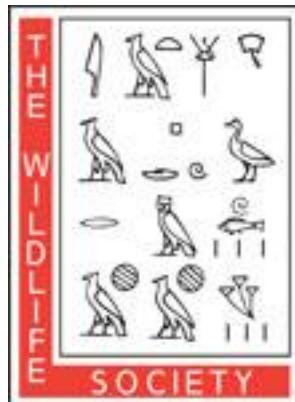


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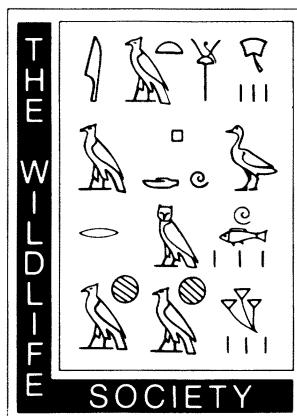


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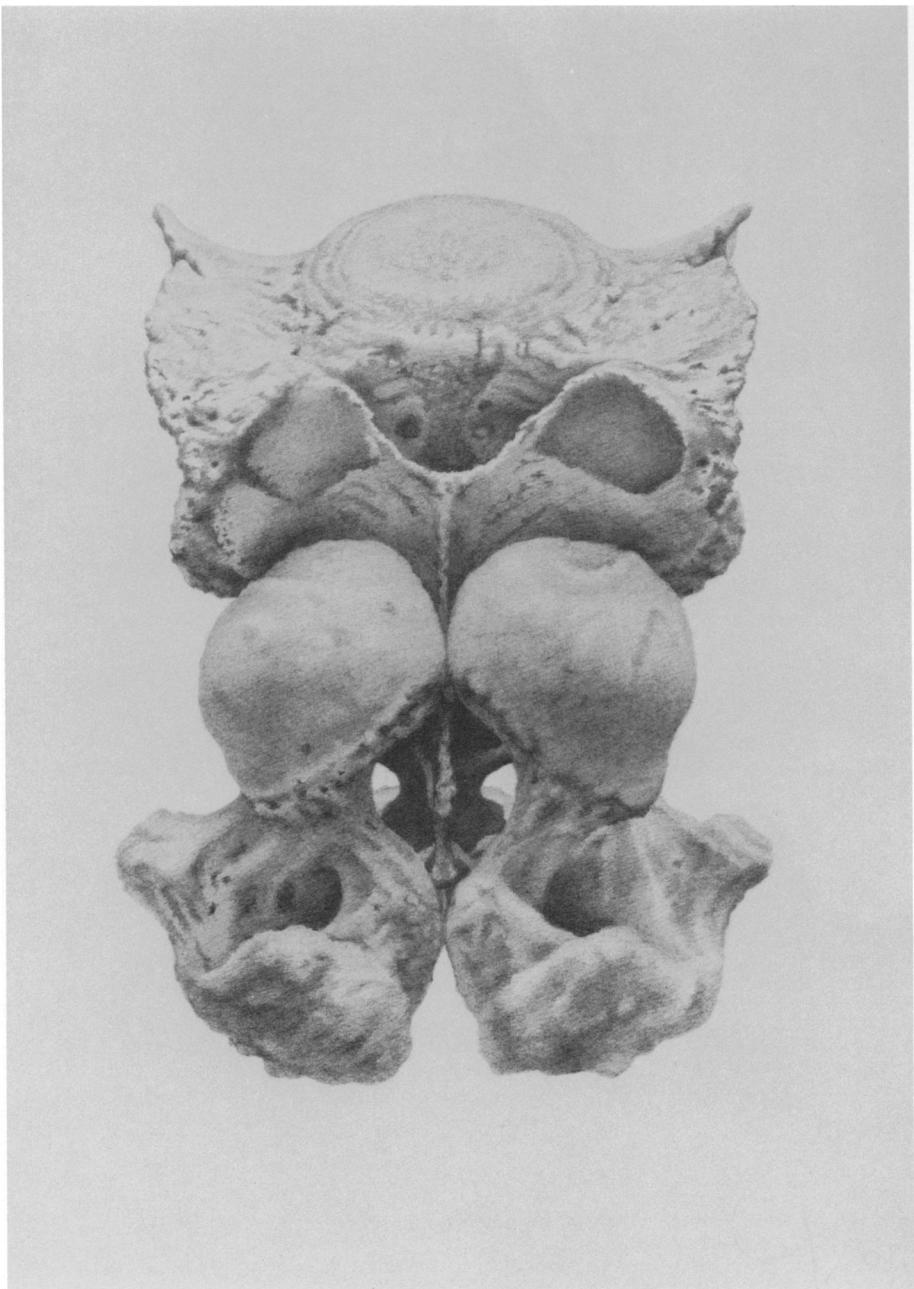
POPULATION DYNAMICS OF WOLVES IN NORTH-CENTRAL MINNESOTA

by

TODD K. FULLER

NO. 105

OCTOBER 1989



FRONTISPIECE. Untitled configuration of wolf relics (sacral and femural), pencil and paper, 365:305 mm, by Gendron Jensen © 1987.

POPULATION DYNAMICS OF WOLVES IN NORTH-CENTRAL MINNESOTA

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Abstract: During September 1980–December 1986, 81 radio-collared wolves (*Canis lupus*) were monitored in and near the 839-km² Bearville Study Area (BSA) in north-central Minnesota. Each year winter-territory size averaged 78–153 km²; no territories had road densities >0.72 km/km². From zero to 30% of radio-marked pup, yearling, or adult wolves left their territories each month. Pups left natal packs during January–March and older wolves left frequently during September–April. Wolves temporarily leaving territories moved 5–105 km away and were absent 3–118 days; up to 6 exploratory moves were made prior to dispersal. Dispersing wolves traveled 5–100 km away during periods of 1–265 days. One disperser joined an established pack, but 16 others formed new packs. Annual dispersal rates were about 0.17 for adults, 0.49 for yearlings, and 0.10 for pups.

Each year mean pack size ranged from 5–9 in November–December to 4–6 in March. Annual wolf density (including 16% lone wolves) ranged from 39–59 wolves/1,000 km² in November–December to 29–40 wolves/1,000 km² in March. Annual immigration was 7%. The observed mean annual finite rate of increase was 1.02, and annual rates of increase were correlated with mean number of pups per pack in November. Litters averaged 6.6 pups at birth and 3.2 by mid-November, at which time pups made up 46% of pack members. Annual survival of radio-marked wolves >5 months old was 0.64. Despite legal protection, 80% of identified wolf mortality was human caused (30% shot, 12% snared, 11% hit by vehicles, 6% killed by government trappers, and 21% killed by humans in some undetermined manner); 10% of wolves that died were killed by other wolves.

During sample periods in 2 winters, wolves were located twice daily to estimate predation rates on white-tailed deer (*Odocoileus virginianus*). Estimated minimum kill rates during January–February ($\bar{x} = 21$ days/kill/wolf) did not differ between winters with differing snow depths. Winter consumption averaged 2.0 kg deer/wolf/day (6% wolf body wt/day). Scat analyses indicated deer were the primary prey in winter and spring, but beaver (*Castor canadensis*) were an important secondary prey (20–47% of items in scats) during April–May. Neonatal deer fawns occurred in 25–60% of scats during June–July whereas the occurrence of beaver declined markedly. Overall, deer provided 79–98% of biomass consumed each month. Adult wolves consumed an estimated 19 deer/year of which 11 were fawns.

A review of North American studies indicates that wolf numbers are directly related to ungulate biomass. Where deer are primary prey, territory size is related to deer density. Per capita biomass availability likely affects pup survival, the major factor in wolf population growth. Annual rates of increase of exploited populations vary directly with mortality rates, and harvests exceeding 28% of the winter population often result in declines. Management decisions concerning wolf and ungulate densities and ungulate harvests by humans can be made using equations that incorporate estimates of wolf density, annual ungulate kill per wolf, ungulate densities, potential rates of increase for ungulates, and harvest.

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INTRODUCTION

Minnesota is the only state of the contiguous 48 states within the U.S. with a large (approximately 1,200 [Berg and Kuehn 1982]) self-sustaining wolf (*Canis lupus*) population, and, consequently, the species is legally protected and classified as "threatened" under the federal Endangered Species Act. Since repeal of the wolf bounty in 1965 and complete federal protection in 1974, controversy over wolves in Minnesota has abounded (Van Ballenberghe 1974, Llewellyn 1978, Kellert 1986). Some Minnesota residents believe wolves seriously compete with hunters for white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*) or cause major livestock depredations; such individuals thus feel that wolf numbers should be reduced. Others view wolves as a symbol of wilderness, having only incidental impact on ungulate populations or livestock and often believe that wolves should be rigorously protected. Although aspects of these opposing views are sometimes both correct, responsible management of wolves in Minnesota and elsewhere continues to rely heavily on sound knowledge of wolf population dynamics, prey relationships, and interactions with humans.

In the Great Lakes region, the primary ungulate prey of wolves is white-tailed deer. Olson (1938a,b) initially observed wolf population characteristics and interactions with deer in northeastern Min-

nesota. Stenlund (1955) provided more detailed information from the same area. Pimplott et al. (1969) documented wolf and deer densities and distribution in Algonquin Provincial Park, Ontario, and estimated kill rates of deer by wolves. With the advent and application of radiotelemetry to wolf studies (Kolenosky and Johnston 1967), the quantity and quality of population data gathered increased greatly. Since 1968, studies of wolf biology where deer are the primary prey have been conducted in Ontario (Kolenosky 1972, Theberge and Strickland 1978), Quebec (Potvin 1988), Wisconsin (Thiel 1978, 1985), northeastern Minnesota (e.g., Mech 1973, 1977a,b, 1980, 1986, 1987; Peters and Mech 1975; Van Ballenberghe et al. 1975; Harrington and Mech 1979), northwestern Minnesota (Fritts and Mech 1981), and north-central Minnesota (Berg and Kuehn 1980, 1982). Impacts of wolf predation on livestock in Minnesota and subsequent efforts to minimize such depredations also have been reported (Fritts 1982; Fritts et al. 1984, 1985). These and studies conducted elsewhere in North America (e.g., Gasaway et al. 1983; Peterson et al. 1984; Messier 1985a,b; Ballard et al. 1987) suggest that (aside from human-caused mortality) food resources of varying size, availability, and distribution are the ultimate factors and social behavior is the major proximate factor that cause changes in wolf populations (Packard and Mech 1980).

Studies of wolf population dynamics were reviewed and summarized by Keith (1983) who found that 4 factors dominate wolf population dynamics: wolf density, ungulate density, human exploitation, and ungulate vulnerability. Yet many of the relationships between rates of wolf population change and human-caused mortality, food supply, and wolf behavior (e.g., dispersal) are poorly quantified, particularly where numbers of deer and hunters are relatively high. The Minnesota Department of Natural Resources (MDNR) initiated studies of deer habitat use and population trend in 1968 on such an area in north-central Minnesota (Kohn and Mooty 1971; Mooty 1979; Mooty et al. 1984, 1987); preliminary wolf studies began there in fall 1977 (Berg and Kuehn 1982). I began expanded radiotelemetry studies of wolves and deer, surveys of alternate prey species, and monitoring of deer harvest by hunters there in autumn 1980 to document and interpret interrelationships between wolves, prey, and humans.

For this study, field work on wolves was carried out during September 1980–December 1986 (Fuller 1988a). Specific objectives were to relate wolf density and annual rates of population increase to wolf reproduction, survival, dispersal, and feeding ecology. Results of this study were combined with those of other wolf studies throughout North America to provide summary models that predict the impact of various management strategies on wolf and ungulate population dynamics.

Acknowledgments.—I gratefully acknowledge the field assistance of D. W. Kuehn and R. K. Markl, who trapped and handled most of the wolves, J. A. Markl, who analyzed most of the scats and participated in all other aspects of the project, J. W. Burch, P. L. Coy, S. L. Emerson, S. H. Fritts, W. F. Jensen, P. E. Lederle, T. J. Meier, T. P. Moore, K. V. Noyce, B. E. Ott, W. J. Paul, A. S. Perendy, J. Pernat, M. K. Tenney, B. A. Toms, and the pilots of Mesaba Aviation. W. E. Berg and D. W. Kuehn shared ideas and the results of their work on the study area during 1977–80. P. D. Karns initiated the project and,

along with J. A. Summers, G. B. Joselyn, J. M. Engel, and W. H. Longley, provided valuable administrative and logistical support. D. M. Heisey and R. E. Pace provided statistical advice, W. J. Snow provided computer assistance, and S. A. Loegering and D. R. Castle provided clerical help. W. H. Oldegard, D. J. Lund, and their staffs of the Minnesota Department of Corrections (Thistledew Camp) and L. P. Hoyt and L. P. Childs of Minnesota Department of Natural Resources Division of Forestry gave much needed logistical support. W. B. Ballard, D. L. Garshelis, L. B. Keith, D. W. Kuehn, J. A. Litvaitis, and L. D. Mech reviewed the manuscript and provided many helpful suggestions for improvement.

STUDY AREA

Wolf research centered on the 839-km² Bearville Study Area (BSA; lat. 47°45'N, long. 93°15'W), located 50 km north-northeast of Grand Rapids, Minnesota (Fig. 1). Most data were collected on 5–8 contiguous wolf packs whose territories encompassed part of the BSA, but dispersing wolves that settled up to 70 km away were monitored on an intermittent basis. The BSA is adjacent to a relatively uninhabited, forested area to the north and on the developed, populated Iron Range to the south. It lies within primary wolf range in Minnesota (Fig. 1), but also is on the northern edge of an area designated as Zone 4 by the Eastern Timber Wolf Recovery Team (Bailey 1978). The Team considered that, within wolf range, this zone had the highest potential for wolf–human conflicts and thus was the area where wolves should be harvested if a change in legal status allowed such activity.

Topography in the BSA is gently to strongly rolling, and soils are primarily sandy loams (Arneman 1963). Lakes cover about 6% of the area. Vegetation is mostly boreal coniferous–hardwood forest (Maycock and Curtis 1960, Kohn and Mooty 1971, Mooty 1979); about 66% of the BSA is covered with upland vegetation and only 2% is nonforested (Fuller and Heisey 1986).

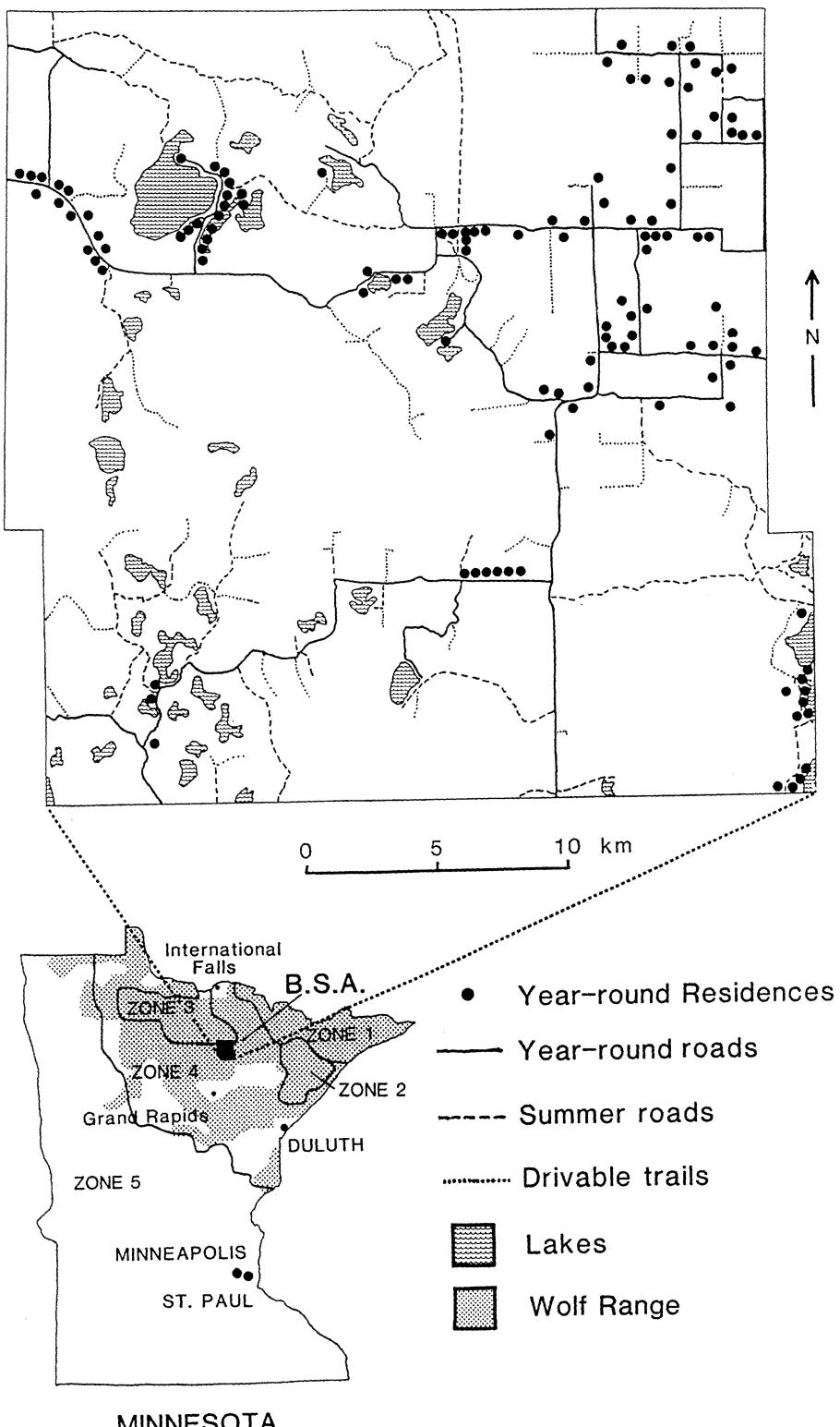


Fig. 1. Map of the Bearville Study Area (BSA) in north-central Minnesota and its location in relation to the boundaries of wolf management Zones 1–5 (as designated by the Eastern Timber Wolf Recovery Team; Bailey 1978) and the estimated distribution of reproducing packs of wolves (Mech et al. 1988).

Approximately 66% of the land in the BSA is in public ownership (40% state and 26% county); the remaining private land is owned by paper companies (20%) or private citizens (14%). Densities of roads and trails in the study area averaged 0.44 km/km². Most year-round residences (0.13/km² overall) occur in the northeastern part of the BSA, whereas residences not used in winter are concentrated around lakes. Estimated hunter density in the BSA during opening day of the 16-day deer-hunting season in November was about 2.5/km² (Fuller 1988b).

The mean January temperature at Grand Rapids is -14 C; the July mean is 19 C (U.S. Dep. Commer., unpubl. data). Annual precipitation averages 67 cm, 66% of which falls as rain during May–September. Snow cover >10 cm usually is present from early December through mid-April. Mean weekly snow depths at Grand Rapids were moderate ($\bar{x} = 36\text{--}44$ cm) during December–March 1980–81, 1982–83, and 1984–85 and shallow ($\bar{x} = 13\text{--}16$ cm) during 1981–82, 1983–84, and 1985–86.

Midwinter density of white-tailed deer declined about 50% during 1982–86, but averaged about 6/km² (T. K. Fuller, unpubl. data). Moose density was about 1/50 km² (Fuller 1986). Density of beaver (*Castor canadensis*) colonies increased from 0.58 to 0.86/km² during 1981–85 (Fuller and Markl 1987), and numbers of snowshoe hares (*Lepus americanus*) peaked during 1977–80 and declined precipitously during 1981–84 (Fuller and Heisey 1986).

METHODS

Capture, Handling, and Radiotelemetry

Wolves were captured in steel foothold traps (Kuehn et al. 1986) during April–May and August–October and immobilized with ketamine mixed with either promazine or xylazine (Fuller and Kuehn 1983) or immobilized with etorphine (Fuller and Keith 1981a). Individuals were then weighed, measured, ear-tagged, fitted with a mortality-sensing radio collar

(164–165 MHz; Telonics, Inc., Mesa, Ariz.), and injected with an antibiotic. A blood sample also was taken.

Wolves were classified as pups (<12 months old starting 1 Apr), yearlings (12–24 months old), or adults (>24 months old). Pups were classified by tooth eruption patterns and body size (Van Ballenberghe and Mech 1975). Wolves considered yearlings when monitored were either of known age (captured and marked previously as pups; $n = 18$) or, if caught in April–May, of assumed age ($n = 3$) from their tooth wear and reproductive status or pack history. Some wolves caught in August–October when 16–18 months old may have been classified as adults because they were not otherwise distinguishable.

Radio-marked wolves were located from a Cessna 172 fixed-wing aircraft (Mech 1974, Gilmer et al. 1981). For each location, wolf numbers and activity, time of day, and cover type (Mooty 1979, Fuller and Heisey 1986) were recorded. Locations were plotted on topographic maps (1:24,000) and recorded as metric grid coordinates.

Territory Size and Movements

Estimated wolf pack territory boundaries sometimes shifted between winters, and therefore territory sizes were calculated for a “summer” (15 Apr–14 Sep) and a “winter” (15 Sep–14 Apr) period each year. The beginning and ending dates correspond to documented changes in pack cohesiveness related to denning (Fuller 1989) and travel as a pack (see Radiotelemetry). Territory boundaries of all but 1 pack with radio-collared wolves were estimated by the minimum-convex-polygon method (Odum and Kuenzler 1955); during winter 1980–81, calculation of the Sturgeon Lake Pack’s territory excluded an area with high human density that pack members avoided. Locations considered to be the result of temporary extraterritorial excursions (e.g., notably isolated [≥ 5 km, see below] from other locations) or inside other pack territories were excluded from boundary determination and calculations

of territory size; these averaged 1.2 locations/pack (range = 0–6, $n = 41$ packs) in winter and 0.3 locations/pack (range = 0–5, $n = 33$ packs) in summer. Areas for territories determined from <30 locations may have been incompletely described (Fuller and Snow 1988) and were not included in territory size summaries.

Monthly rates at which resident wolves left packs temporarily (temporary excursion) or permanently (dispersal), or non-resident wolves established new packs or joined packs already present (i.e., settled) were extrapolated from estimates of daily rates, similar to mortality rate calculations (see below; Trent and Rongstad 1974, Keith et al. 1984:21, Heisey and Fuller 1985). Similar to Messier (1985b), only excursions ≥ 5 km outside territory boundaries ($\bar{x} = 0.4$ territory diameters away in this study) were included in these rate calculations to assure that movements were outside of territories that may have been incompletely described. The maximum distance that wolves making extraterritorial excursions were located away from home territories was measured from the most distant wolf location to the closest point of the home territory boundary. The approximate duration of an excursion was calculated from the difference in middates between consecutive locations inside and outside of territories (Messier 1985b). Annual dispersal rates for each age cohort of resident wolves were calculated by simultaneously applying age-specific dispersal and mortality rates each month to a 1 April population of 100 wolves, summing the total loss in 1 year resulting from dispersal, and dividing this total by the initial number of wolves in the cohort (100).

Pack Size, Density, and Population Change

Pack size in “early” (Nov–Dec) or “late” (Mar) winter was the maximum number of wolves that were observed together or that could be accounted for during telemetry flights (e.g., 7 observed plus 1 radioed wolf 2 km away but within the territory = 8). Early winter counts provided a max-

imum estimate of the number of adult-size wolves present each year, and late winter counts (just before denning) provided an estimate at the population nadir. Proportion of lone wolves in the population was estimated from their proportion (as subsequently determined by radiotelemetry) in the sample of wolves captured during spring.

Annual wolf density during early and late winter was estimated by first delineating a census area that encompassed all adjacent winter territories in the BSA and the area between them (Peterson et al. 1984, Ballard et al. 1987). The summed maximum pack sizes plus the estimated proportion of lone wolves were divided by this census area to give an overall density. Not all wolf packs in the study area contained marked wolves each winter (4 of 44 pack-winters overall), and limited aerial searches were conducted to identify pack size in these territories. The territories of these packs were assumed to be similar to their territory in previous or subsequent years when 1 or more pack members were marked. Radio-marked packs whose territories may have been inadequately described ($n = 7$; $\bar{x} = 18$ locations/territory; range = 11–28) also were included in the estimates of resident wolf numbers; most (5 of 7) were included in the 1985–86 estimate.

Finite rates of increase (λ) of the wolves were determined from the ratio of successive yearly population estimates in late winter. Mean annual finite rate of increase was calculated by taking the antilogarithm of the mean annual exponential rates of increase ($r = \ln \lambda$) for the population; this is the same as taking the fifth root of the ratio of the population estimates in year 6 and year 1.

Immigration rates of pack wolves were estimated from numbers of wolves outside the census area that established new packs in areas where other radio-marked packs in the census area had disappeared (these are maximum rates because some unmarked resident wolves may have established packs in the census area). In addition, some wolves from outside the census area

likely joined already-established packs. To calculate their numbers, I assumed that the ratio of wolves joining packs to those starting new packs was similar for both marked and unmarked wolves. Thus, the proportion of immigrants in the study area was the proportion of new wolves (probably not born in the study area) in the census area in late winter.

Reproduction and Survival

Mean litter size was estimated from counts of placental scars of 4 radio-collared wolves that died and observations of presumably complete litters of pups in 4 consecutive years at 1 natal den. The reproductive tract of 1 of the radio-collared wolves had 2 sets of placental scars—1 heavily pigmented and the other faintly pigmented; these were interpreted as indicating 2 consecutive litters (as did Peterson et al. 1984), though the faded set may have provided an underestimate of litter size (cf. Lindstrom 1981).

Pup survival from birth to about 7 months of age was estimated from the difference between numbers born and numbers observed in packs the following October–December. During autumn and early winter, pups were identified by their smaller size and behavioral characteristics (Peterson and Page 1988). When such identification was tenuous, reduction in pack size due to known mortality and dispersal of yearlings and adults also was taken into account (e.g., 4 adults in pack in spring; 1 known to have died during the summer, 7 wolves in pack in autumn = ≥ 4 pups).

Age-specific survival rates of radio-collared wolves were estimated by extrapolation of daily survival rates (Trent and Rongstad 1974); the relative importance of various mortality factors was similarly derived (Heisey and Fuller 1985). For simplicity, the biological year was designated as beginning on 1 April. Each month was considered an interval during which daily survival rates were relatively constant. Wolves were classified as residents when inside or within 5 km of their normal ter-

ritory (see below) and nonresidents when they were alone and traveling outside their territory boundaries.

When radio signals of wolves could not be located by routine monitoring, searches were conducted up to 100 km from the study area within the next several weeks, and their frequencies continued to be monitored in the study area for the next several months to determine if dispersing wolves had returned. Resident wolves whose radio signals disappeared during the 16-day-firearms deer-hunting season in November were presumed illegally shot and their transmitters destroyed. Similarly, socially dominant resident wolves (not likely to disperse) that disappeared during the legal trapping and snaring season for other large furbearers (Dec–Jan) were presumed captured and illegally killed. If radio contact was lost immediately after a wolf had dispersed from its territory, or soon after it had made ≥ 1 exploratory movement out of its home territory, I assumed that the animal was alive at last contact and had moved beyond range of our monitoring equipment. Expected life of radio transmitters was 3 years; signals not received after that time span were assumed to be a result of battery failure. Using all these criteria, I could not ascertain probable fates for only 5 animals, all of whose signals disappeared during March–May. For purposes of calculation, these animals were considered alive on the last day of radio contact, and the resulting estimates of survival are thus maximal. Overall, this assumption had little effect on my estimates as pooled annual survival rates were not significantly different ($z = 0.61$, $P = 0.54$) between the maximum estimate (0.64) and the resulting minimum estimate if all 5 wolves had died (0.60).

Feeding Ecology

Carcasses observed when radio-collared wolves were located from aircraft were examined on the ground to determine sex, age, and condition. Sex was determined from skull or pelvis characteristics (Taber 1956), and age was estimated from tooth

replacement, wear, or cementum annuli (Severinghaus 1949, Gilbert 1966) or from hind foot length for fawns versus adults (Fuller et al. 1989).

Wolf predation rates on ungulates during winter are most accurately determined by locating wolves on consecutive days and following their entire path of travel (Burkholder 1959, Mech 1966, Kolenosky 1972, Peterson 1977, Peterson et al. 1984, Ballard et al. 1987). Wolf trails were not followed in this study because tracking conditions were never suitable due to adverse snow and vegetation characteristics. Therefore preliminary winter kill rates were estimated from the frequency wolves were found near recently killed deer (Mech 1977b, Fritts and Mech 1981). For example, if a pack was found at kill sites on 2 of 14 days they were located, the estimated kill rate would be 1 kill/7 days. Kill rates were estimated during January–February when visibility of packs ($\bar{x} = 76\%$ of locations) was highest each winter.

Extrapolating kill rates from the proportion of days wolves are located at kills, however, assumes wolves remain at kills an average of exactly 24 hours. Kill rates would be overestimated if wolves remained >24 hours, on average, as at moose kills (Fuller and Keith 1980, Peterson et al. 1984, Ballard et al. 1987) and underestimated if carcasses were abandoned in <24 hours (Fritts and Mech 1981, Carbyn 1983). Because a pack of wolves can consume a white-tailed deer in <24 hours (Pimlott et al. 1969:46, Mech 1970:181), unadjusted kill rates for wolves killing deer could be low. To help correct for this potential bias, radio-collared wolves in packs of 2–9 were located in early morning and in late afternoon for multiple periods of 2–7 consecutive days during portions of January and February 1984 and 1985. A pack located away from a future kill site 1 morning, on the kill that afternoon, and away from the kill the next morning was at the kill an estimated 12 hours. This is the mean of the minimum time possible at the kill (0 hours—i.e., the pack killed and left the carcass immediately) and the maximum time possible (24 hours—i.e.,

the kill was made just after they were located the first morning, and they left the kill just before being located the next morning). Thus, uncorrected kill rates were underestimated by at least 50% ($[12 \div 24]100$). Because only 2 flights/day were made, it could not be determined if wolves stayed an average of <12 hours at kills; thus even corrected estimates of predation rates (2 times uncorrected rates) are minimal. To obtain uncorrected kill-rate estimates during this period (when 2 flights were made in 1 day) that were comparable to those observed in other winters, 1 of 2 observations was randomly selected to be included in the uncorrected estimate.

Wolf scats found on snow during November–March and those collected on 138 km of roads searched at least once per month in April–October were assigned to the appropriate month of deposition. Scats collected at den and rendezvous sites were dated from my knowledge of when radio-marked wolves had used these sites (Fuller 1989). Scats at dens or rendezvous sites were classified as from pups or adults on the basis of diameter. Because a few coyotes occurred in the study area, only scats >25 mm in diameter collected on roads or trails were considered to be from wolves (Thompson 1952, Weaver and Fritts 1979). Prey remains in scats were identified by comparison with known material; if identification from gross examination was uncertain, hair-scale impressions were examined microscopically (Adorjan and Kolenosky 1969).

Relative biomass and relative numbers of prey consumed were estimated from scat-analysis data (Floyd et al. 1978, Traves 1983). Similar to Ballard et al. (1987), the total number of deer consumed during April–October, when only 4 aerial observations of kills were made, was estimated from (1) the consumable weight of both adult and fawn deer, accounting monthly for changes in fawn size, (2) the relative biomass provided by both adults and fawns in the diet each month, and (3) mean monthly consumption rates of deer by adult wolves. Consumption rates (kg/day) by adults in summer were assumed equiva-

lent to winter rates. Even though wolf metabolic rate may be somewhat lower in summer than in winter (Schmidt-Nielsen 1975:319), wolves have the additional burden of providing food for pups. In addition, summer predation rates on both caribou (*Rangifer tarandus*) (James 1983) and moose (Ballard et al. 1987) have been found to be similar to those in winter, even though Peterson et al. (1984) reported many moose were scavenged in summer and suggested this implied lower consumption rates than in winter.

Statistical Tests

Differences in means were examined with *t* tests, and differences in ratios were tested by chi-square; samples of unpaired, non-normal measurements were compared with Mann-Whitney *U* tests (Snedecor and Cochran 1973). Correlations were tested with linear and multiple regression techniques (Draper and Smith 1981); weighted regression (weight = *n*) was used when appropriate. Survival and dispersal rates (Heisey and Fuller 1985) were compared with *z* statistics (Bishop et al. 1975). Unless stated otherwise, only $P \leq 0.05$ was considered statistically significant.

RESULTS AND DISCUSSION

Radiotelemetry

During September 1980 to August 1985, 81 wolves were radio-collared in the BSA. The proportion of wolves in each sex and age class within the monitored sample did not differ ($P > 0.50$) among years ($\bar{x} = 25$, range = 13–32); average numbers monitored were 7 adult males (range = 6–9), 9 adult females (3–11), 2 yearling males (0–4), 2 yearling females (0–3), 2 male pups (0–5), and 3 female pups (0–6). Sex ratios of 48 adults and yearlings (46% male) and 33 pups (42% male) did not differ from parity.

Radio-marked wolves were located, on average, every 6.8 days. However, wolves were located more frequently (31% of all

locations) during January and February when we often flew twice per day, and less in other months. Most flights were conducted between 0900–1100 hours (49%) or 1400–1600 hours (18%). Marked wolves or associated pack members were observed most often (76% of attempts) during January–February when snow cover was complete and least often (16%) during May–October when leaves were on trees. Overall observability of solitary marked wolves was lower (31 vs. 46%) than for those found in groups. Variation in observability among winter months largely reflected differences in snow depth ($r = 0.76$, 17 df, $P < 0.01$); wolves were seen more often during January–March when snow was deepest.

Marked pups and 41 older wolves initially were members of 12 packs; 7 others were solitary (i.e., not associated with a pack as determined by subsequent monitoring). During November–December each year, 23–54% ($\bar{x} = 36\%$) of wolves in packs whose territories were included wholly or partly within the BSA were radio-collared.

Many (49%) radio-marked wolves were monitored for <1 year, but 21% were monitored for >2 years (overall $\bar{x} = 438$ days, range = 12–1,494 days). Survival, dispersal, and settling rates were based on a total of 34,826 transmitter-days. Thirteen packs with all or part of their territories in the BSA were monitored for 1–6 years ($\bar{x} = 2.9$); 5 of these were formed during the study period and reoccupied vacant territories. An additional 10 pairs or packs monitored 1–3 years ($\bar{x} = 1.2$) had territories wholly outside of the BSA; 9 of these territories were formed by wolves that dispersed from the BSA.

Pairs of radio-marked pack members were together (Cohesion Index; Peterson et al. 1984) more often (chi-square tests, $P < 0.001$) during September–March ($\bar{x} = 62\%$, range = 51–71%) than during May–August ($\bar{x} = 29\%$, range = 18–40%). In Alaska, the Cohesion Index declined when pups were born in May and increased as pups began traveling with the pack in October (Peterson et al. 1984).

Table 1. Minimum winter territory sizes, number of pack locations per territory, and mean early and late winter sizes of radio-marked wolf packs in north-central Minnesota.

Winter	No. of packs	Territory size (km ²)		No. of locations		No. of wolves per pack				Change	
		Mean	Range	Mean	Range	Nov-Dec		Mar		No.	%
						Mean	Range	Mean	Range		
1980-81	5	153	72-223	62	33-104	6.2	0-10	4.6	3-9	-1.6	-26
1981-82	7	109	50-159	64	41-82	4.7	1-10	3.9	2-7	-0.8	-17
1982-83	8	109	79-135	51	31-63	6.4	2-10	4.0	1-6	-2.4	-37
1983-84	6	96	69-122	46	40-53	5.8	2-9	4.4	2-9	-1.4	-24
1984-85	4	153	107-197	94	72-136	9.3	7-12	6.3	4-9	-3.0	-30
1985-86	3	78	51-104	34	33-35	8.0	5-10	5.0	4-6	-3.0	-37
Mean		116		59		6.7		4.7		-2.0	-29

Movements

Territory Size and Location.—Mean minimum winter territory sizes of packs in part or all of the BSA ranged from 78 to 153 km² over the years of the study (overall $\bar{x} = 116$ km², $n = 33$), and individual territory sizes ranged from 50 to 223 km² (Table 1). For comparison, 3 winter territories wholly outside the BSA (determined from 34 to 50 locations each) were 40–135 km². Individual summer territories based on 30–85 locations each ($\bar{x} = 45$) ranged from 54 to 226 km² ($\bar{x} = 110$ km², $n = 20$) and were not different from winter territories ($P > 0.05$). Deer densities within each territory were not known, but a review of studies where wolves prey primarily on white-tailed deer indicates wolf territories are smaller and territory size per wolf is lower where deer are more numerous (Table 2; weighted regressions, $P \leq 0.007$). These regression analyses exclude the large mean winter-territory size in a newly protected population in northwest Minnesota (Fritts and Mech 1981); however, as wolf numbers increased there, territory size decreased 35–45%.

Within any winter, little overlap of territory boundaries occurred among adjacent marked packs in the BSA (Fig. 2). Wolves may be more territorial in Minnesota where territories are smaller and thus boundaries easier to maintain (Mech 1973, 1977b; Peters and Mech 1975; Harrington and Mech 1979), but, as pointed out by Ballard et al. (1987), apparent overlap in other studies may be the result of

the method used to depict boundaries and may not reflect temporal separation of packs.

Relatively stable, long-established territorial boundaries in the BSA likely fluctuate little with short-term changes in pack size. Thus it is not surprising that there were only weak positive correlations between territory size in the BSA and early- and late-winter pack size ($r = 0.37$ and 0.43, respectively; $P < 0.05$). Pack size and territory size have been correlated in other areas (Peterson et al. 1984, Ballard et al. 1987) where wolf densities were lower, territories larger, and exploitation was higher than in the BSA. In some areas, territories have expanded, contracted, disappeared, or been established when wolf mortality was high and prey availability or distribution changed (Peterson 1977; Carbyn 1980, 1982; Fuller and Keith 1980; Messier 1985a; Ballard et al. 1987; Peterson and Page 1988).

Most territories in the BSA encompassed relatively roadless tracts of land (cf. Figs. 1 and 2). Density of maintained roads in the BSA (from county highway maps only) was higher outside of pack territory boundaries than inside (0.59 vs. 0.38 km/km²). Similarly, the number of permanent residences was higher outside territories (0.41 vs. 0.07/km²). Road density within all pack territories ranged from 0.15 to 0.72 km/km² but was not related to the rate of human-caused mortality of radio-collared wolves (weighted $r = 0.20$, 17 df, $P = 0.49$; weighted by number of wolf transmitter-days in each territory). How-

Table 2. Mean territory size and territory area per wolf vs. deer density^a for wolf populations whose major prey is white-tailed deer.

Location	Territory size (km ²)		Mean pack size	Territory area per wolf (km ²)	Deer density (No./km ²)	Reference
	\bar{x}	n				
Northeast Minnesota	110	5	8.0	14	5.1	Van Ballenberghe et al. 1975
North-central Minnesota	116	33	5.7	20	6.2	This study
East-central Ontario	175	4	7.0	25	5.8	Pimlott et al. 1969
North-central Minnesota	192	3	6.0	32	6.0	Berg and Kuehn 1980 ^b
Southern Quebec	199	21	5.6	36	3.0	Potvin 1988
East-central Ontario	224	1	8.0	28	3.1	Kolenosky 1972
Northeast Minnesota	243	11	7.0	35	2.1	Mech 1973 ^b
Northwest Minnesota	260 ^c	22	4.6	56	5.0	Fritts and Mech 1981 ^b

^a Correlation between territory size and deer density: weighted $r = -0.91$, 5 df, $P = 0.003$. Correlation between territory area per wolf and deer density: weighted $r = -0.87$, 5 df, $P = 0.007$. Both of the above exclude data from Fritts and Mech (1981).

^b Recalculated values from figures of territories.

^c Newly established population.

ever, these results corroborate work elsewhere (Thiel 1985, Jensen et al. 1986, Mech et al. 1988) that suggests road densities $>0.6\text{--}0.8 \text{ km/km}^2$ provide enough access for humans to limit wolf numbers through legal or illegal trapping or shooting.

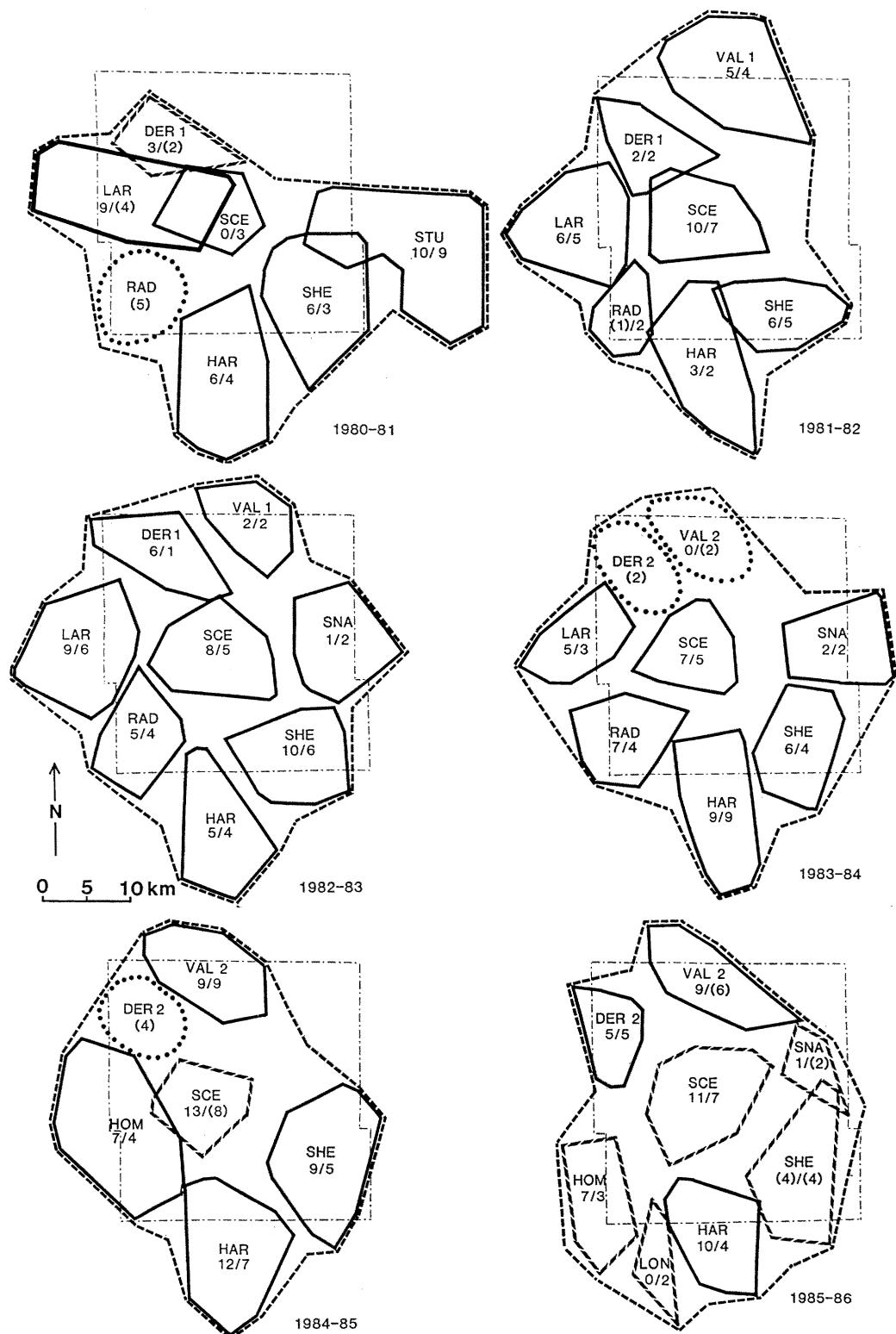
Extraterritorial Movements.—Each month, up to 30% of wolves of any 1 age class in the BSA left their territories (i.e., moved $\geq 5 \text{ km}$ away) (Fig. 3); some wolves returned (temporary excursions), but other wolves never returned and died or settled elsewhere (dispersals). Monthly rates of departure did not differ between sexes within an age class ($P > 0.46$), but yearlings did differ in both rate and pattern of departure ($P < 0.003$). Most departures of pups occurred during January–March when they were 9–11 months old, and departure rates of new yearlings (12 months old) were very high in April when new pups were born. Older yearlings left their territories most often during September–January and in March. Monthly rates of departure for adults generally were low throughout the year, but, as with pups and yearlings, were highest in months preceding or following breeding in February and during April when parturition occurred.

Intrapack conflict may precipitate extraterritorial movements, and aggression in captive packs is highest during December–January and March–May (Zimen 1976). In Quebec, most departures of pups occurred after February, those of yearlings during December–March, and those of

adults during December–August (Messier 1985b). Overall rates of departure were slightly higher for adults than for yearlings in Quebec, contrary to the findings in the BSA. In Alaska, departure rates were highest in February, coinciding with the beginning of the breeding season there, and extraterritorial movements of pups were negligible (Peterson et al. 1984).

Of the temporary excursions made by 25 wolves in the BSA, 79% were made alone. All 5 excursions by yearlings were solitary, but 2 of 6 by pups and 10 of 45 by adults were with other pack members. Yearling wolves in the BSA that left their territories ($n = 5$) only made 1 temporary excursion each and pups sometimes made 2 ($\bar{x} = 1.5$, $n = 4$), but adults made up to 10 ($\bar{x} = 2.8$, $n = 16$). Maximum distance ($\bar{x} = 17 \text{ km}$, range = 5–105 km, $n = 43$) and duration ($\bar{x} = 20 \text{ days}$, range = 2–118 days) of temporary excursions from the BSA did not differ between wolves traveling alone or with other pack members, or by sex or age (Mann-Whitney U tests, $P > 0.05$).

Extraterritorial forays have been reported from several other areas as well (Fritts and Mech 1981, Van Ballenberghe 1983a, Ballard et al. 1987). In Quebec, 71% of excursions were solitary, and those by packs were to deer wintering areas (Messier 1985b). In contrast to the BSA wolves, yearlings in Quebec initiated an average of 3 extraterritorial movements per year and adults only 1. Pack excursions



were more frequent in northeast Minnesota when prey was scarce (Mech 1977b), but none on the Kenai Peninsula seemed associated with food shortage (Peterson et al. 1984). Distance and duration of excursions for wolves in Quebec were similar to the BSA where ungulate biomass per wolf was similar, but excursion distance and duration were somewhat greater for packs living in areas of lower prey abundance (Messier 1985b).

Twenty-eight radio-collared wolves from the BSA dispersed from their home territories; 2 of these settled and subsequently dispersed again. At least 12 of 28 dispersing wolves had previously made at least 1, and up to 6, extraterritorial excursions (\bar{x} minimum = 0.9). Dispersing wolves in Quebec had made a mean minimum of 2.1 predispersal trips (Messier 1985b).

One BSA wolf left its home territory with 2 other unmarked pack members; another left with its mate (the only other pack member) after <1 year in a newly formed territory. The remaining 28 dispersals (93%) were solitary. Seven of 9 dispersers in Quebec dispersed alone (Messier 1985b), as did 18 of 21 dispersers in Alaska (Peterson et al. 1984).

The proportion of wolves that dispersed from BSA packs each month ranged from 0 to 11% ($\bar{x} = 3\%$) for pups ≥ 5 months old and 0 to 7% ($\bar{x} = 2\%$) for adults, but 0 to 20% ($\bar{x} = 9\%$) for yearlings ($P < 0.01$) (Fig. 3, Appendix A). Six of 17 dispersing “adult” wolves were known to be >2.0 years old, although others could have been misclassified yearlings (1.0–2.0 years old) because of the method used to assign ages. Of 18 dispersers of known age on the Kenai Peninsula, Alaska, 1 was a pup, 11 were yearlings and 2-year-olds, and 6 were ≥ 3.0 years old (Peterson et al. 1984). Similarly,

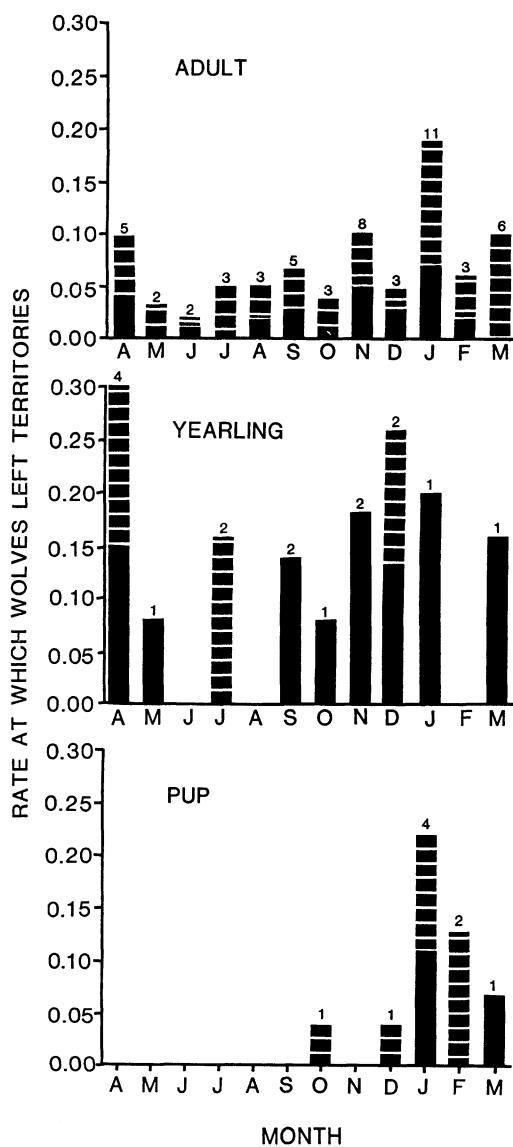


Fig. 3. Monthly rates (wolves leaving/total wolves) at which radio-collared wolves in packs (residents) left their territory each month, either temporarily (dashed bar) or permanently (solid bar). Number of wolves leaving indicated for each month for each age class.

←

Fig. 2. Annual wolf territory boundaries, early winter/late winter pack size estimates, and annual census area for wolf packs (dashed line) monitored in the Bearville Study Area (dot-dash line). Three-letter abbreviations identify packs. Solid line indicates that a territory was described by >30 radiotelemetry locations, and slanted dashed lines by <30 . Dotted lines indicate approximate locations of packs not radio-monitored in that year, but identified by aerial tracking.

40% of female and 50% of male dispersers in south-central Alaska were ≤ 2.0 years old (Ballard et al. 1987). At least 3 of 8 dispersers in northwest Minnesota were yearlings (Fritts and Mech 1981), as were 4 of 7 known-aged wolves that definitely dispersed in northeast Minnesota (Mech 1987).

Most wolves that dispersed from the BSA did so during November–January and March–May (Fig. 3). Wolves in other areas dispersed during autumn when pack members begin traveling together, prior to the breeding season, and/or in spring after pups are born (Fritts and Mech 1981, Berg and Kuehn 1982, Peterson et al. 1984, Messier 1985b, Ballard et al. 1987, Mech 1987).

There were no sex-related differences in dispersal rates of wolves in the BSA ($P > 0.16$), nor did maximum distance and duration of movements differ ($P > 0.05$) by sex. Ballard et al. (1987) reported higher dispersal rates for males. Peterson et al. (1984) also reported a preponderance of male dispersers during the first 4 years of their study, but in the fifth year more females dispersed and overall there was no significant sex-related difference.

Average dispersal distances of males and females are not consistently different: Peterson et al. (1984) reported females tended to disperse a shorter distance than males; Ballard et al. (1987) documented that, excluding a record movement of 2 males (732 km; Ballard et al. 1983), females dispersed farther than males; and Mech (1987) found no clear differences in dispersal distance. However, males predominate in reports of farthest dispersing wolves (Pulliainen 1965, Van Camp and Gluckie 1979, Fritts and Mech 1981, Berg and Kuehn 1982, Stephenson and James 1982, Ballard et al. 1983, Fritts 1983, Peterson et al. 1984).

Annual age-specific dispersal rates of resident wolves in the BSA were 17% for adults, 49% for yearlings, and 10% for pups > 5 months old. Only 1 radio-marked pup dispersed on the Kenai Peninsula (Peterson et al. 1984), and recalculation of dispersal and mortality data indicates that the annual dispersal rate of older wolves was

about 19%. Similarly, no pups dispersed in Quebec (Messier 1985b), but recalculated data indicate an annual dispersal rate of about 16% for yearlings and 25% for adults. Overall, dispersal rates were higher for pups and yearlings in the BSA than in Quebec or Alaska, but differences cannot clearly be attributed to prey density (biomass index per wolf = 161, 162, and 345, respectively), pack size (5.7, 4.7, and 11.2, respectively), annual survival (0.64, 0.64, and 0.67, respectively), or percent pups in packs (46% in the BSA vs. 36% in Alaska) (see Demography).

Survival rates sometimes are lower for wolves traveling outside home territories (Peterson et al. 1984, Messier 1985a), so extraterritorial excursions might be more common when opportunity to establish new packs is high, food is scarce within territories, or chances to breed in natal packs are low (Mech 1987). Fritts and Mech (1981:74) found “a high rate of dispersal of young wolves” in an expanding, newly protected population, and Ballard et al. (1987:21) reported apparently “higher rates of dispersal from areas of relatively low ungulate densities,” although no quantitative data concerning these rates were presented in either study. On Isle Royale, more wolves left packs when food supplies decreased (Peterson and Page 1988).

Five of 28 wolves that dispersed from packs in the BSA died while traveling alone, 10 likely dispersed beyond the range of our receiver, 1 was still alone at the end of the study, and 12 others settled 13 times after traveling for 4–210 days ($\bar{x} = 79$ days) and moving 5–70 km from home territories ($\bar{x} = 29$ km). Four lone wolves that settled established territories 3–76 km ($\bar{x} = 32$ km) from capture locations after traveling 142–267 days ($\bar{x} = 187$ days). Fifteen of these 17 settlers found mates and established territories as a pair, 1 yearling male wolf joined 2 radio-marked females that were the only remaining members of an already-established pack, and 1 wolf established a pack with 2 others that likely were pack mates. Four wolves settled during September–October, and 13 settled during December–February. The propor-

tion of wolves that settled each month did not differ by sex or age ($P > 0.80$) and ranged from 0 to 25% ($\bar{x} = 7\%$; Fig. 4, Appendix A). Four wolves from the BSA established territories immediately adjacent to their home territories, and 1 wolf marked as a pup joined an adjacent pack. The 8 other dispersers established territories 8–70 km ($\bar{x} = 39$ km) away from home territories.

Whether dispersing wolves pair and settle in a vacant area or join already-established packs, either adjacent to or far from home territories, success likely depends on a combination of relative prey abundance, the availability of vacant territories, and survival rates of breeding pack wolves. In Quebec, where prey was relatively scarce, a pair of dispersers acquired another associate and formed a pack, and 2 others were accepted by adjacent packs (Messier 1985b). In south-central Alaska, where pack sizes were reduced by high human harvest, 8 of 23 dispersing wolves later found with other wolves were in pairs and at least 8 more were apparently accepted into existing packs (Ballard et al. 1987). Of the 5 settlers on the Kenai Peninsula, where prey was abundant but mortality high, 3 paired with another wolf and 2 joined 2 other wolves (Peterson et al. 1984). In northwest Minnesota where the wolf population was rapidly expanding, all 9 radio-marked lone wolves paired rather than join a pack, but at least 1, and possibly 3, nonradioed wolves were thought to have joined packs (Fritts and Mech 1981). Also, 6 of 7 dispersers there paired within 8–30 days ($\bar{x} = 17$), and 3 lone wolves paired and settled in 95–148 days ($\bar{x} = 116$; Fritts and Mech 1981).

Demography

Pack Size and Lone Wolves.—Mean number of wolves per pack monitored in the BSA each year ranged from 4.7 to 9.3 (overall $\bar{x} = 6.7$) in early winter versus 3.9 to 6.3 ($\bar{x} = 4.7$) in late winter (Table 1). Individual pack size was as large as 13 in early winter and 9 in late winter (Fig. 2). Overwinter declines in mean pack size (\bar{x}

= −29%; −2.0 wolves) were correlated with early winter pack size ($r = 0.92$, 4 df, $P = 0.006$); larger packs lost more wolves through mortality and dispersal each winter than did small packs. The large increase in mean early winter pack size in 1984 was a result of the large number of pups that survived to that autumn (see Reproduction); the next year this cohort continued to compose a large proportion of the population.

Four of 25 new yearlings and adults captured in spring were lone wolves (nonresidents). Three of 23 yearling and adult wolves captured in autumn were nonresidents, but 33 pups also were captured then. Thus nonresidents composed only 5% of all autumn captures. However, the percentage of pups in the catch (33 of 53 residents = 62%) was higher than the percentage of pups in the resident population (46%; see Reproduction). Thus for every 23 yearlings and adults captured in autumn, one would expect there to be only 20 pups (46% of all wolves), and the adjusted proportion of nonresidents would be 7% ($3 \div [23 + 20]$).

Lone wolves and pairs without territories have been ignored in some population estimates (Fritts and Mech 1981, Peterson et al. 1984, Mech 1986), but have composed 2–29% of winter populations elsewhere (Mech 1966, Pimlott et al. 1969, Mech 1973, Fuller and Keith 1980, Messier 1985a, Ballard et al. 1987, Peterson and Page 1988). Lone wolves are difficult to census because (1) the chances of observing them incidentally is likely less than for larger groups and (2) capture rates may be biased if trapping is concentrated inside territories where lone wolves are less likely to travel (Fritts and Mech 1981). Modeling wolf mortality, dispersal, and settling rates may help estimate and identify seasonal changes in the proportion of lone wolves in a population (Fuller 1988a).

Density and Population Change.—During winters 1980–81 to 1985–86, density of wolves increased from 39 to 50/1,000 km² ($\bar{x} = 44.5/1,000$ km²) in early winter and from 31 to 35/1,000 km² ($\bar{x} = 32.8/1,000$ km²) in late winter (Table 3);

Table 3. Early (Nov-Dec) and late (Mar) winter density of wolves and annual rates of population change in north-central Minnesota.

Winter	Census area ^a (km ²)	No. of resident wolves ^a		Estimated no. of nonresident wolves ^b		Total		Density (wolves/1,000 km ²)		Annual rate of population increase	
		Early	Late	Early	Late	Early	Late	Early	Late	Finite (λ)	Exponential (r = ln λ)
1980–81	1,166	39	30	7	6	46	36	39	31	0.935	-0.067
1981–82	1,103	33	27	6	5	39	32	35	29	1.103	0.098
1982–83	1,140	46	30	9	6	55	36	48	32	0.938	-0.064
1983–84	1,248	38	31	7	6	45	37	36	30	1.333	0.287
1984–85	1,087	54	37	10	7	64	44	59	40	0.875	-0.134
1985–86	1,124	47	33	9	6	56	39	50	35		
Mean								44.5	32.8		

^a As in Fig. 2.

^b Assumes 16% of total population is composed of nonresidents (see text).

thus, average midwinter density was about 39/1,000 km². The number of packs in the census area did not increase (Fig. 2), but the mean number of wolves per pack increased from 6.2 to 8.0 in early winter and 4.6 to 5.0 in late winter; also, mean territory size was somewhat smaller (Table 1).

From 1 year to the next, some packs disappeared and others reoccupied vacant territories or settled in other unoccupied areas. Each March, 6–8 packs composed of 27–37 wolves had territories that encompassed all or part of the BSA (Fig. 2), and 1 or 2 of these packs (total = 19% of 43 pack-years), each consisting of 2–4 wolves (total = 10% of 188 wolf-years), had reoccupied vacant areas. Most of these "new" packs were composed of wolves that probably were not originally members of BSA packs, i.e., were immigrants (total = 13 of 19 wolves in "new" packs and 7% of all wolves). In addition to these immigrants, a wolf or 2 may have joined already-existing packs; 1 of 17 radio-marked wolves that dispersed and settled joined a pack rather than establishing its own.

The annual finite rate of increase in the BSA varied from 0.88 to 1.33 among late-winter estimates (Table 3), and the mean annual rate during 1980–81 to 1985–86 was 1.02. Annual exponential rates of increase ($r = \ln \lambda$) were not correlated ($P > 0.90$) with annual survival estimates (all ages, see below), but were correlated

(weighted $r = 0.89$, 3 df, $P < 0.02$) with mean number of pups per pack the previous autumn (see below).

Pimlott (1967) suggested that an intrinsic control of wolf numbers limited density to a maximum of about 39 wolves/1,000 km² in most areas. Mech (1973) concurred, but noted exceptions where prey densities were extremely high. Packard and Mech (1980) submitted that food supply critically affects wolf numbers over the long term. Subsequent research has demonstrated that if a limit occurs, densities are much higher than previously suggested. Densities in the BSA reached 59 wolves/1,000 km² in early winter and 40/1,000 km² in late winter 1984–85. On Isle Royale, density exceeded 80/1,000 km² during the 1970's and peaked at 92/1,000 km² in 1980; Peterson and Page (1988) concluded that the only natural limits to wolf density are those ultimately imposed by food.

Changes in wolf density due to varying ungulate density have been documented by long-term studies in northeast Minnesota (Mech 1977a, 1986) and Isle Royale (Peterson and Page 1988) and in areas of varying moose density in southwest Quebec (Messier and Crete 1985). A compilation of additional studies throughout North America (Appendix B) confirms that, regardless of prey type or stability of wolf populations (Keith 1983), average wolf densities are clearly correlated with biomass of ungulates (Fig. 5; $r^2 = 0.72$). The

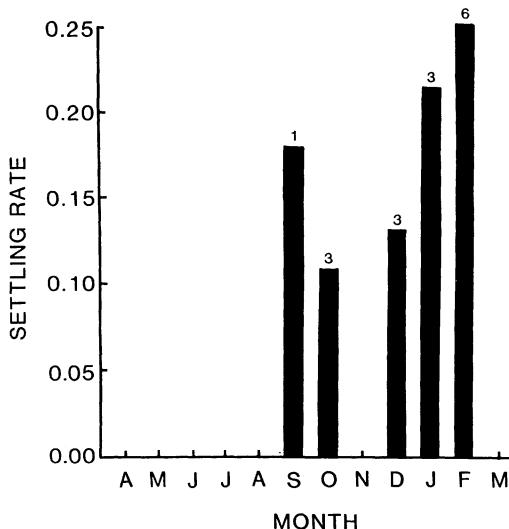


Fig. 4. Monthly rates at which lone wolves (nonresidents) settled (i.e., established their own packs or joined other than their natal packs). Number of wolves settling indicated for each month.

ungulate biomass index per wolf is highest for heavily exploited (Ballard et al. 1987) or newly protected wolf populations (Fritts and Mech 1981) and lowest for unexploited wolf populations (Oosenbrug and Carbyn 1982, Mech 1986) or those where ungulates are heavily harvested (Kolenosky 1972). In the BSA, where both wolf and white-tailed deer densities were high and deer were heavily harvested (Fuller 1988b), the ungulate biomass index per wolf (161) was well below the mean (249) and median (225) (Appendix B).

Reproduction.—Mean litter size for 5 females from the BSA whose reproductive tracts were examined (one who had 2 sets of placental scars) and one whose pups were seen outside of the natal den in 4 consecutive years was 6.1; mean size of all 9 litters was 6.6 (range = 4–8). Litter size was small for an unexploited population in Ontario ($\bar{x} = 4.9$; Pimlott et al. 1969) but large for exploited populations in Alaska ($\bar{x} = 6.5$; Rausch 1967) and northeast Minnesota ($\bar{x} = 6.4$; Stenlund 1955), leading Van Ballenberghe et al. (1975) and Keith (1983) to suggest that litter size may increase with

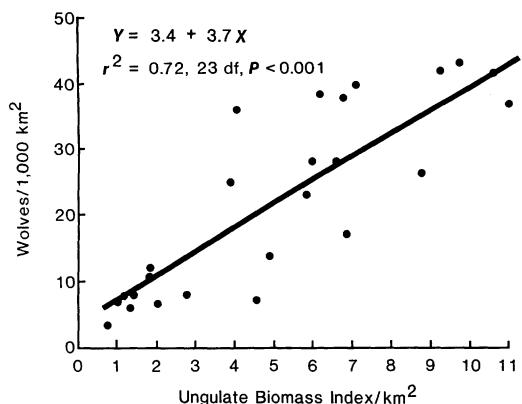


Fig. 5. Relationship between ungulate biomass and wolf density for various areas of North America. Ungulate density, wolf density, and ungulate biomass index values from Appendix B.

greater ungulate biomass per wolf. A summary of 8 studies does not support this contention (weighted $r = 0.37$, 6 df, $P = 0.45$; Table 4).

No packs in the BSA ($n = 36$ pack litters) were known to have produced >1 litter each year. Most wolf packs produce only 1 litter of pups per year (Packard and Mech 1980, Packard et al. 1983), although 2 litters per pack (by different females) have been reported (Murie 1944, Harrington et al. 1982, Van Ballenberghe 1983b, Peterson et al. 1984, Ballard et al. 1987). Consequently, if there are >2 female wolves ≥ 2 years old per pack, some likely do not breed, and populations with larger packs have a lower proportion of breeders (Peterson et al. 1984, Ballard et al. 1987). Peterson et al. (1984) found that increased harvest on the Kenai Peninsula resulted in smaller packs and territories and in establishment of new packs in vacated areas. As a result, breeders made up a higher proportion of the population, and the rate of pup production increased.

One female and 1 male wolf in the BSA, both captured and marked as pups, were 22 months old when they first bred; each, with its mate, successfully raised pups. Mech and Seal (1987) reported that the youngest wild female wolf known to have produced pups was 3.0 years old, although 1 known 2.0-year-old wolf in Alaska pro-

Table 4. Ungulate biomass index per wolf ratios vs. litter size, percent pups in packs, and number of pups per pack during late autumn to early winter in North America.^a

Location	Ungulate biomass index per wolf ^b	Litter size		Percent pups in packs	No. pups per pack		Reference
		\bar{x}	n		\bar{x}	No. packs	
North-central Minnesota	161	6.6	9	46	3.2	36	This study
Northeast Minnesota	166 ^c			41	2.6	24	Harrington et al. 1983
Interior Alaska	175	4.4	12				Gasaway et al. 1983
East-central Ontario	179	4.9	10				Pimlott et al. 1969
North-central Minnesota	214			45	3.3	3	Berg and Kuehn 1982, pers. commun.
Southern Quebec	214	5.6	10				Potvin 1988
Northeast Minnesota	221			43	3.4	5	Van Ballenberghe et al. 1975
Northeast Alberta	231			43	3.8	5	Fuller and Keith 1980
Northeast Minnesota	252	6.4	8				Stenlund 1955
Isle Royale, Michigan	264			48	3.1	7	Peterson and Page 1988
Denali Park, Alaska	334			39	5.4	5	Haber 1977
Kenai Peninsula, Alaska	345	5.0	5	35	3.8	15	Peterson et al. 1984
Jasper Park, Alberta	364			45	4.4	5	Carbyn 1974
Northwest Minnesota	400	7.0	1	57	3.2	12	Fritts and Mech 1981, Harrington et al. 1983
South-central Alaska	659	6.1	16	67	5.4	28	Ballard et al. 1987

^a Correlation between ungulate biomass index per wolf and litter size: weighted $r = 0.37$, 6 df, $P = 0.45$. Correlation between ungulate biomass index per wolf and percent pups in packs: $r = 0.73$, 9 df, $P = 0.005$. Correlation between ungulate biomass index per wolf and number of pups per pack: weighted $r = 0.88$, 9 df, $P = 0.001$.

^b From Appendix B.

^c Mean of ratios for Mech's study area in northeast Minnesota during 1967–69 and 1976–84 because data in Harrington et al. (1983) are from that area during 1970–78.

duced pups (Peterson et al. 1984) as have several 1-year-old and 2-year-old captive wolves (Rabb et al. 1967, Lentfer and Sanders 1973, Medjo and Mech 1976). Thus, all wolves except pups probably are capable of producing young, and the proportion that do breed is a function of age structure, pack size, and number of packs versus lone wolves in the population. It is not surprising that some radio-marked 2.0-year-olds in the BSA produced pups, as the proportion of pups (and subsequently yearlings) and dispersal rates of yearlings were relatively high and pack sizes were relatively small.

By November each year, an average of 3.2 pups (range = 2.7–5.0) remained in each pack, composing about 46% of pack members (range: 32–57%; Table 5). The greatest number of pups that survived in a pack until late autumn was 8; median and modal number of pups was 3. Though mean numbers of pups per pack changed almost twofold between some years, numbers did not correlate ($P > 0.99$) with either the number of adults or the number of

auxiliaries per pack, similar to Peterson et al. (1984) and Ballard et al. (1987), but different from Harrington et al. (1983). Pup numbers also did not vary with several annual indices of food abundance: the previous winter's severity (mean weekly snow depth during Dec–Mar, indexing spring ungulate vulnerability [Nelson and Mech 1986a]), the previous winter's deer : wolf ratio, or the mean number of beaver colonies in the BSA the same autumn ($P > 0.61$). Also, number of pups in each pack did not correlate (weighted regression; $P = 0.40$) with beaver colony density within a pack's territory the same autumn ($n = 25$ packs, $\bar{x} = 11\%$ areal coverage/territory).

Keith (1974:34) noted that the proximate and ultimate factors affecting wolf pup mortality rates during the first 5 months were almost wholly unknown and, because both summer food abundance and pup mortality are difficult to measure, represented "the single greatest enigma in wolf biology today." In northeast Minnesota, pup survival apparently decreased as the

Table 5. Wolf pup : adult ratios in October–December ($\bar{x} = 11$ Nov) of radio-marked packs with part or all of their territories on the Bearville Study Area as determined from direct observations and from spring-to-fall increases in pack size.

Pack	1980	1981	1982	1983	1984	1985	1986	Total
Sherry	4:2	3:3	5:5	2:4	6:3			
Hartley		0:4	3:2	5:4	4:8	5:7	3:4	
Scenic		7:3	4:4	3:4	8:5	3:8	4:7	
Larson	3:6	3:3	4:5	1:3				
Raddison Lake			3:2	4:4				
Homestead						3:4		
Deer Lake 1	1:2	0:2	4:2				2:3	
Deer Lake 2								
Valley River 1		3:3	0:2	1:1				
Valley River 2					7:2	1:8	2:5	
Snake					0:1			
Long							5:2	
Total	8:10	16:18	23:22	16:19	25:19	14:30	14:18	116:136
Percent pups	44	47	51	46	57	32	44	46
\bar{x} no. pups/pack	2.7	2.7	3.3	2.7	5.0	2.8	3.5	3.2
\bar{x} no. ad./pack	3.3	3.0	3.1	3.2	3.8	6.0	4.5	3.8
\bar{x} pack size	6.0	5.7	6.4	5.9	8.8	8.8	8.0	7.0

ungulate food base declined (Seal et al. 1975, Van Ballenberghe and Mech 1975, Mech 1977a). Percent pups in packs was highest ($r = 0.73$, 8 df, $P = 0.008$; Table 4) in newly protected (Fritts and Mech 1981) and heavily exploited populations (Ballard et al. 1987) and likely reflects higher pup survival where ungulates are abundant (see below). Mean ungulate biomass per wolf and mean number of pups per pack in autumn or early winter populations also were correlated ($r = 0.88$, 8 df, $P < 0.001$).

Survival.—A pup survival rate of 0.48 from birth (in mid-Apr; Fuller 1989) through mid-November was estimated from mean numbers of pups per pack at both times (6.6 and 3.2, respectively) and is lower than the rate of 0.76 on the Kenai Peninsula (Peterson et al. 1984) or 0.89 in south-central Alaska (Ballard et al. 1987). This may be related to ungulate availability; ungulate biomass per wolf was only 161 in the BSA versus 345 and 659, respectively, for the 2 areas in Alaska.

Forty-six radio-collared wolves died or were assumed to have died during this study. There were no significant differences ($P > 0.23$) related to sex or age in annual survival rates or survival during each month, and survival of resident wolves

≥5 months old (0.67) was not statistically greater ($P = 0.22$) than that of nonresidents (0.52). Mean annual survival rate for all radio-collared wolves was 0.64 and did not differ ($P > 0.25$) among years (range = 0.57–0.71). Survival of radio-collared pups from mid-November through March was not different ($P > 0.40$) than for marked yearling and adult pack members ($\bar{x} = 0.77$), and thus annual pup survival was 0.37 (0.48×0.77).

The annual survival of dispersing adults on the Kenai Peninsula was only 0.38 versus 0.73 for resident adults (Peterson et al. 1984). Mortality of wolves traveling outside versus inside territories also was higher in Quebec (Messier 1985a). On the Kenai Peninsula, as in the BSA, survival of pups during October–April was similar to that of older wolves (0.88 vs. 0.85; Peterson et al. 1984), but annual pup survival was similar to resident adult survival (0.70 vs. 0.73) and thus much higher than in the BSA. In contrast, November–April pup survival (0.43) was lower than annual survival of adults and yearlings in south-central Alaska (0.59 and 0.68, respectively), but was 0.35 annually, similar to pup survival in the BSA.

In the BSA, no mortality of marked wolves occurred during April–May, but

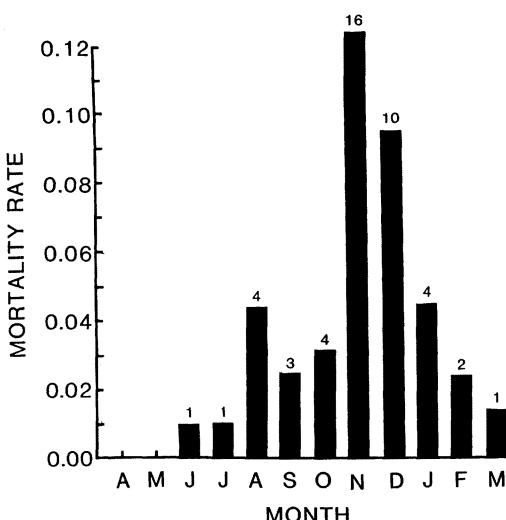


Fig. 6. Monthly mortality rates of radio-collared wolves ≥ 5 months old monitored in north-central Minnesota during 1980–86. Number of wolves dying indicated for each month.

some mortality occurred throughout the summer and increased significantly ($P = 0.007$) during the November deer-hunting season (Fig. 6, Appendix A). Mortality also was high in December (the major fur-taking season), then decreased through the winter. Despite legal protection, at least 80% of wolf mortality was human caused (Table 6); some deaths attributed to unknown causes (8% of all mortality) also might have been human related. Many wolves (26% of mortality) were shot by deer hunters during the 16-day season in

November, and others (27%) were shot, snared, or hit by a vehicle in other months. Two wolves also were killed by federal depredation trappers (6%) in July and August at a farm where pack members had killed livestock. Intraspecific aggression (10%) occurred only during October–December. One wolf died of pneumonia (2%) in February and perhaps was predisposed by a previous infection of canine distemper (G. R. Ruth, Univ. Minn., pers. commun.). Road density within 2 km of sites of death was higher ($t = 2.25$, 24 df, $P = 0.034$) for wolves killed by humans ($\bar{x} = 0.55 \text{ km/km}^2$, $n = 20$) than for those dying from intraspecific strife and disease ($\bar{x} = 0.27 \text{ km/km}^2$, $n = 6$).

Potential rates of wolf population increase should be higher after human exploitation because increased per capita food availability results in increased pup production and survival (Keith 1983; see above). However, reproduction may not fully compensate for exploitation rates that are too high. After summarizing demographic variables, Keith (1983) estimated that maximum sustainable exploitation was probably <30% of the early winter population. The human-caused mortality rate in the BSA was at least 29%, and the population was stable or slightly increasing. Peterson et al. (1984) reported that wolf density on the Kenai Peninsula declined following 2 annual kills of >40%, but increased after harvests of <35%. Gasaway

Table 6. Cause-specific mortality rates (Heisey and Fuller 1985) and relative importance of mortality factors for 81 radio-marked wolves ≥ 5 months old monitored during September 1980–December 1986 in north-central Minnesota.

Cause	Resident (31 mortalities)		Nonresident (10 mortalities)		Total		
	Rate	%	Rate	%	Rate	95% CI	%
Shot by deer hunter	0.08	23	0.19	38	0.09	0.05–0.14	26
Shot by other	0.01	3	0.04	8	0.02	0.00–0.04	4
Snared	0.04	12	0.04	7	0.04	0.01–0.08	12
Hit by a vehicle	0.03	8	0.11	22	0.04	0.01–0.07	11
Depredation complaint ^a	0.03	8			0.02	0.00–0.05	6
Killed by humans ^b	0.08	22	0.07	13	0.08	0.03–0.12	21
Killed by wolves	0.03	11	0.06	12	0.04	0.01–0.07	10
Pneumonia	0.01	3			0.01	0.00–0.02	2
Unknown ^c	0.03	10			0.03	0.00–0.06	8

^a U.S. Fish and Wildlife Service depredation program.

^b Undetermined human caused (possibly hit by car, trapped, snared, or shot).

^c Cause not determined.

Table 7. Mean rates of population increase vs. annual total and human-caused mortality rates of exploited wolf populations in North America.^a

Location	No. of years	Annual finite rate of population increase (λ)	Exponential rate of population increase (r)	Annual mortality rate		Reference
				Total	Human-caused	
Northwest Alberta	2	0.40	-0.92	(0.68) ^{b,c}	0.68 ^b	Bjorge and Gunson 1983
Interior Alaska	4	0.69	-0.37	(0.46) ^{b,c}	0.46 ^b	Gasaway et al. 1983
South-central Alaska	8	0.88	-0.13	0.45	0.36	Ballard et al. 1987 ^d
North-central Minnesota	3	0.93	-0.08	0.31	0.31	Berg and Kuehn 1982, pers. commun.
North-central Minnesota	6	1.02	0.02	0.36	0.29	This study
Kenai Peninsula, Alaska	6	1.06	0.06	0.33	0.27	Peterson et al. 1984 ^d
Southwest Quebec	4	1.11	0.10	0.36	0.19	Messier 1985 ^{a,d}
Northwest Minnesota	5	1.19	0.17	0.28	0.17	Fritts and Mech 1981 ^a
Northeast Alberta	2	1.21	0.19	0.15	0.15	Fuller and Keith 1980 ^d

^a Correlation between exponential rate of increase and annual total mortality rate: weighted $r = -0.90$, 7 df, $P < 0.001$. Correlation between exponential rate of increase and annual human-caused mortality rate: weighted $r = -0.98$, 7 df, $P < 0.001$ (see Fig. 7).

^b Mortality rate of early winter population; assumes summer survival of adults = 1.00.

^c Minimum total mortality rate because only includes human-caused mortality.

^d Recalculated.

et al. (1983) reported stable populations following harvests of 16–24% of the early-winter population, but found numbers declined 20–52% after harvests of 42–61% of the population. Ballard et al. (1987:29) estimated that human exploitation of >40% of the autumn population would cause a population decline. I reanalyzed their data (W. B. Ballard, Alas. Dep. Fish and Game, pers. commun.) using transformed values of finite rates of increase (i.e., exponential rates of increase) as a regression variable with percent overwinter mortality results to increase model fit (i.e., reduce residuals). The revised model suggested, on average, a stable population ($\lambda = 1.00$) with an overwinter mortality of 35% and harvest rate of 28% ($r = -0.81$, $P < 0.001$); however, 8 of 25 packs with >35% mortality (about 28% harvest) had subsequent rates of increase ≥ 1.00 (W. B. Ballard, pers. commun.). For the unexploited wolf population on Isle Royale, annual mortality of adult-sized wolves was 13–16% when numbers were increasing or stable at high numbers, 51% during a population crash, and 33–34% when the population subsequently stabilized (Peterson and Page 1988).

Summary analyses indicate that observed exponential rates of increase (r) during sustained exploitation (Table 7) are

negatively correlated with both total (weighted $r = -0.90$, 7 df, $P < 0.001$) and human-caused annual mortality rates (weighted $r = -0.98$, 7 df, $P < 0.001$) of adult-sized wolves. These relationships suggest that population size would stabilize ($r = 0.00$, $\lambda = 1.00$) with an overall mortality rate of 0.35, or a human-caused rate of 0.28 (Fig. 7). However, these values may vary with the age and sex structure of the population. For example, a population with a high proportion of pups may be able to withstand somewhat higher overall mortality because pups (nonreproducers) may be more vulnerable to some harvest techniques and make up a disproportionate part of the harvest. Also, net immigration or emigration may mitigate effects of harvest.

Feeding Ecology

Winter Predation.—Wolves located from aircraft were observed at ungulate carcasses on 176 occasions. Of these, 145 were fresh kills of which 74 were identified during ground investigations, 61 were identified only from the air by signs of a chase or fresh blood, and 10 were assumed to be kills because packs stayed in areas of dense conifer cover on successive days and 3–15 ravens (*Corvus corax*) were present.

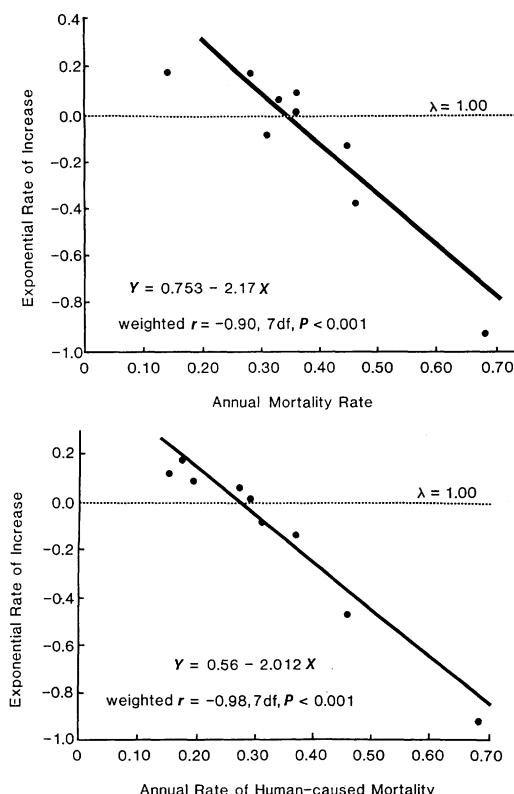


Fig. 7. Relationship between exponential rates of increase and annual mortality rates of 9 wolf populations in North America (Table 7). Intercepts of regression lines with dotted line indicate rates of mortality that would result in a stationary population (total mortality—0.35; human-caused mortality—0.28).

Of the 31 carcasses that were not fresh kills, 18 were investigated on the ground, 7 were known to be revisited kills (i.e., first observed as fresh kill of radioed wolves earlier), 4 were identified from aircraft by the presence of antlers on male carcasses in February (males usually drop antlers by mid-January; T. K. Fuller, pers. observ.),

and 2 were assumed not to be fresh kills because of a lack of any blood on the snow or tracks indicating a chase.

The proportion of flights during which single wolves or packs of 2–10 were observed at carcasses of deer they had killed during January–February did not vary between winters with shallow versus moderately deep snow ($P > 0.17$). The proportion of days packs were at kill sites (Table 8) varied with pack size ($\chi^2 = 32.8$, 4 df, $P < 0.001$) as did the number of days per kill per wolf ($\chi^2 = 15.6$, 4 df, $P < 0.01$), but neither did so linearly ($P > 0.10$). The best estimate of the overall, unadjusted kill rate is the unweighted mean for all packs (42.4 days/kill/wolf; Table 8). However, no packs, regardless of size [n kills (pack size) = 2(2), 1(3), 1(4), 5(6), and 8(9)] stayed at kill sites an average of more than 12 hours (i.e., none were found at sites on 2 consecutive flights), and thus unadjusted kill rates were underestimated by at least 50% (see Methods). The corrected mean kill rate is 21.2 days/kill/wolf (42.4 \times 0.5), and the minimum total number of deer killed per wolf per winter (1 Nov–31 Mar) was 7.1 (151 days \div 21.2 days/kill).

Kill rates vary with pack size in other areas where moose are the primary prey (Ballard et al. 1987), but wolves stay at moose kills 1–8 days (Fuller and Keith 1980, Ballard et al. 1987) and daily locations of packs are adequate to document kill rates of packs of different sizes. Deer, however, are about one-sixth the size of moose, and it is not surprising that no packs in the BSA stayed at deer kill sites >24 hours. Large packs in the BSA likely remained at kills <12 hours (resulting in an apparently lower kill rate per wolf than

Table 8. Frequency of radio-marked wolf packs at kill sites in north-central Minnesota during January–February 1981–86.

	Pack size					
	1–2	3–4	5–6	7–8	9–10	Total
(A) No. of locations at kills	17	27	28	5	19	96
(B) No. of pack locations	350	176	230	58	126	840
(C) Mean pack size	1.7	3.6	5.5	7.1	9.2	4.9
(D) No. of wolf-days ($B \times C$)	593	637	1,267	413	1,165	4,075
(E) Days per kill per pack ($B \div A$)	20.6	6.5	8.2	11.6	6.6	8.8
(F) Days per kill per wolf ($D \div A$)	34.9	23.6	45.3	82.6	61.3	42.4

for smaller packs [Table 8]), and thus overall kill rates likely were underestimated.

Fawns composed 54% of wolf-killed deer examined *in situ* for which sex and/or age could be determined ($n = 74$), and females composed 60% of deer ≥ 1.0 year old ($n = 25$). Given these observed sex and age ratios, the average whole-body weight of adult deer was about 78 kg versus 39 kg for fawns (Hamerstrom and Camburn 1950, Fuller et al. 1989), and the weighted mean weight of kills was 57 kg ($[78 \times 0.46] + [39 \times 0.54]$). Edible portions of deer would not include bones (without marrow), rumen contents, or hide, estimated to weigh about 10, 8, and 8% of deer, respectively (Short et al. 1969, Hakonson and Whicker 1971, Anderson et al. 1974), or 26% of whole weight (similar to Peterson's [1977] estimate for moose). Given a mean edible weight of about 42 kg (0.74×57) for all wolf-killed deer, the total deer biomass eaten per wolf per winter would then be 298 kg (7.1×42 kg). The average daily consumption would be 2.0 kg/wolf ($298 \div 151$), or 0.06 kg/kg wolf/day, based on an average adult wolf weight of 34 kg.

This estimate assumes complete consumption of edible parts and does not include any small prey such as snowshoe hares or food scavenged from deer or moose dying of other causes. Only 6 of 78 (8%) deer killed by wolves in winter and examined *in situ* were not totally consumed (all meat and many bones), and only 2 of those had $>2-5$ kg of meat remaining. Also, hares likely composed $\leq 2\%$ of food biomass in winter (see Scat Analyses). Wolves were seen at 24 (14% of 169) carcasses of deer that had died previously and were being scavenged, but at least 7 of these were kills made earlier by the wolves. No wolf-killed moose were observed, but carcasses of 7 adult moose (1–2 each winter) also were scavenged (Fuller 1986).

Messier and Crete (1985) reported that among adjacent study areas with differing but low moose densities, there were higher kill and consumption rates of moose by wolves where densities of moose were higher. However, daily food availability per wolf on Isle Royale was not clearly

related to wolf : moose ratios (Peterson and Page 1988). A review of various studies (Table 9) indicates that ungulate biomass correlates moderately well with mean winter consumption rates (kg/wolf/day— $r = 0.56$, 12 df, $P = 0.02$; kg/kg wolf/day— $r = 0.46$, 12 df, $P = 0.08$). Some rates may be high because carcass utilization was not quantified; thus they reflect the rate at which prey were killed, not consumed (i.e., rate of availability). Also, Pimlott et al. (1969) and Mech et al. (1971a) reported wolves abandoned partially eaten deer kills during winters with deep snow, and Carbyn (1983) found that wolves consumed only about half the biomass of elk they killed in a winter with relatively deep snow. Such weather-related influences cannot be incorporated into this analysis. Also, some variation likely is due to the vagaries of estimating wolf predation rates on deer (see Methods).

Scat Analyses.—Deer remains composed 45–91% of identified items in scats each month, depending on time of year and collection site (Table 10; $n = 2,386$ scats). During winter, deer and snowshoe hares composed the majority of prey, but, in April and May, beaver occurred as 20–47% of items. In June and July, occurrence of beaver diminished and deer fawns became most common (25–60% of all occurrences, 32–69% of deer occurrences). Occurrence of beaver increased during August–October (3–22%), but not to the high level of spring. Vegetation (mainly berries) increased in occurrence during July–September (4–52%).

Extrapolations of scat data (Table 11) indicate that deer provided 79–98% of animal biomass consumed by wolves each month; beavers provided >10% of biomass consumed only in April and May (12 and 19%, respectively). Deer fawns were eaten 4 times more often than adults in June, but by July were eaten only as often as adults, similar to the ratio in winter (see above). Snowshoe hares were apparently killed and consumed about as often as deer in most months, but this was true for beaver only in April and May.

Wolf food habits, as assessed through

Table 9. Ungulate biomass index per wolf vs. estimated winter consumption rates of ungulates by wolves during winter in North America.^a

Location	Major prey species	Ungulate biomass index per wolf ^b	Mean consumption rate in winter		Reference
			kg/wolf/day	kg/kg of wolf/day	
East-central Ontario	Deer	112	2.9	0.10 (30) ^c	Kolenosky 1972
Northern Alberta	Bison	152	5.3	0.14 (38)	Oosenbrug and Carbyn 1982
West-central Yukon	Sheep	153	3.0	0.08 (37)	Sumanik 1987
North-central Minnesota	Deer	161	2.0	0.06 (34)	This study
Southwest Quebec	Moose	162	2.2 ^d	0.07 ^d (30)	Messier and Crete 1985
Northeast Minnesota	Deer	178	2.9	0.10 (30)	Mech 1977b
Isle Royale, Michigan	Moose	225	7.2 ^e	0.22 ^e (33)	Peterson 1977
Northeast Alberta	Moose	231	5.5	0.14 (38)	Fuller and Keith 1980
Isle Royale, Michigan	Moose	264	4.9 ^e	0.15 ^e (33)	Peterson and Page 1988
Denali Park, Alaska	Moose	334	4.5	0.11 (40)	Haber 1977
Southwest Manitoba	Elk	336	6.8	0.21 (32)	Carbyn 1983
Kenai Peninsula, Alaska	Moose	345	4.8 ^e	0.12 ^e (40)	Peterson et al. 1984
Northwest Minnesota	Deer	400 ^f	2.9 ^e	0.09 ^e (32)	Fritts and Mech 1981
South-central Alaska	Moose	659 ^g	7.1	0.18 (40)	Ballard et al. 1987

^a Correlation between the natural logarithm (ln) of ungulate biomass index per wolf and kg/wolf/day: $r = 0.56$, 12 df, $P = 0.02$. Correlation between ln ungulate biomass index per wolf and kg/kg wolf/day: $r = 0.46$, 12 df, $P = 0.08$.

^b From Appendix B.

^c Estimated mean mass (kg) of wolf in each area.

^d Does not include 15–40% other food items.

^e Amount available, not necessarily amount consumed.

^f Wolf population newly protected.

^g Wolf population heavily exploited.

scat analyses, differ by month and site (Table 10; Kuyt 1972, Theberge et al. 1978, Fuller and Keith 1980, Scott and Shackleton 1980); if not taken into account, such

differences may confound interpretation of summer food habits. Moreover, not all ungulates eaten may be killed by wolves; Peterson et al. (1984) surmised that on the

Table 10. Annual food habits of wolves in and near the Bearville Study Area as represented by 2,386 scats containing 2,711 food items that were collected on trail and roads (T) and at den and rendezvous sites (D) during November 1980–December 1983.

Species	Percent occurrence of food items											
	Apr ^a		May ^a		Jun ^a		Jul ^a		Aug–Sep ^a		Oct	Nov–Mar
	T	D	T	D	T	D (ad)	D (pup)	T	D	T	D	T
Deer (adult)					27	53	26	52	19			
Deer (fawn)					60	38	60	25	30			
Total deer	61	71	45	70	87	91	86	77	49	56	65	72
Beaver	30	20	47	23	5	2	2	2		3	22	8
Snowshoe hare	7	8	5	6	2	6	5	9		7	4	8
Other mammal ^b	2	1	1	<1	6	2	3	8		5	<1	4
Vegetation ^c	<1	<1	<1			4	4	52	20	9		1
Bird	<1	<1		<1					1			8
Grasshopper									8			
No. of items	145	706	215	739	85	55	125	92	27	197	116	25
												184

^a Occurrence of beaver in scats at Apr and May den and rendezvous sites was significantly less (chi-square tests, $P < 0.05$) than in scats collected on trails. In Jun, pup scats and scats collected on trails contained more fawn hair than did scats of adults collected at rendezvous sites. In Jul, a small sample of pup scats from a rendezvous site had a high occurrence of raspberries, and in Aug, less beaver and more vegetation were in scats collected on trails.

^b Includes microtines (12 items), woodchuck (*Marmota monax*) (12 items), red squirrel (*Tamiasciurus hudsonicus*) (12 items), wolf (2 items), striped skunk (*Mephitis mephitis*) (4 items), black bear (*Ursus americanus*) (6 items), bobcat (*Felis rufus*) (1 item), badger (*Taxidea taxus*) (2 items), and chipmunk (*Tamias striatus*) (1 item).

^c Includes raspberries (*Rubus* spp.), blueberries (*Vaccinium* spp.), and grasses.

Table 11. Estimated number (relative to total deer) and percent biomass of prey consumed by wolves in north-central Minnesota as extrapolated (Floyd et al. 1978, Traves 1983) from analyses of scats collected on roads and trails and at den and rendezvous sites (data pooled) during November 1980–December 1983.^a

Prey	Apr	May	Jun	Jul	Aug-Sep	Oct	Nov-Mar
Relative no. of prey consumed							
Deer (adult)			0.2	0.5			
(fawn) ^b			0.8	0.5			
Total	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Beaver	0.5	0.9	<0.1	<0.1	0.2	0.1	
Snowshoe hare	1.2	1.0	0.2	1.2	0.7	1.0	0.9
Percent biomass of prey consumed							
Deer (adult)			59	80			
(fawn)			37	15			
Total	85	79	96	95	91	94	98
Beaver	12	19	2	1	7	4	
Snowshoe hare	3	2	2	3	2	3	2

^a Whole weight estimates (kg): total deer (assumes fawn : adult ratio = 54:46; from winter kill data) for Aug = 42, Sep = 46, Oct = 50, and Nov–May = 53; adult deer for Jun–Jul = 78; fawn deer for Jun = 7 and Jul = 18; beaver = 12.5; snowshoe hare = 1.2. Assumes edible weight of total deer (Aug–Nov) and adult deer (Jun–Jul) = 74%; fawn deer (Jun–Jul), beaver, and snowshoe hare = 90%.

^b Fawns born 1 Jun; hair from adults and fawns not distinguishable in scats after Jul.

Kenai Peninsula, wolves scavenged carcasses of adult moose extensively in summer. Nevertheless, a majority of studies indicates that even though alternate foods are most available in summer (and ungulate prey are less important than in winter), ungulates usually compose >75% of biomass consumed by wolves at that time (Thompson 1952, Pimlott et al. 1969, Frenzell 1974, Van Ballenberghe et al. 1975, Voigt et al. 1976, Peterson 1977, Theberge et al. 1978, Fuller and Keith 1980, Fritts and Mech 1981, Reimann 1983, Peterson et al. 1984, Ballard et al. 1987). Although wolves likely consume 1 to 9 times more newborn ungulates than adult ungulates, no studies have identified the factors influencing rates of predation on juveniles (Mech 1966, Crete et al. 1981, Messier and Crete 1985, and studies cited above).

Beaver often provide a major alternative summer food source for wolves, and more are consumed as their numbers, relative to ungulates, are high (Mech 1966:152, Shelton 1966, Pimlott et al. 1969, Hall 1971 in Peterson 1977, Voigt et al. 1976, Peterson 1977:53, Carbyn and Kingsley 1979, Fuller and Keith 1980, Peterson et al. 1984, Messier and Crete 1985). The peak period of utilization of beaver differs among areas,

but generally occurs during April–August (Van Ballenberghe et al. 1975, Voigt et al. 1976, Peterson 1977, Scott and Shackleton 1980, Crete et al. 1981, Fritts and Mech 1981). Increased beaver abundance may result in increased pup survival, but only Peterson (1977) has been able to demonstrate such a relationship.

Numbers of Deer Killed.—Given a summer consumption rate of 59 kg deer/wolf/month (1.9 kg/day × 31 days), 7.2 fawns and 4.5 adults are consumed per wolf during April–October in the BSA (Table 12). Of the 7.1 deer consumed per wolf in winter (15 Nov–31 Mar), 3.8 were fawns (54% fawns × 7.1) and 3.3 were adults. Thus, total annual per capita consumption in the BAS was 11.0 fawns (7.2 + 3.8) and 7.8 adults (4.5 + 3.3), or 18.8 deer/wolf/year.

Mech (1971) guessed that wolves killed 15 deer/wolf/year, and Keith (1983) extrapolated an average winter kill rate in 3 studies to summer, resulting in an annual average of 16.6 deer/wolf. Pimlott (1967) estimated an annual kill of 36.7 deer/wolf, but assumed daily consumption was 3.6 kg/wolf/day, almost twice that in the BSA (2.0 kg/wolf/day), but lower than for areas where ungulates other than deer are the primary prey of wolves (Table 9).

Table 12. Estimated number of fawn (≤ 1.0 year old) and adult deer consumed per wolf during April–October in north-central Minnesota as extrapolated from scat analyses (Floyd et al. 1978, Traves 1983) and estimated consumable weights of deer. For this example, monthly consumption is assumed to be 59 kg/wolf.

Variable	Apr		May		Jun		Jul		Aug		Sep		Oct	
	Fawn	Ad												
(A) Consumable wt (kg)	32	57	32	57	6	57	12	57	16	57	22	57	29	57
(B) Total biomass consumed (kg) ^a	20	31	19	29	17	41	10	47	14	41	17	38	21	35
(C) Total no. individuals consumed ($B \div A$)	0.6	0.5	0.6	0.5	0.5	2.8	0.7	0.8	0.8	0.9	0.7	0.8	0.7	0.6
Total no. of fawns consumed = 7.2														
Total no. of adults consumed = 4.5														

^a Calculated from equations

$$R(X \div F) = Y \div A$$

where R = ratio of adult to fawn deer consumed (0.85 during Apr–May and Aug–Oct, 0.25 in Jun, and 1.0 in Jul; Table 11), X = biomass of fawns consumed, Y = biomass of adults consumed, F = consumable weight of fawns, and A = consumable weight of adults

$$X + Y = W(Z)$$

where W = monthly biomass consumption per wolf and Z = percent biomass of diet comprised by deer.
Whole weight (kg) estimates for fawn deer are: Aug = 20, Sep = 28, Oct = 36, Nov–Apr = 40, and others as in Table 11.

Management

Rates of wolf population increase are most affected by relative ungulate biomass availability (directly affecting survival of pups < 6 months old) and human-caused mortality. Fortunately, the most direct manipulative tool in managing these 2 parameters is legal regulation of both wolf and ungulate harvests. A prerequisite for responsible management, however, is accurate monitoring of population density and harvest.

Ungulate biomass availability depends on ungulate size, density, and vulnerability, but, in most calculations, ungulate density is the major component of availability because size is known and factors affecting vulnerability can rarely be used in a predictive way. Relative “condition” of a population is seldom known, age structures are not highly correlated with vulnerability, and effects of winter weather on food availability are imperfectly known (Fuller 1988a). On the other hand, ungulate densities can be estimated by a number of methods, and regulation of ungulate harvest is a major concern for all government agencies in areas where wolves occur.

Several techniques have been used to survey wolves (e.g., Mech 1966, Pimlott et al. 1969, Rausch 1969, Kolenosky 1972, Carbyn 1975, Theberge and Strickland 1978, Crete and Messier 1987, Fuller and Sampson 1988), though in forested areas, actual censuses are best done with the aid of radiotelemetry (Mech 1973, 1982; Fuller 1982; Fuller and Snow 1988). Lone wolves and pairs without territories compose 2–29% of winter populations and should not be ignored.

In areas where wolves are legally harvested, the total number killed often is monitored closely through registration. Thus, changes in wolf numbers are predictable, given a reliable estimate of wolf population density and relatively constant natural mortality due to disease (Chapman 1978, Carbyn 1982) and intraspecific strife

(Mech 1977a). In Minnesota, however, wolves are legally killed only through depredation control, but many are killed illegally and accidentally (Mech 1977a, Fritts and Mech 1981, Berg and Kuehn 1982; see Survival); this mortality cannot be enumerated, except through intensive radiotelemetry studies. Nevertheless, human-related wolf mortality is correlated with distribution and density of roads; therefore, regulating road access (especially during hunting seasons) likely can control human-caused mortality of wolves.

It is apparent that under certain circumstances wolves can regulate ungulate numbers (Pimlott 1967, Mech 1970, Gasaway et al. 1983, Keith 1983, Messier and Crete 1985, Bergerud and Ballard 1988). Ungulate populations that declined precipitously in several areas due to severe winter weather, habitat change, overhunting, and/or predation remained low because of low ungulate:wolf ratios (Mech and Karns 1977, Gasaway et al. 1983, Bergerud and Elliot 1986, Ballard et al. 1987). In some areas, hunting of ungulates was restricted and/or wolf numbers were reduced; this increased ungulate:wolf ratios and sometimes was followed by immediate increases in ungulate numbers (Gasaway et al. 1983, Crete and Messier 1984, Bergerud and Elliot 1986, Ballard et al. 1987). In areas where providing a huntable surplus of ungulates is a major management concern, restricted hunting combined with wolf reductions may, over a short time, result in increased ungulate numbers, greater ungulate harvest, and, eventually, higher wolf densities (Gauthier and Therberge 1987). In south-central Alaska where wolf numbers were reduced 58%, they recovered to 81% of former levels within 1 denning season after control was terminated and exceeded precontrol numbers after 3 seasons (Ballard and Stephenson 1982, Ballard et al. 1987).

Management of ungulate:wolf ratios also must consider the effects of hunter harvest on ungulate populations. Keith (1983) provided a model to predict the number of ungulates required per wolf to

maintain a stable ungulate population, given a certain harvest level by humans:

$$N = \frac{K}{(\lambda_p - 1)(1 - H)}$$

where

N = ungulate numbers per wolf in spring before birth,

K = annual ungulate kill per wolf,

λ_p = annual finite rate of increase for an ungulate population with adequate food and no wolves or hunters (subsequently referred to as the potential rate of increase), and

H = proportion of annual increment removed by hunting (including legal kill and wounding loss).

This model also assumes that wolf predation and hunting mortality are completely additive to other mortality factors.

Minimum ungulate:wolf ratios needed to maintain stable ungulate populations can be derived with this formula by assuming there is no hunting mortality. Using Keith's (1983) mean potential rate of increase for moose ($\lambda_p = 1.24$) and mean annual moose kill per wolf (8.5/year), the required ratio is 35:1 ($8.5 \div [1.24 - 1]$). This represents an ungulate biomass index of 210:1 (35×6 ; Appendix B), similar to that on Isle Royale (where no hunting occurs) during 1970–74 when wolf and moose populations were stable (Peterson 1977). It also is similar to that for northeast Alberta where hunting did occur, wolves were increasing, and moose were declining (Fuller and Keith 1980, Hauge and Keith 1981) and is higher than that in southwest Quebec where wolves likely were controlling moose numbers (Messier and Crete 1985).

The deer:wolf ratio was 100:1 in an unhunted deer population in Ontario, and Pimlott (1967) estimated that a finite rate of increase of deer of ≥ 1.37 was required to support the annual kill by wolves of 36.7 deer/wolf. The annual potential rate of increase for deer in northern forests probably is less than the 1.40 observed for a captive herd having adequate food and no

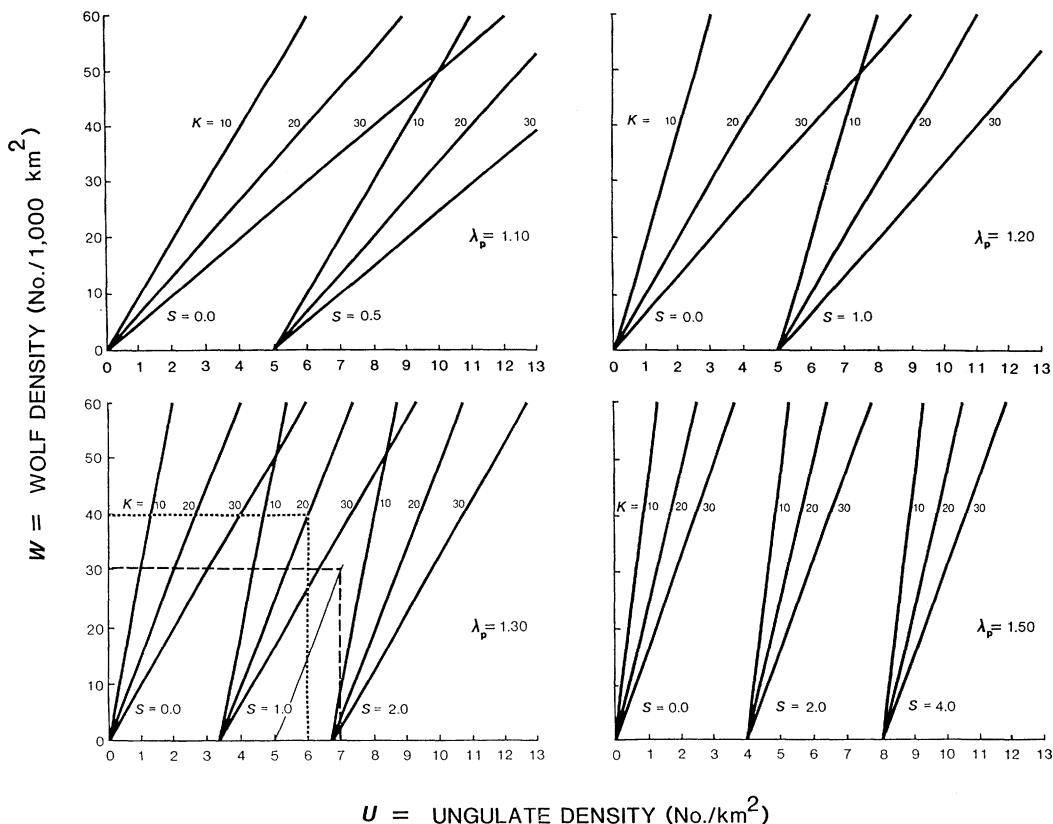


Fig. 8. Models of interactions of ungulate density (U), wolf density (W), potential rate of increase for an ungulate population with adequate food and no hunter or wolf mortality (λ_p), hunter harvest per km 2 (S), and annual ungulate kill per wolf (K) that aid in estimating the effect of various management strategies on the stability of ungulate numbers. See text for interpretation of dotted and dashed lines.

human-related losses (Ozoga and Verme 1982). The annual potential rate of increase for radio-collared deer in the BSA (T. K. Fuller, unpubl. data) was about 1.21 when excluding wolf predation, hunting, and wounding loss (but including car kills and poaching). These rates are substantially lower than the mean rate (1.55) in Keith (1983), but likely are more applicable to deer in the northern forest. Given an annual kill rate of about 19 deer/wolf/year in the BSA, the deer : wolf ratio required to maintain a stable deer population (without hunting) would be 90:1 (19 \div [1.21 – 1.0]), less than the ratio in Ontario (Pimlott 1967).

Modifications of Keith's (1983) model result in several equations that can be used to explore relationships among wolves, un-

gulates, and hunters. The following formula allows for estimates of wolf density that would result in a stationary ungulate population, given a specific ungulate density, hunter kill, estimated potential rate of increase, and estimated wolf kill:

$$W = \frac{[U(\lambda_p - 1) - S]}{K} \times 1,000$$

where

U = number of ungulates/km 2 ,

W = number of wolves/1,000 km 2 ,

λ_p = potential finite rate of increase for the ungulate population,

S = hunter kill/km 2 , and

K = annual ungulate kill/wolf.

Similarly, those wanting to maintain spec-

ified wolf and ungulate densities can rearrange the equation above to calculate the maximum allowable ungulate harvest,

$$S = U(\lambda_p - 1) - \frac{K \times W}{1,000},$$

or to estimate the density of ungulates needed to support given wolf density and hunter harvest,

$$U = \frac{S}{(\lambda_p - 1)} + \frac{K \times W}{1,000 (\lambda_p - 1)}.$$

Variation in wolf and ungulate density, wolf predation rates, harvest rates by hunters, and potential rates of increase for ungulates also can be examined graphically to quickly survey the expected outcome of various management schemes that will result in a stationary ungulate population (Fig. 8). For example, let us suppose that one wants to know how many wolves an area could support without causing the deer population to decline, given a deer density (U) of $6/\text{km}^2$, a hunter harvest (S) of $1.0/\text{deer}/\text{km}^2$, a potential rate of increase (λ_p) of 1.30 , and an annual ungulate kill per wolf (K) of $20 \text{ deer/wolf/year}$. In Figure 8, locate the graph where $\lambda_p = 1.30$ and follow the dotted line drawn perpendicular from the X -axis at $U = 6$ up to where it intersects the line indicating $S = 1.0/\text{km}^2$ and $K = 20$. Following the dotted line perpendicular to the Y -axis indicates about $40 \text{ wolves}/1,000 \text{ km}^2$ (W) could be supported in the area. If deer density increased to $7/\text{km}^2$ and hunter harvest was subsequently increased to $1.5/\text{km}^2$, the dashed perpendicular line from $U = 7$ would intersect at $K = 20$, $S = 1.5$ (thin solid line paralleling the $K = 20$ lines and halfway between $S = 1.0$ and 2.0) and would indicate about $30 \text{ wolves}/1,000 \text{ km}^2$ could be supported.

Some scenarios may result in nonsense plots, e.g., given $\lambda_p = 1.30$ and $U = 6$, S cannot be greater than about 1.7 , even with no wolves, or the population will decline. Also, high human-caused mortality of wolves may keep a wolf population from reaching its equilibrium density. Conse-

quently, the ungulate population will increase unless hunter harvest of ungulates is increased or human mortality of wolves is decreased. Clearly, any estimates resulting from the use of these relationships are only as good as the input data, but the general estimates that are produced certainly will help in evaluating wolf, human, and ungulate interactions.

CONCLUSIONS

1. Small territory size ($\bar{x} = 116 \text{ km}^2$) and high wolf density ($39/1,000 \text{ km}^2$ in mid-winter) in north-central Minnesota likely resulted from relatively high white-tailed deer numbers in January ($6.2/\text{km}^2$).
2. Extraterritorial forays, usually made alone, were common for wolves and many resulted in permanent dispersal. Yearlings dispersed at a higher rate than did adults or pups. Overall decreases in pack size from early to late winter (including dispersal and mortality) were greatest for large packs.
3. Wolf numbers were stable to slowly increasing ($\lambda = 1.02$) because pup recruitment was moderate (3.2 pups/pack in autumn) and mortality of wolves ≥ 5 months old was not excessive (annual survival = 0.64). Annual rates of population change directly reflected the proportion of pups in the population the previous autumn.
4. Despite the fact that wolves were legally protected, 80% of mortality was human caused. Road density was higher where wolves died of human-related causes. No wolf pack territories had road densities $> 0.72 \text{ km/km}^2$.
5. Wolves killed mostly fawn deer in both summer and winter, but, in terms of biomass, older deer still were of primary importance. Winter consumption rates were low (2.0 kg/wolf/day), but may have reflected the inaccuracy, in general, of techniques used to estimate predation on deer.
6. A majority of studies in North America, including this one, indicate that wolf numbers in North America are directly

- related to ungulate biomass, and potential wolf density (with no human-caused mortality) ultimately is limited only by ungulate availability.
7. Consumption rates of wolves in North America likely increase with higher per capita food availability; this likely results in the higher pup survival observed where ungulate biomass is higher.
 8. Annual rates of wolf population increase vary in direct response to mortality rates, and, where wolves are killed by humans, harvests exceeding about 28% of the autumn or early winter population often result in population declines.

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APPENDIXES

Appendix A. Monthly mortality rates and age-specific dispersal and settling rates of radio-collared wolves ≥ 5 months old monitored in north-central Minnesota during September 1980–December 1986.

Month	Mortality rate			Dispersal rate			Settling rate		
	All ages ^a		Adult	Yearling		Pup	All ages ^a		
	Mean	95% CI	Mean	95% CI	Mean	95% CI	Mean	95% CI	
Apr	0	0.039	0.000–0.091	0.147	0.000–0.335	0	0	0	0
May	0	0	0.000–0.031	0.077	0.000–0.222	0	0	0	0
Jun	0.011	0.000–0.032	0.015	0.000–0.043	0				
Jul	0.011	0.000–0.032	0						
Aug	0.044	0.000–0.086	0.016	0.000–0.046	0				
Sep	0.025	0.000–0.052	0.028	0.000–0.067	0.144	0.000–0.328	0	0.179	0.000–0.344
Oct	0.032	0.001–0.062	0		0.084	0.000–0.243	0	0.107	0.000–0.237
Nov	0.131	0.069–0.189	0.054	0.003–0.105	0.186	0.000–0.418	0	0	
Dec	0.095	0.044–0.149	0.031	0.000–0.073	0.126	0.000–0.357	0	0.133	0.000–0.290
Jan	0.044	0.001–0.086	0.076	0.002–0.145	0.199	0.000–0.547	0.111	0.000–0.257	0.215
Feb	0.024	0.000–0.056	0.020	0.000–0.059	0		0	0.254	0.006–0.381
Mar	0.015	0.000–0.037	0		0.164	0.000–0.459	0.078	0.000–0.224	0.047–0.424

^a Adults, yearlings, and pups ≥ 5 months old

Appendix B. Mean ungulate and wolf densities and ungulate biomass index per wolf during winter in various areas of North America.

Location	Years	Prey species	Number/1,000 km ²			Ungu-late biomass index per wolf ^a	Reference
			Ungu-lates	Index ^a	Wolves		
North-central Canada	1968	caribou	5,500	11,000	37	297	Parker 1973
Isle Royale, Michigan	1984–86 ^b	moose	1,762	10,570	40	264	Peterson and Page 1988
Isle Royale, Michigan	1970–74 ^b	moose	1,616	9,696	43	225	Peterson 1977
Northeast Minnesota	1970–71	deer moose	5,100 700	9,300	42	221	Van Ballenberghe et al. 1975
Southwest Manitoba	1975–78	elk moose deer	1,200 800 340	8,740	26	336	Carbyn 1982, 1983
Northeast Minnesota	1967–69	deer moose	3,500 600	7,100	40	178	Mech et al. 1971b, Peek et al. 1976, Nelson and Mech 1986b
Northwest Minnesota	1972–77	deer moose	5,000 300	6,800	17 ^c	400 ^c	Fritts and Mech 1981
East-central Ontario	1958–64	deer moose	5,769 169	6,783	38	179	Pimplott et al. 1969
Southern Quebec	1980–84	deer moose	3,000 300	6,600	28	236	Potvin 1988
North-central Minnesota	1980–86	deer moose	6,160 20	6,280	39	161	This study, unpubl. data
North-central Minnesota	1978–79	deer	6,000	6,000	28	214	Berg and Kuehn 1980, pers. commun.
Northeast Minnesota	1946–53	deer moose	3,475 386	5,791	23	252	Stenlund 1955
Kenai Peninsula, Alaska	1976–81	moose caribou	800 13	4,826	14	345	Peterson et al. 1984
South-central Alaska	1975–82	moose caribou	665 311	4,612	7 ^d	659 ^d	Davis 1978, Ballard et al. 1987
East-central Ontario	1969	deer moose	3,098 154	4,021	36	112	Pimplott et al. 1969, Kolenosky 1972
Northeast Minnesota	1976–84	deer moose	600 550	3,850	25	154	Mech 1986; Nelson and Mech 1986a,b; MDNR files ^e
Jasper Park, Alberta	1969–72	elk sheep goat moose deer caribou	500 470 120 80 80 40	2,730	8	364	Carbyn 1974
Denali Park, Alaska	1966–74	moose sheep caribou	164 478 270	2,002	6	334	Haber 1977
South-central Ontario	1975–79	moose caribou	296 13	1,802	12	150	Bergerud et al. 1983
Southwest Quebec	1980–84	moose	300	1,800	11	162	Messier and Crete 1985
Interior Alaska	1975–78	moose caribou	185 145	1,400	8	175	Gasaway et al. 1983
Northeast Alberta	1975–77	moose caribou	225 17	1,384	6	231	Fuller and Keith 1980, 1981b; Hauge and Keith 1981
Northern Alberta	1979	bison	153	1,224	8	152	Oosenbrug and Carbyn 1982

Appendix B. Continued.

Location	Years	Prey species	Number/1,000 km ²			Ungulate biomass index per wolf ^a	Reference
			Ungulates	Index ^a	Wolves		
West-central Yukon	1985–86	moose	62	1,073	7	153	Sumanik 1987
		caribou	10				
		sheep	681				
Denali Park, Alaska	1984–85	moose	94	848	3	282	Singer and Dalle-Molle 1985
		caribou	106				
		sheep	86				

^a Bison (*Bison bison*), moose, elk, caribou, bighorn sheep (*Ovis canadensis*), Dall sheep (*O. dalli*), mountain goat (*Oreamnos americanus*), mule deer (*Odocoileus hemionus*), and white-tailed deer assigned relative biomass values of 8, 6, 3, 2, 1, 1, 1, and 1, respectively, similar to Keith (1983).

^b Years with relatively stable moose and wolf numbers.

^c Wolf population newly protected.

^d Wolf population heavily exploited.

^e M. S. Lenarz, Minn. Dep. Nat. Resour., pers. commun.