; such dispersal could have been secondary to an earlier natal dispersal.

The distance traveled was estimated by measuring the distance between the last location in the known territory and the first location in the newly established territory or the place where the animal was killed. The number of territories crossed during dispersal (i.e., effective dispersal, Shields 1987) was either counted from known territory boundaries or, in the case of long-range dispersers, we used a distance of 15 km to represent the diameter of a territory traversed by an animal, assuming a mean 170-km^2 territory size (Mech and Fenzel 1971; Mech 1974; Van Ballenberghe et al. 1975). The initial and final directions in which a wolf dispersed were classified into four directional quadrants: northeast (1–90°), southeast (91–180°), southwest (181–270°), and northwest (271–360°).

Reproduction is considered one of the ultimate objectives of an animal's dispersal (Howard 1960; Lidicker 1975; Endler 1979). We measured dispersal success in three different stages leading towards reproduction: settling, pairing, and denning. A wolf was considered settled if it was accepted into a different territory or established a new territory. A wolf was considered paired if consistently observed with another wolf. Denning was indicated by sighting of the den, usually from the air, and a high frequency of telemetry locations near the den. We used only known-fate animals in our analysis, and did not include wolves with which we lost radio contact. Wolves that were killed were considered unsuccessful.

Holekamp (1984, 1986) reported that body weight played a major role in determining when young male ground squirrels (*Spermophilus beldingi*) dispersed. Using the relative weights of pups (Van Ballenberghe and Mech 1975; Harrington et al. 1983), we examined the relationship between wolf weight and the age of dispersal. The use of relative weights allowed for standardization of pups captured at different times of the year and pooling of the sexes. We calculated the relative weight of the dispersers by dividing their capture weight by the average weight of other pups captured during the same 2-week period. We hypothesized that the weight of the disperser would influence the time the animal dispersed, as was found by Holekamp (1984, 1986) and Holekamp and Sherman (1989).

Pups captured in their natal territory were used in our analysis of predispersal forays because we could document the forays from an early age; yearlings and adults may have made forays prior to capture. The number of forays documented is a minimum estimate because animals were usually located every 3–5 days, so shorter forays may have been undetected. Our sample included those wolves reported by Mech (1987).

Results and discussion

A total of 316 wolves were captured and fitted with radio collars between 1969 and 1989. Many wolves had operating transmitters for >1 year and were carried over as available dispersers to subsequent years. Thus, the 316 radio-collared wolves were followed for 542 wolf-years, representing 358 adult-, 63 yearling-, and 121 pup-years. Pups and yearlings were shifted into subsequent age-classes as they grew older. The sex ratio (162 males, 154 females) was not significantly different from parity ($\chi^2 = 0.20$, 1 df, $P > 0.50$).

Sex and age of dispersers

Of the 316 radio-collared wolves, 75 were classified as dispersers. Forty-eight (64%) of the dispersers were animals of known age, 21 (28%) were believed to be aged accurately according to our aging criteria, and 6 (8%) were aged as adults but could have been yearlings (i.e., their age was not discernible).

The dispersers consisted of 39 males and 36 females ($\chi^2 = 0.12$, 1 df, $P > 0.50$), of which 24% were adults ($n = 18$), 53% yearlings ($n = 40$), and 23% pups ($n = 17$). Of the 542 wolf-years accumulated during the study, 5% represented dispersal as an adult, 63% as a yearling, and 14% as a pup ($\chi^2 = 153.91$, 2 df, $P < 0.005$). Of the adult dispersers, 12 were males and 6 were females ($\chi^2 = 2.00$, 1 df, $P > 0.10$); of yearling dispersers, 21 were males and 19 were females ($\chi^2 = 0.10$, 1 df, $P > 0.50$); and of dispersing pups, 6 were males and 11 were females ($\chi^2 = 1.47$, 1 df, $P > 0.10$).

Most dispersing wolves left their natal territory as pups or yearlings (Fig. 1). Many wolves left at 11–12 months old, with another peak at 17–19 months old. Some animals delayed

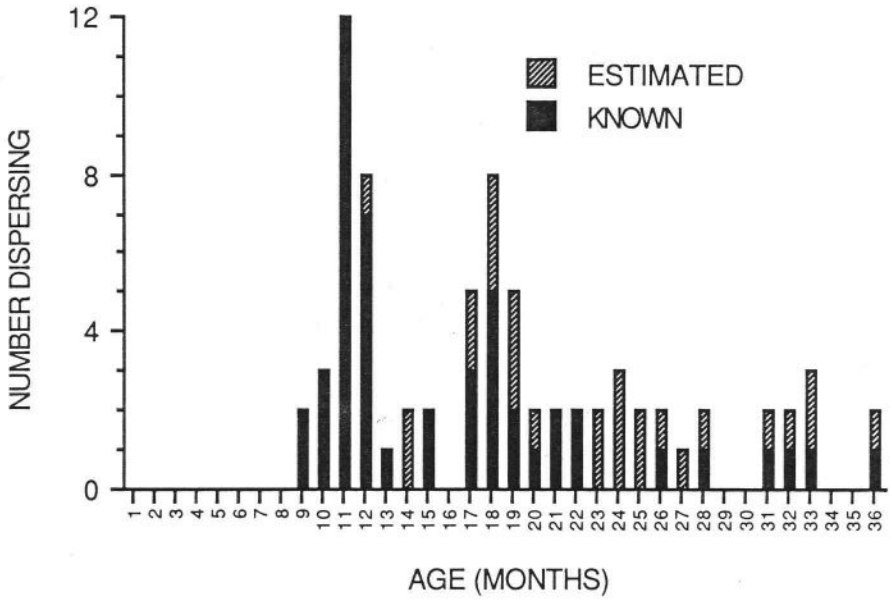

FIG. 1. Age at dispersal for 48 known-age and 27 estimated-age wolves, Superior National Forest, Minnesota, 1969–1989.

dispersing until they were adults. One known-age wolf did not disperse from its natal territory until it was 54 months old. All the known-age and 20 of the estimated-age dispersers left their known natal territory. Only seven (all adults) of the dispersers may have been making a breeding dispersal, which may represent a dispersal move for the second time following a prior natal dispersal.

Many studies have documented the dispersal of wolves. Ballard et al. (1987) reported that 38 (28%) of 135 wolves dispersed from their original area; 74% of the dispersers were males and 40% were females, and 50% of the male dispersers were ≤24 months old. Peterson et al. (1984) found 21 of 64 radio-collared wolves dispersed form their original packs, no sex-biased dispersal rate, and yearlings and 2-year olds comprising 11 of 21 dispersers. Fritts and Mech (1981) reported only 8 of 39 wolves dispersed in northwestern Minnesota; 7 of these 8 were < 24 months old. In neither Fuller's (1989) nor our study were sex-biased dispersal rates found in Minnesota wolves.

The common trend in wolf dispersal is a preponderance of young wolves. Wolves can become sexually mature as early as 10 months of age (Medjo and Mech 1976). In captive wolves, Zimen (1976) noted young, low-ranking individuals exhibiting dispersal tendencies, apparently in response to aggression from conspecifics; adults may view these young wolves as competing for mating privileges. This increased aggression during the breeding season may be triggered by secretion of reproductive hormones (Seal et al. 1979).

Low prey numbers may also cause young, subordinate wolves to be evicted from their pack, or voluntarily leave it (Zimen 1976, 1982). Messier (1985*a*) and Ballard et al. (1987) documented a higher rate of yearling dispersal in an area of low prey density than in an area of high prey density. On Isle Royale, dispersal of wolves increased when the prey base declined (Peterson and Page 1988).

Time of dispersal

Dispersal frequency varied throughout the year. Most wolves dispersed from February through April and October through November. Males and females both followed this trend, but female dispersal peaked in April, and male dispersal in October

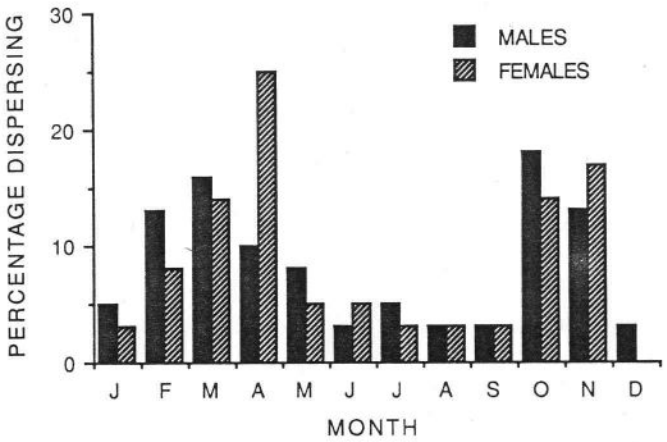

FIG. 2. Month of dispersal for 39 male and 36 female wolves, Superior National Forest, Minnesota, 1969–1989.

(Fig. 2). Adult dispersal peaked in February and October, yearling dispersal peaked in April and October–November, and pup dispersal peaked from February to April (Fig. 3).

In Alaska, Ballard et al. (1987) reported wolves dispersing primarily from April through June and in October and November. Fuller (1989) reported most pups dispersing during January through March, and older wolves left during September through April. Most other studies (Fritts and Mech 1981; Mech and Hertel 1983; Peterson et al. 1984) have documented wolf dispersal occurring usually during the breeding season, when aggression is high (Zimen 1976), or prior to denning. Studies of captive wolves showed that reproducing adults showed greater aggression towards and exerted greater dominance over pack members during the breeding season (Rabb et al. 1967; Zimen 1976; Packard et al. 1983).

The annual percentage of wolves dispersing varied over time (Fig. 4). Dispersal increased from 1970 to 1974, then declined until 1981. Two subsequent dispersal peaks occurred in 1984 and 1988. Dispersal was estimated by dividing the number of dispersers in a given year by the total number of wolves with operating radio collars in that year. The estimates were therefore

TABLE 1. Interaction between different phases of wolf population change and wolf dispersal patterns, Superior National Forest, Minnesota, 1969–1989

	Population trend	Age-class	No. of wolves available	Wolves dispersing	
				No.	%
1969–1970 to 1974–1975	Decline	Adult	76	5	7
		Yearling	10	7	70
		Pup	32	6	19
1975–1976 to 1984–1985	Stable	Adult	193	10	5
		Yearling	30	14	47
		Pup	66	3	4
1985–1986 to 1988–1989	Increase	Adult	89	3	3
		Yearling	23	19	83
		Pup	23	8	35

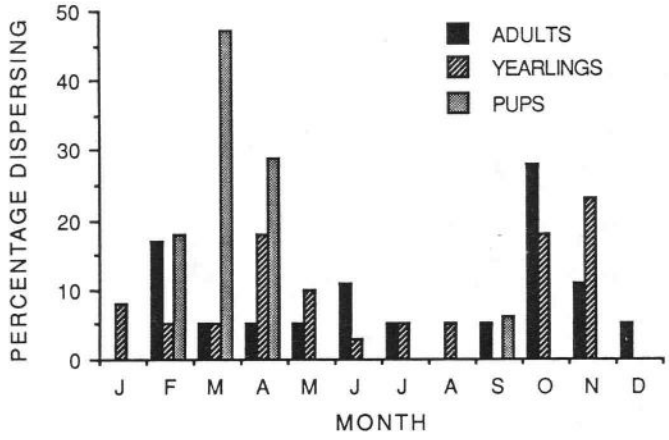

FIG. 3. Month of dispersal for three age-classes of dispersing wolves, Superior National Forest, Minnesota, 1969–1989.

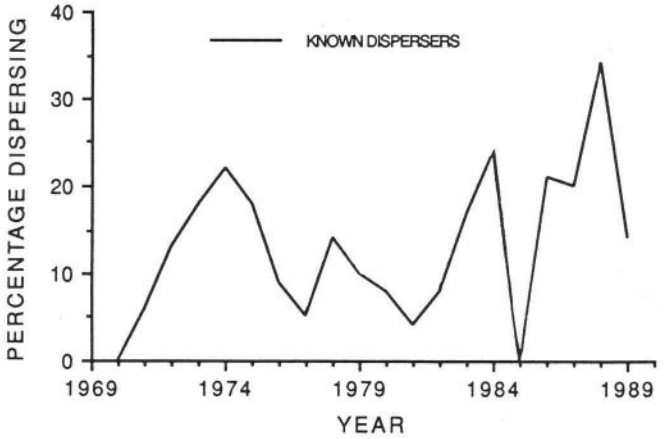

FIG. 4. General trend in annual wolf dispersal, Superior National Forest, Minnesota, 1969–1989.

influenced by the high variation in numbers of radio-collared yearlings available for dispersal, but probably reflect general trends in dispersal, if not absolute rates.

Wolf population trends in the study area seemed to affect the amount of dispersal by radio-collared wolves. From 1969–1970 through 1974–1975 the wolf population declined steeply (Mech 1986), from 1975–1976 through 1984–1985 the rate of decline lessened and the population stabilized at a low level, and from 1985–1986 through 1988–1989 it was low but increasing (L. D. Mech, unpublished data). During the steep decline, yearling dispersal was 70% and pup dispersal 19% (Table 1). While the wolf population was stable, there was 47% yearling and 4% pup dispersal. During the recent population increase, yearling dispersal was 83%, and pup dispersal 35%. Dispersal of adults was unrelated to the changes in the wolf population level ($\chi^2 = 0.94$, 2 df, $P > 0.50$). Both yearlings and pups dispersed at a higher frequency during the population decline and increase than during the more stable population phase (yearlings: $\chi^2 = 7.42$, 2 df, $P < 0.025$; pups: $\chi^2 = 13.91$, 2 df, $P < 0.005$).

The high level of yearling dispersal during the wolf population decline was likely due to the declining deer population. A declining prey base often results in a higher rate of dispersal (Messier 1985*a*; Ballard et al. 1987; Peterson and Page 1988), and may be evidence of dispersal due to resource competition. When the deer population stabilized, dispersal of yearlings and pups declined from higher levels. Food abundance and wolf density may have been balanced, hence more offspring could remain. During the recent wolf population increase, prey were more abundant, and yearling and pup dispersal increased. Fritts and Mech (1981) also documented increased dispersal and success at pairing in an expanding wolf population with an ample prey base. Resource competition may have declined with increasing prey numbers, but there was still competition for mates, favoring dispersal to find a mate.

Distance and direction of dispersal

Wolves traveled 8–354 km after leaving their territories. The longest movement was by a yearling male in 1987. The mean minimum distance traveled by all dispersers was 77 km (median 35 km). The mean minimum distance traveled was 88 km (median 49 km) by male dispersers and 65 km (median 37 km) by females dispersers ($T = 1.10$, $P > 0.25$). Mean minimum distance traveled by adults, yearlings, and pups was 36 (median 19 km), 87 (median 38 km), and 95 km (median 66 km), respectively ($F = 0.95$; 2,70 df, $P > 0.25$).

The distribution of minimum distance traveled by wolves in the three age-classes showed that adults of both sexes usually dispersed <50 km from their territories (Fig. 5). Yearling males dispersed over both short (<50 km) and long (>200 km) distances, whereas yearling females predominantly dispersed over short distances. Pups of both sexes dispersed mainly over short to moderate distances, with a few long-distance dispersals (Fig. 5). The distribution of distances traveled was signifi-

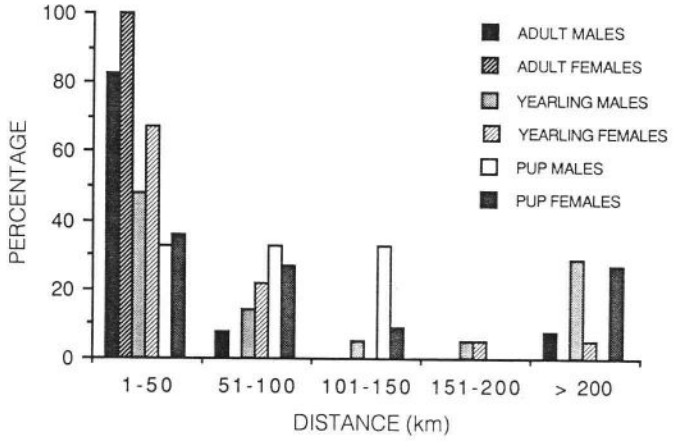

FIG. 5. Distance traveled by dispersing wolves in three age-classes, Superior National Forest, Minnesota, 1969–1989.

TABLE 2. Percentages of wolves of three age-classes dispersing over different numbers of territories away from the home territory, Superior National Forest, Minnesota, 1969–1989

No. of territories crossed	% of age-class		
	Adult	Yearling	Pup
1–3	89	69	47
4–6	5	5	29
7–9	0	3	6
≥10	5	25	18

cantly different among the three age-classes ($\chi^2 = 16.98$, 8 df, $P < 0.05$).

The distribution of the number of territories through which the dispersing wolves traveled, like the distance traveled, was related to age (Table 2) ($\chi^2 = 12.70$, 2 df, $P < 0.05$). In most cases, adults traveled to an adjacent or nearby territory (Table 2). Many yearlings and most pups dispersed to either nearby territories or very distant territories.

In some studies a sex-biased dispersal distance has been found in wolves. Males predominate in long-range dispersal distances reported in the literature (Van Camp and Gluckie 1979; Ballard et al. 1983; Fritts 1983). Peterson et al. (1984) found females to disperse over shorter distances than males. In contrast, Ballard et al. (1987) reported females dispersed farther than males. In Fuller's (1989), Mech's (1987), and this study, no difference in dispersal distance was found between males and females. In northwestern Minnesota, wolves were able to quickly find a vacant area a short distance from the natal area because of the low density and expanding population of wolves (Fritts and Mech 1981), whereas, Messier (1985*a*) documented wolves traveling great distances before they found a vacancy because of saturated wolf habitat.

Dispersers initially moved to the southwest 31% of the time, the northeast 27%, the northwest 25%, and the southeast 16% ($\chi^2 = 3.14$, 1 df, $P > 0.05$). Adults and yearlings dispersed in all directions equally ($\chi^2 = 2.88$, 1 df, $P > 0.05$ for adults; $\chi^2 = 0.99$, 1 df, $P > 0.25$ for yearlings), whereas pups dispersed mainly to the southwest ($\chi^2 = 5.42$, 1 df, $P < 0.025$). Males of all ages initially dispersed all directions equally ($\chi^2 = 1.55$, 1 df, $P > 0.10$), whereas females tended to avoid the southeast (10%) ($\chi^2 = 4.48$, 1 df, $P < 0.05$).

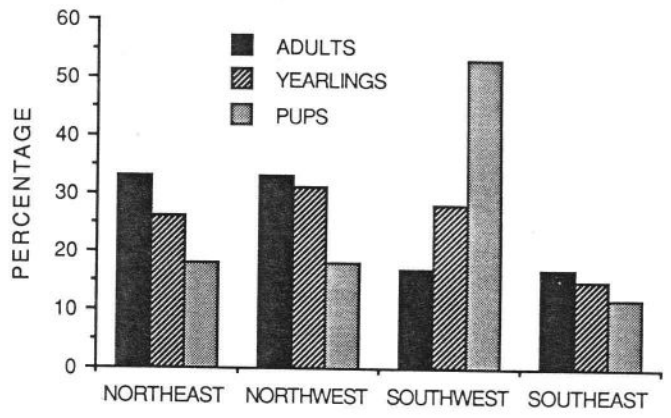

FIG. 6. The final direction, with respect to natal territory, in which dispersing wolves in three age-classes settled, Superior National Forest, Minnesota, 1969–1989.

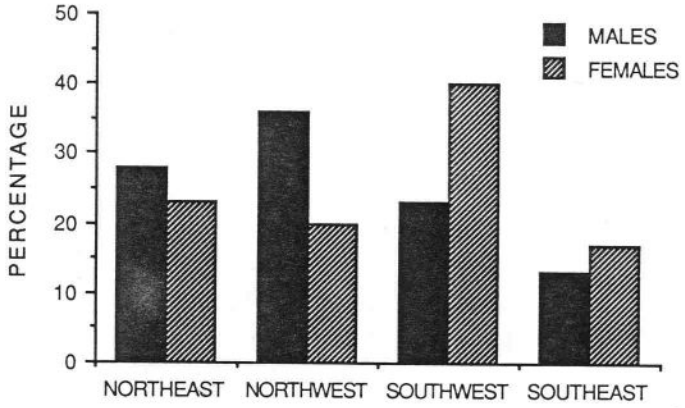

FIG. 7. The final direction, with respect to natal territory, in which dispersing male and female wolves settled, Superior National Forest, Minnesota, 1969–1989.

The final direction at which a wolf completed its dispersal move and settled in a new territory, or was killed, was the southwest 31% of the time, the northwest 28%, the northeast 26%, and the southeast 15% ($\chi^2 = 2.90$, 1 df, $P > 0.05$). Adult and yearling dispersers settled in all directions equally (adults: $\chi^2 = 2.00$, 1 df, $P > 0.10$; yearlings: $\chi^2 = 2.13$, 1 df, $P > 0.10$), whereas most pups settled primarily to the southwest ($\chi^2 = 7.24$, 1 df, $P < 0.01$) (Fig. 6). Males of all ages settled mostly to the north and tended to avoid the southeast ($\chi^2 = 4.38$, 1 df, $P < 0.05$); in contrast, females settled to the southwest but also avoided the southeast ($\chi^2 = 4.42$, 1 df, $P < 0.05$) (Fig. 7). The avoidance of the southeast is likely due to Lake Superior acting as a barrier to dispersal. Any wolf dispersing to the east is forced by the lake to go northeast or southwest along the lakeshore.

Dispersal success

The success of a wolf in finding a vacant territory or becoming accepted into a pack, pairing with a mate, and producing pups will ultimately determine its lifetime reproductive success. We found that the age of the wolf at dispersal affected its success (Table 3). The three age-classes were equally successful at settling in new territories. Adults had a high success is pairing, yearlings moderate success, and pups low success. Adults were more successful at denning after dispersal than yearlings and pups (Table 3).

Adults dispersed mostly over short distances (Fig. 5) and had a high degree of success in settling, pairing, and denning in a new territory (Table 3). We investigated the relationship between

TABLE 3. Percent success of settling, pairing, and denning in a new territory for dispersing wolves of three age-classes , Superior National Forest, Minnesota, 1969–1989

Age at dispersal	Settled		Paired		Denned	
	%	n	%	n	%	n
Adult	83	18	87	15	67	15
Yearling	68	31	61	28	31	26
Pup	67	12	25	8	25	8
χ^2	1.62		8.54		6.15	
P	>0.25		<0.025		<0.05	

distance and settling success by examining the distribution of dispersal distances for successful and unsuccessful dispersers. For adults, sample size of distant dispersers was too small for proper analysis. For yearlings and pups there was a significant relationship between dispersal distance and settling success (Table 4). Many of the yearlings and pups successfully settled a short distance from their natal territory, whereas unsuccessful wolves dispersed farther. Perhaps adults are accepted, or can establish, in a new area within a short distance because of their size, age, experience, and sexual maturity. In contrast, when a yearling or pup disperses, the availability of vacancies in nearby areas will probably determine their success in settling. If there are no vacancies, these young wolves are probably displaced easily because of their youth, inexperience, and sexual immaturity, so they continue to disperse farther. The time required to successfully settle and pair in a new area was similar among all ages, but the degree of success was high for adults, moderate for yearlings, and low for pups.

Dispersal success is dependent upon prey abundance, availability of vacant territories, and survival of mates (Fuller 1989). Fritts and Mech (1981) reported a high degree of success in finding a vacant area and a mate in northwestern Minnesota in an area of abundant prey base and an unsaturated wolf population. They believed that dispersers played a major role in the population increase observed in northwestern Minnesota by creating new packs in areas devoid of existing social units (Fritts and Mech 1981). Peterson et al. (1984) found high dispersal success on the Kenai Peninsula, where prey was abundant. Ballard et al. (1987) documented, in an area with low wolf density and many vacant areas due to human exploitation, that most single wolves eventually became members of other packs, either by pairing with another wolf or being accepted into an existing pack.

Adult and yearling wolves dispersed in all directions, whereas pups favored the southwest. We examined the relationship between the final direction of dispersal and success in settling, pairing, and denning in a new territory for all wolves. We found that for all ages combined, success in settling, pairing, and denning did not differ significantly among the four directional quadrants (Table 5).

We examined the relationship between the changes in the wolf population and success in settling, pairing, and denning. We found no significant relationship between success and population changes for any of the three age-classes (Table 6). Apparently, the population changes affected the dispersal rates of yearlings and pups, but not dispersal success. Our finding that dispersal success was not influenced by population changes conflicts with the apparently high success of pairing and becoming a social unit in an expanding population (Fritts and Mech 1981). However, the SNF wolf population was saturated and no vacant areas existed, whereas in northwestern Minnesota the wolf population was newly protected and vacant territories were available (Fritts and Mech 1981).

Duration of dispersal

The duration of dispersal ranged from 1 week to 12 months. Adult wolves averaged 2.9 ± 4.0 months between dispersing and settling; yearlings and pups averaged 2.0 ± 2.8 and 4.1 ± 3.5 months, respectively. Adult males took significantly longer to settle than adult females (Table 7). Yearlings and pups did not differ between the sexes. The period between dispersing and successfully pairing with another wolf in the new territory ranged from 1 week to 11 months. Adults, yearlings, and pups averaged 3.7 ± 3.9, 2.2 ± 2.5, and 5.1 ± 4.7 months, respectively, between dispersing and pairing. There were no significant differences in the dispersal-to-pairing period between the sexes for any age-class (Table 7). These times are estimated only from wolves that successfully settled and paired.

Fritts and Mech (1981) reported a short interval of time between dispersal and pairing for wolves in northwestern Minnesota and believed that this indicated an abundance of dispersers and an unsaturated wolf population with an abundant prey base. In contrast, in an area of low availability of prey, wolves had to disperse farther and travel for longer in search of vacant areas favorable for reproduction (Messier 1985*a*, 1985*b*).

Natal philopatry versus dispersal

We examined the prevalence of philopatry (Waser and Jones 1983) and dispersal of known-age wolves captured as pups. Of 171 wolf pups captured, 139 were radio-collared. Of these, 74 pups remained whose fate was known for >1 year. During their 1st year, 17 (23%) pups dispersed. During their 2nd year, 25 dispersed, bringing the total to 42 (57%) wolves dispersing within 2 years. Four wolves dispersed at 28–32 months old, and two more left when they were over 41 months old, bringing the total of dispersers to 48 (65%) of the original 74 animals whose fate was known. The remaining 26 wolves remained in their natal territories for >2 years. Many of those that stayed were killed, or last located, in their natal territory before their radios failed at 2–3 years. Seven wolves with functioning transmitters remained in their natal territory after 3 years; two wolves remained for >7 years.

Assistance of yearlings and other pack members does not necessarily influence the survival of pups (Harrington and Mech 1982; Harrington et al. 1983; Peterson et al. 1984). It is likely that pups which remain are "biders" (Packard and Mech 1983), having the eventual "goal" of reproducing in the pack. Philopatric wolves gain the advantage of acquiring a territory and mate, as well as increased survival, by remaining in a familiar territory (Packard and Mech 1983; Peterson et al. 1984; Messier 1985*a*).

Effect of weight on dispersal

We examined the relationship between weight and age at dispersal using the relative weight of pups (Van Ballenberghe and Mech 1975; Harrington et al. 1983), which made comparisons valid; we found no significant relationship ($R^2 = 0.008$, $F = 0.31$, $P = 0.58$). We were only able to capture pups from August through November, hence we could not monitor their weights immediately before dispersal. Furthermore, because pups are growing throughout the capture period, we could not directly compare the weights of individuals caught at different ages.

We also found no relationship between the relative weight of

TABLE 4. Relationship between distance dispersed from the natal territory and the success of a wolf settling in a new territory, Superior National Forest, Minnesota, 1969–1989

Distance dispersed (km)	No. of adults		No. of yearlings and pups	
	Successful	Unsuccessful	Successful	Unsuccessful
1–50	13	3	21	3
51–100	1	0	3	4
101–150	0	0	0	3
151–200	0	0	0	1
>200	1	0	4	3
χ^2	0.64		15.19	
P	>0.95		<0.005	

TABLE 5. Percent success in settling, pairing, and denning for wolves dispersing in four final directions, Superior National Forest, Minnesota, 1969–1989

	% settled	% paired	% denned
Northeast	64	61	45
Southeast	82	80	33
Southwest	72	50	25
Northwest	71	69	61
χ^2	0.90	2.65	4.26
P	>0.75	>0.25	>0.10

TABLE 6. Percent success in settling, pairing, and denning for wolves of three age-classes during three phases of population change, Superior National Forest, Minnesota, 1969–1989

Age-class	Population trend	% settled	% paired	% denned
Adult	Decline	80	80	60
	Stable	90	89	62
	Increase	67	100	100
	χ^2	1.01	0.67	1.69
	P	>0.50	>0.50	>0.25
Yearling	Decline	60	60	40
	Stable	60	56	25
	Increase	73	64	29
	χ^2	0.65	0.18	0.34
	P	>0.50	>0.90	>0.75
Pup	Decline	100	0	0
	Stable	83	50	50
	Increase	25	25	25
	χ^2	5.12	1.34	1.34
	P	>0.05	>0.50	>0.50

the disperser and its dispersal success. We divided relative weights into three classes, light (<85% relative weight), average (85–115% relative weight), and heavy (>115% relative weight), and examined the interaction between weight class and success of settling, pairing, and denning. There was no significant interaction between relative weight class and successful settling ($\chi^2 = 1.67$, 2 df, $P > 0.25$), successful pairing ($\chi^2 = 1.69$, 2 df, $P > 0.25$), or successful denning ($\chi^2 = 1.79$, 2 df, $P > 0.25$).

The above analyses examined only the dispersing cohort, so we also investigated the interaction between relative weight class and the tendency for a pup to disperse. We found that 64% of philopatric pups were of relatively average weight and 32% were heavy, whereas 23% of dispersing pups were light, 44% were average, and 33% were heavy ($\chi^2 = 4.76$, 2 df, $P = 0.09$). Perhaps young, lighter pups are the low-ranking individuals in the pack (Knight 1978) and receive most of the aggression from larger litter mates; thus, they do not maintain their weight because of low food consumption so they disperse from the pack.

TABLE 7. Number of months between dispersing, settling, and pairing for radioed wolves of three age-classes, Superior National Forest, Minnesota, 1969–1989

		Settled			Paired		
Age-class	Sex	Mean	SD	n	Mean	SD	n
Adult	M	4.4*	4.7	9	4.9	4.5	9
	F	0.8	1.1	6	2.1	2.4	6
Yearling	M	3.0	4.1	7	3.5	3.7	6
	F	1.2	0.9	9	1.9	1.0	8
Pup	M	4.2	2.5	3	4.0	—	1
	F	4.1	4.0	7	5.4	5.3	4

*Significantly different from females in the same age-class; Student's t-test, $P < 0.05$.

Predispersal forays

Forays outside the natal territory prior to dispersal were common for many dispersers. The number of forays ranged from 0 to 5, with a mean of 0.97 forays per dispersing wolf. Forty-seven percent of the dispersers made no forays, 31% made 1 trip, 11% made 2 trips, and 11% made ≥3 trips outside the territory prior to dispersal. Philopatric pups made an average of 0.81 forays each (range 0–5 trips). Fifty-nine percent of the philopatric pups made no trips, 22% made 1 trip, 7% made 2 trips, and 11% made ≥3 trips during their 1–2 year tenure in their natal territory prior to radio failure or death. The numbers of forays made by dispersers and philopatric wolves were not significantly different ($\chi^2 = 1.10$, 3 df, $P > 0.75$).

The duration of extraterritorial forays ranged from 2 to 40 days. Forays by dispersers and philopatric pups lasted an average of 14 days (range 2–40 days) and 13 days (range 2–27 days), respectively ($T = 0.64$, $P > 0.50$). Forays by dispersers were <1 week (32%), 1–2 weeks (26%), 2–3 weeks (19%), or >3 weeks (23%) in length. Forays by philopatric pups were <1 week (28%), 1–2 weeks (22%), 2–3 weeks (39%), or >3 weeks (11%) in length, not significantly different from those of dispersers ($\chi^2 = 2.54$, 3 df, $P > 0.25$).

The distance traveled during extraterritorial forays averaged

25 km (range 8–71 km) and 21 km (range 10–40 km) for dispersers and philopatric pups, respectively ($T = 0.97$, $P > 0.20$). During a predispersal foray, dispersers and philopatric pups usually favored the southwest (39%) or northwest (29%) and avoided the southeast (14%) and northwest (18%) ($\chi^2 = 8.57$, 1 df, $P < 0.005$). The direction of the foray did not differ between dispersers and philopatric pups ($\chi^2 = 3.03$, 3 df, $P > 0.25$).

Predispersal forays by wolves are well known (Fritts and Mech 1981; Van Ballenberghe 1983; Messier 1985*a*; Fuller 1989). Dispersing wolves show a variety of movement patterns prior to and after leaving the natal territory. In some cases, dispersal appeared to be gradual, with many previous extraterritorial movements, whereas in other cases, yearling wolves left quickly (Fritts and Mech 1981; Van Ballenberghe 1983; Mech 1987). Fritts and Mech (1981) documented that most young wolves dispersed early, formed new social units, and experienced a high probability of reproductive success in a low-density, newly protected population that was expanding. In Alaska, Van Ballenberghe (1983) found that some wolves returned to their territory following a predispersal foray, probably because of the low probability of encountering favorable conditions in a largely saturated population.

Sibling dispersal patterns

We investigated sibling dispersal in relation to dispersal time, distance, and direction. The 48 known-age dispersers came from 19 packs. Of these packs, we had only six pairs and one trio of littermates that dispersed; none of these pups dispersed together. Two pairs left their natal territory during the same month, but dispersed in opposite directions. Most pups dispersed 5–6 months apart. Two pups in the trio dispersed the same direction, but 1 month apart, and were 72 km apart when their dispersal move was completed. Two pairs of pups dispersed approximately the same distance from their natal territory, but in different directions and 5 months apart.

We also examined the time, distance, and direction of dispersal of pups born in the same pack in consecutive years. The Perch Lake pack (Mech 1987) showed a high degree of variation in its general dispersal patterns, utilizing various strategies in response to environmental opportunities. Other packs ($n = 5$) showed similar variation among siblings in consecutive years, dispersing in different directions and distances at different ages. Of 14 litters born a year apart, in only one case did two siblings (both male) from different years disperse in the same direction and for the same distance, and eventually associate with one another in the same new pack and territory.

The apparent lack of influence of parental dispersal on offspring dispersal is illustrated by one case in which an adult male dispersed at 41 months of age a distance of 14 km to the southeast. His offspring also dispersed short distances (19 and 11 km), but in different directions (southwest and northwest) and at different ages (15 and 20 months). Thus, it appears that wolves have great variation in their dispersal patterns, and genetically related individuals display different dispersal characteristics (Mech 1987). Plasticity in dispersal strategies would be advantageous in allowing for adjustment to environmental opportunities. Parents with offspring that can disperse for short distances into adjacent territories or for long distances to alien packs will greatly facilitate the survival and propagation of their valuable offspring (i.e., genes).

Ultimate theories proposed to account for wolf dispersal include resource competition, mate competition, and inbreeding avoidance. The role each of these factors plays in wolf dispersal is only speculative and requires further examination and testing. There is some evidence that resource competition might play a role in wolf dispersal. In southwestern Quebec, yearling females tended to dissociate from the pack and to make forays outside the territory during times of low availability of moose carcasses (Messier 1985*a*). When prey declined on Isle Royale, more wolves left their packs (Peterson and Page 1988). During times of undernutrition, aggression may increase in a wolf pack, forcing young subordinate animals to leave (Zimen 1976). Aggression also increases during the breeding season (Zimen 1976), the time when most yearling wolves typically disperse.

Mate competition may also play a role in wolf dispersal. Social stress increases during the breeding season, with a concomitant increase in aggression by dominant wolves over subordinate wolves (Rabb et al. 1967; Zimen 1982). Perhaps younger, maturing animals are viewed by the older wolves as competition for mating opportunities. Alienation from the natal pack prior to dispersing is well documented (Messier 1985*a*; Mech 1987; Fuller 1989).

Inbreeding in a wolf pack is believed to be common (Mech 1966; Woolpy and Eckstrand 1979; Mech 1987). Incestuous matings occur in captivity (Packard et al. 1985) and probably in the wild (Peterson et al. 1984). The occurrence of short-distance dispersal into adjacent packs containing individuals potentially related to the disperser, plus the observation of many long-distance dispersals, indicates that a balance between inbreeding and outcrossing may exist (for more details see Mech 1987). Many theoretical assumptions about inbreeding avoidance remain to be tested, mainly whether inbreeding or outcrossing increases the genetic fitness of an individual.

We suggest that wolf parents maximize their lifetime reproductive success by producing offspring (genes) capable of being biders within the pack (Packard and Mech 1983), moving to an adjacent territory, or dispersing a long distance should conditions (i.e., resources or mates) be inadequate. The plasticity provided by the availability of different dispersal strategies (including not dispersing) allows an individual wolf to respond to different environmental and social opportunities, thereby increasing its chances of survival and of passing these traits to future generations.

Acknowledgements

This study was supported by the U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, the U.S. Department of Agriculture North Central Forest Experiment Station, and the Big Game Club of Minneapolis. We thank M. E. Nelson, many bush pilots, and numerous technicians for field assistance, U. Swain for data tabulation and reduction, and trappers and hunters in Canada for reporting kills of radio-collared wolves.

BALLARD, W. B., FARNELL, R., and STEPHENSON, R. O. 1983. Long distance movement by gray wolves, *Canis lupus*. Can. Field-Nat. **97**: 333.

BALLARD, W. B., WHITMAN, J. S., and GARDNER, C. L. 1987. Ecology of an exploited wolf population in southcentral Alaska. Wildl. Monogr. **98**: 1–54.

BLAIR, W. F. 1953. Population dynamics of rodents and other small mammals. *In* Advances in genetics. *Edited by* M. Demerec. Academic Press, New York. pp. 1–41.

BURT, W. H. 1949. Territoriality. J. Mammal. **30**: 25–27.

CHRISTIAN, J. J. 1970. Social subordination, population density, and mammalian evolution. Science (Washington, D.C.), **168**: 84–90.

——— 1971. Fighting, maturity and population density in *Microtus pennsylvanicus*. J. Mammal. **52**: 556–567.

ENDLER, J. A. 1979. Gene flow and life history patterns. Genetics, **93**: 263–284.

FRITTS, S. H. 1983. Record dispersal by a wolf from Minnesota. J. Mammal. **64**: 166–167.

FRITTS, S. H., and MECH, L. D. 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. Wildl. Monogr. **80**: 1–79.

FULLER, T. K. 1989. Population dynamics of wolves in north-central Minnesota. Wildl. Monogr. **105**: 1–41.

GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. **28**: 1140–1162.

GREENWOOD, P. J., HARVEY, P. H., and PERRINS, C. M. 1979. Inbreeding and dispersal in the great tit. Nature (London), **271**: 52–54.

HAMILTON, W. D. 1972. Altruism and related phenomena, mainly in social insects. Annu. Rev. Ecol. Syst. **3**: 193–232.

HARRINGTON, F. H., and MECH, L. D. 1982. Patterns of homesite attendance in two Minnesota wolf packs. *In* Wolves of the world: perspectives of behavior, ecology, and conservation. *Edited by* F. H. Harrington and P. C. Paquet. Noyes Data Corp., Park Ridge, NJ. pp. 81–109.

HARRINGTON, F. H., MECH, L. D., and FRITTS, S. H. 1983. Pack size and wolf pup survival: their relationship under varying ecological conditions. Behav. Ecol. Sociobiol. **13**: 19–26.

HOLEKAMP, K. E. 1984. Natal dispersal in Belding's ground squirrels (*Spermophilus beldingi*). Behav. Ecol. Sociobiol. **16**: 21–30.

——— 1986. Proximal causes of natal dispersal in Belding's ground squirrels (*Spermophilus beldingi*). Ecol. Monogr. **56**: 365–391.

HOLEKAMP, K. E., and SHERMAN, P. W. 1989. Why male ground squirrels disperse. Am. Sci. **77**: 232–239.

HOWARD, W. E. 1960. Innate and environmental dispersal of individual vertebrates. Am. Midl. Nat. **63**: 152–161.

KNIGHT, S. W. 1978. Dominance hierarchies of captive coyote litters. M. thesis, Utah State University, Logan.

KUEHN, D. W., FULLER, T. K., MECH, L. D., PAUL, W. J., FRITTS, S. H., and BERG, W. E. 1986. Trap-related injuries to gray wolves in Minnesota. J. Wildl. Manage. **50**: 90–91.

LIDICKER, W. Z. 1975. The role of dispersal in the demography of small mammals. *In* Small mammals: productivity and dynamics of populations. *Edited by* K. Petrusewicz, E. B. Golley, and L. Ryszkowski. Cambridge University Press, London. pp. 103–128.

MECH, L. D. 1966. The wolves of Isle Royale. Fauna Ser. No. 7, U.S. National Park Service. U.S. Government Printing Office, Washington, D.C.

——— 1974. Current techniques in the study of elusive wilderness carnivores. *In* Proceedings of the 11th International Congress of Game Biologists, Stockholm, Sweden, 3–7 September 1973. *Edited by* I. Kjerner and P. Bjurholm. Liber Distribution, Vallingby, Sweden. pp. 315–322.

——— 1977*a*. Productivity, mortality, and population trends of wolves in northeastern Minnesota. J. Mammal. **58**: 559–574.

——— 1977*b*. Population trend and winter deer consumption in a Minnesota wolf pack. *In* Proceedings of the 1975 predator symposium, Missoula, MT, 1975. *Edited by* R. L. Phillips and C. Jonkel. Bull. Montana Forest Conservation Experiment Station, University of Montana, Missoula. pp. 55–83.

——— 1979. Making the most of radio tracking—a summary of wolf studies in northeastern Minnesota. *In* A handbook on biotelemetry and radiotracking. *Edited by* C. J. Amlaner, Jr., and D. W. MacDonald. Pergamon Press, New York. pp. 85–95.

——— 1983. Handbook of animal radio-tracking. University of Minnesota Press, Minneapolis.

——— 1986. Wolf population in the central Superior National Forest, 1967–1985. U.S. Dep. Agric. For. Serv. Res. Rep. NC-270. pp. 1–6.

——— 1987. Age, season, distance, direction, and social aspects of wolf dispersal from a Minnesota pack. *In* Mammalian dispersal patterns: the effects of social structure on population genetics. *Edited by* B. D. Chepko-Sade and Z. T. Halpin. University of Chicago Press, Chicago. pp. 55–74.

MECH, L. D., and FRENZEL, L. D. 1971. Ecological studies of the timber wolf in northeastern Minnesota. U.S. Dep. Agric. For. Serv. Res. Rep. NC-52. pp. 1–52.

MECH, L. D., and HERTEL, H. H. 1983. An eight-year demography of a Minnesota wolf pack. Acta Zool. Fenn. **174**: 249–250.

MECH, L. D., and KARNS, P. D. 1977. Role of the wolf in a deer decline in the Superior National Forest. U.S. Dep. Agric. For. Serv. Res. Rep. NC-148. pp. 1–23.

MEDJO, D. C., and MECH, L. D. 1976. Reproductive activity in nine- and ten-month-old wolves. J. Mammal. **57**: 406–408.

MESSIER, F. 1985*a*. Solitary living and extraterritorial movements of wolves in relation to social status and prey abundance. Can. J. Zool. **63**: 239–245.

——— 1985*b*. Social organization, spatial distribution, and population density of wolves in relation to moose density. Can. J. Zool. **63**: 1068–1077.

MOORE, J., and ALI, R. 1984. Are dispersal and inbreeding avoidance related? Anim. Behav. **32**: 94–112.

NELSON, M. E., and MECH, L. D. 1981. Deer social organization and wolf predation in northeastern Minnesota. Wildl. Monogr. **77**: 1–53.

——— 1986. Deer population in the central Superior National Forest, 1967–1985. U.S. Dep. Agric. For. Serv. Res. Rep. NC-271. pp. 1–8.

OHMANN, L. F., and REAM, R. R. 1969. Vegetation studies in the BWCA—a brief report on plant communities. Naturalist, **20**: 20–29.

PACKARD, J. M., and MECH, L. D. 1983. Population regulation in wolves. *In* Proceedings of the Symposium on Natural Regulation of Wildlife Populations, March 10, 1978, Vancouver, B.C. *Edited by* F. L. Bunnell, D. S. Eastman, and J. M. Peek. Forest Wildlife and Range Experiment Station, and University of Idaho, Moscow. pp. 151–174.

PACKARD, J. M., MECH, L. D., and SEAL, U. S. 1983. Social influences on reproduction in wolves. *In* Wolves in Canada and Alaska: their status, biology, and management. *Edited by* L. N. Carbyn. Can. Wildl. Serv. Rep. Ser. No. 45. pp. 78–85.

PACKARD, J. M., SEAL, U. S., and MECH, L. D. 1985. Causes of reproductive failure in two family groups of wolves (*Canis lupus*). Z. Tierpsychol. **68**: 24–40.

PETERSON, R. O., and PAGE, R. E. 1988. The rise and fall of Isle Royale wolves, 1975–1986. J. Mammal. **69**: 89–99.

PETERSON, R. O., WOOLINGTON, J. D., and BAILEY, T. N. 1984. Wolves of the Kenai Peninsula, Alaska. Wildl. Monogr. **88**: 1–52.

RABB, G. B., WOOLPY, J. H., and GINSBURG, B. E. 1967. Social relationships in a group of captive wolves. Am. Zool. **7**: 305–311.

SEAL, U. S., PLOTKA, E. D., PACKARD, J. M., and MECH, L. D. 1979. Endocrine correlates of reproduction in the wolf. Part 1. Serum progesterone, estradiol and LH during the estrous cycle. Biol. Reprod. **21**: 1057–1066.

SHIELDS, W. M. 1982. Philopatry, inbreeding, and evolution of sex. State University of New York Press, Albany.

——— 1987. Dispersal and mating systems: investigating their causal connections. *In* Mammalian dispersal patterns: the effects of social structure on population genetics. *Edited by* B. D. Chepko-Sade and Z. T. Halpin. University of Chicago Press, Chicago. pp. 3–24.

SNYDER, R. L. 1961. Evolution and integration of mechanisms that regulate population growth. Proc. Natl. Acad. Sci. U.S.A., **47**: 449–455.

TAYLOR, L. R., and TAYLOR, R. A. J. 1977. Aggregation, migration and population mechanics. Nature (London), **265**: 415–421.

VAN BALLENBERGHE, V. 1983. Extraterritorial movements and dispersal of wolves in southcentral Alaska. J. Mammal. **64**: 168–171.

VAN BALLENBERGHE, V., and MECH, L. D. 1975. Weights, growth, and survival of timber wolf pups in Minnesota. J. Mammal. **56**: 44–63.

VAN BALLENBERGHE, V., ERICKSON, A. W., and BYMAN, D. 1975. Ecology of the timber wolf in northeastern Minnesota. Wildl. Monogr. **43**: 1–43.

VAN CAMP, J., and GLUCKIE, R. 1979. A record long-distance move by a wolf (*Canis lupus*). J. Mammal. **60**: 236–237.

VAN VLECK, D. B. 1968. Movements of *Microtus pennsylvanicus* in relation to depopulated areas. J. Mammal. **49**: 92–103.

WASER, P. M. 1985. Does competition drive dispersal? Ecology, **66**: 1170–1175.

WASER, P. M., and JONES, W. T. 1983. Natal philopatry and solitary mammals. Q. Rev. Biol. **58**: 355–390.

WOOLPY, J. H., and ECKSTRAND, I. 1979. Wolf pack genetics: a computer simulation with theory. *In* The behavior and ecology of wolves. *Edited by* E. Klinghammer. Garland STPM Press, New York. pp. 206–224.

WYNNE-EDWARDS, V. C. 1962. Animal dispersion in relation to social behavior. Oliver and Boyd, Edinburgh.

ZIMEN, E. 1976. On the regulation of pack size in wolves. Z. Tierpsychol. **40**: 300–341.

——— 1982. A wolf pack sociogram. *In* Wolves of the world: perspectives of behavior, ecology, and conservation. *Edited by* F. H. Harrington and P. C. Paquet. Noyes Data Corp., Park Ridge, NJ. pp. 282–322.