Wolf movements and population dynamics in Papineau-Labelle reserve, Quebec

FRANÇOIS POTVIN
Ministère du Loisir, de la Chasse et de la Pêche, 150 St-Cyrille est (5^e), Québec (Québec), Canada G1R 4Y1

Received July 15, 1987

POTVIN, F. 1987. Wolf movements and population dynamics in Papineau-Labelle reserve, Quebec. Can. J. Zool. **66**: 1266–1273.

From 1980 to 1984, wolf ecology was studied in Papineau-Labelle reserve, a 1667-km^2 area characterized by three large deer yards (> 1000 deer) located at the periphery. We obtained 2462 telementry locations from 43 collared wolves belonging to 4–8 packs. Mean pack size on 1 December was 5.6 wolves and density within territories averaged 2.8 animals/100 km^2. Size of territories ranged between 85 and 325 km^2 (mean 199 km^2) and no seasonal variations were noted for most packs. But those packs in contact with a large deer yard generally used that portion of their territory more intensely in winter. The majority of wolves (12/15) dispersed when they were 10–20 months old and traveled an average distance of 40 km. Dispersal likely resulted from the onset of sexual maturity and, possibly, from social stress. Mortality rate of collared wolves (36%) was moderate and similar to that of noncollared wolves. Known causes of mortality were all human related: trapping (23), hunting (6), and road kills (6). Nonetheless, I conclude that this population is regulated largely by social factors and not by food stress.

POTVIN, F. 1987. Wolf movements and population dynamics in Papineau-Labelle reserve, Quebec. Can. J. Zool. **66** : 1266–1273.

De 1980 à 1984, nous avons étudié l'écologie du Loup dans la réserve de Papineau-Labelle, un secteur de 1667 km^2 caractérisé par la présence de trois importants ravages de cerfs (> 1000 cerfs) situés en périphérie. Nous avons obtenu 2462 repérages télémétriques de 43 loups minus d'un collier, loups appartenant à 4–8 meutes. Au 1^er décembre, les meutes comptaient en moyenne 5.6 loups et la densité était de 2.8 loups/100 km^2. Les territoires couvraient 85–235 km^2 (moyenne 199 km^2) et étaient généralement les mêmes en hiver et en été. Cependant, la plupart des meutes en contact avec un important ravage de cerfs utilisaient plus fréquemment cette portion de leur territoire au cours de l'hiver. La plupart des loups (12/15) se dispersaient à l'âge de 10–20 mois, sur une distance moyenne de 40 km. C'est probablement la maturité sexuelle, et peut-être aussi le stress social, qui provoquent le déclenchement de la dispersion. Le taux de mortalité des loups munis d'un collier (36%) s'est avéré modéré et identique à celui des loups sans collier. Les causes de mortalité connues sont toutes d'origine humaine : piégeage (23), chasse (6) et accidents routiers (6). Malgré cela, nous concluons que cette population est surtout régie par des facteurs sociaux et non par la nourriture.

Introduction

With the advent of telemetry, intensive study of such an elusive animal as the wolf (*Canis lupus*) has become possible (Mech 1974). This technique facilitates a better understanding of wolf movement patterns: territoriality, space use, and dispersal. Minimal density estimates are obtained directly by observing packs containing collared animals from the air. Insight into population dynamics can also be gained by studying the fate of radio-collared animals (Heisey and Fuller 1985).

From 1980 to 1984, we used telemetry to study wolf ecology in Papineau-Labelle reserve, Quebec. This area is characterized by the presence of large deer yards where more than 1000 deer (*Odocoileus virginianus*) congregate each winter. Studies from northern Minnesota, on the other hand, show more moderate concentrations (Mech 1975, 1977; Van Ballenberghe et al. 1975; Mech and Karns 1978; Nelson and Mech 1986). Given such a marked difference in deer availability and distribution in winter, our first objective was to document seasonal space-use patterns of wolves. Would territories be the same for both seasons? Would wolves search more intensely in areas with higher deer densities? This paper reports results pertaining to wolf movements which were obtained by telemetry during the 4-year study. As a secondary objective, survival rates were computed and limited productivity data were also obtained. Data pertaining to wolf diet and prey selectivity are presented elsewhere (Potvin et al. 1988).

Study area

The study was conducted in Papineau-Labelle (PL) reserve, a 1667-km^2 area (Fig. 1). This area has a typical Laurentides topography, with altitude normally ranging from 225 to 375 m but sometimes reaching more than 450 m. Lakes, ponds, and streams are numerous. The reserve is forested, with only marginal agriculture in the vicinity. Dominant tree species are sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), white and red pine (*Pinus strobus* and *P. resinosa*), white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), and trembling aspen (*Populus tremuloides*). Typical winters are characterized by 274 cm of snowfall and 33 days with the minimum temperature below −18°C. Snow depth exceeds 50 cm for 62 days, on average, but this may range from 0 to 104 days (Potvin and Breton 1986).

Large mammals present are deer, moose (*Alces alces*), black bear (*Ursus americanus*), and wolf. From December to April most deer occupy three wintering areas located at the periphery. In 1982 these three yards covered 217 km^2 and contained 4500 deer (Ministère du Loisir, de la Chasse et de la Pêche, unpublished data). Summer densities are 3.0/km^2 for deer and 0.6/km^2 for moose. Beaver (*Castor canadensis*) are fairly abundant (0.9 colony/km^2). Although moose is present, wolves use mostly deer in winter (Potvin et al. 1988), so that we consider PL reserve to be a wolf–deer system with a more diversified prey base in summer. No commercial trapping was allowed from 1971, when PL reserve was created, until the summer of 1984. In season, wolves could be trapped or hunted with no bag limit outside the reserve. Big-game hunting is still not permitted in PL reserve. Outside the reserve, only buck deer could be hunted during our study, except for 1 day's hunting of antlerless game in 1981, while moose hunting was not allowed before 1985.

Materials and methods

Wolves were captured in summer along forest roads, using leg-hold traps (Newhouse 4 or modified Newhouse 114). They were classified as young (< 12 months) or adult on the basis of canine eruption and size. Adult females were checked for evidence of lactation. They were fitted with AVM or Telonics radio collars (150–152 MHz fre-

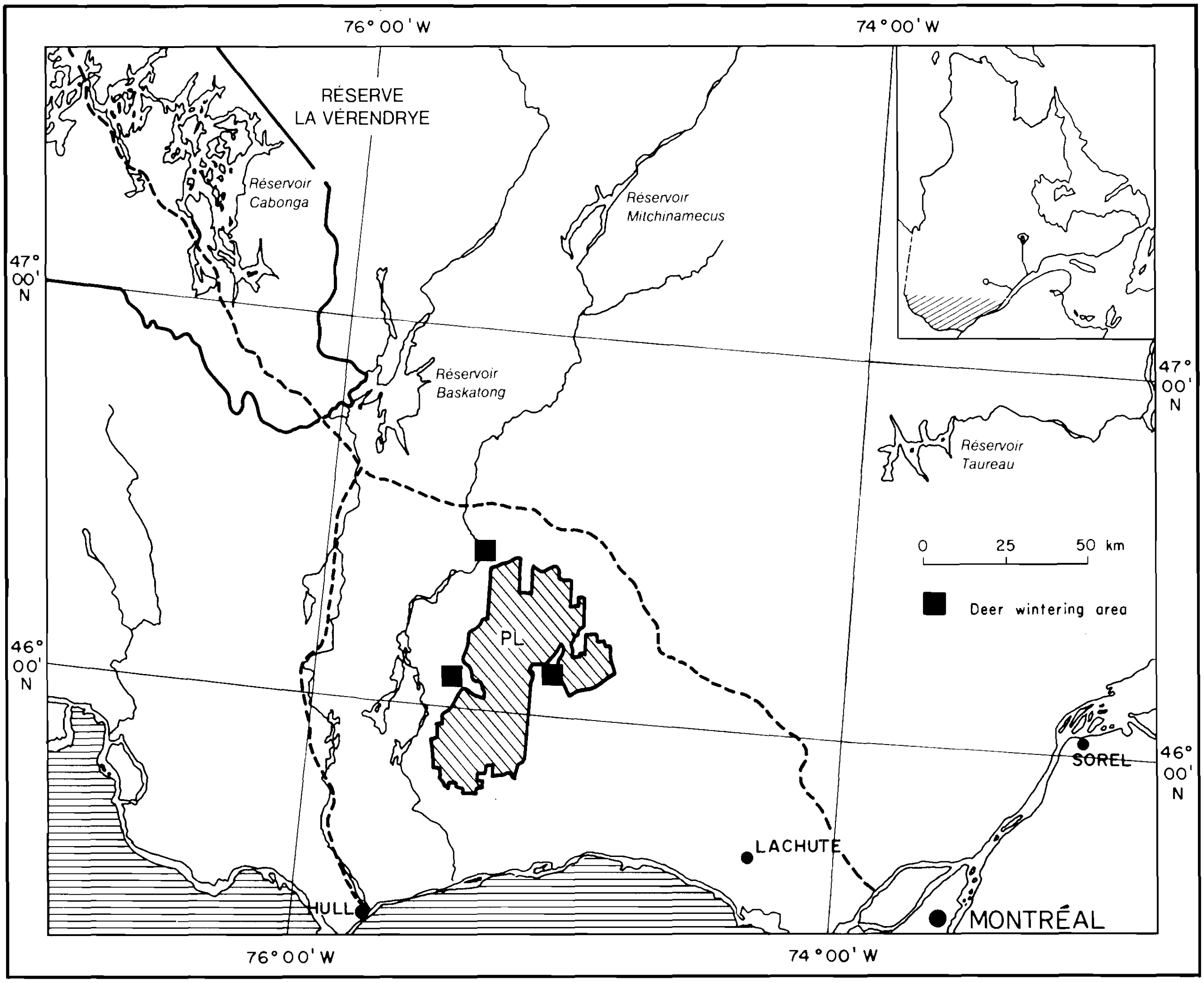

FIG. 1. Map of Outaouais – Laurentides region in Quebec, showing Papineau-Labelle reserve (PL) and the three important deer wintering areas located at the periphery.

quency) and located with a Cessna 185 airplane using techniques described by Gilmer et al. (1981) and Mech (1983). Wolves were located daily, depending on weather conditions, during winter 1982 and winter 1983. Three locations were made every 2 weeks in summer 1983 and one every 1 or 2 weeks during the other periods.

Locations were plotted initially on 1 : 50 000 topography maps using a 100 × 100 m grid. Based on ground checks of collared wolves, the accuracy of such locations was estimated at ±200–300 m. The number of wolves observed was noted whenever possible. Wolves could not be seen in summer because of the cover, but in winter, collared wolves were observed during 24% of locations. Even during winter, however, many animals were not visible because of the dense coniferous cover.

Data were analysed using 1 × 1 km grid units. The territory of each pack was computed using the minimal convex polygon technique (Mohr 1947) by selecting 95% closest location points (Bowen 1982*a*; Bekoff and Mech 1984; Messier 1985*b*). Within each year (from April 16 to April 15 of the following year), locations of all wolves associated in a pack were pooled. Dispersing animals were excluded from the time it was evident that they had left the territory. A curve of number of locations vs. area was drawn, and only territories with an asymptotic curve were accepted as valid (Bekoff and Mech 1984; Laundré and Keller 1984).

Mortality rates of collared wolves according to age-class and sex were computed with MICROMORT (Heisey and Fuller 1985). To take into account the trapping and hunting season we divided the year into two periods: summer (April 16 – October 15) and winter (October 16 – April 15). For each period, the number of days of survival and the number of mortalities were added and put into the model. In order not to bias the mortality rate, collared wolves whose signal had been lost, and that were recovered only at the time of death, were discarded. As an experimental control program was initiated in PL reserve in January 1984, data on survival and mortality from the onset of this program were not used.

Starting in fall 1981, we tried to collect the maximum number of wolf carcasses. Although registration of hunted or trapped wolves is not mandatory, game wardens and most trappers were well aware of our project, particularly during 1982–1983, when we probably missed very few, if any, wolf carcasses resulting from human-induced mortality. Reproductive tracts of females were examined for fresh placental scars (Gier 1968) and ovaries for corpora lutea (Rausch 1967; Jean and Bergeron 1984). Wolves were aged by cementum annuli count in the canine (Linhart and Knowlton 1967; Bowen 1982*b*; Goodwin and Ballard 1985).

We tried to establish reproductive success of known packs each year. Success was recorded for an individual pack if one or more of the following conditions occurred: trapping of pups, observation of tracks or howling from young wolves in summer, capture of a lactating female, or presence of placental scars in the reproductive tract of a killed female known to be associated with the pack. In addition, limitation of the movement of an adult female during the period from May to July, suggesting a den or rendezvous site, was considered to be confirming evidence, though not the sole criterion.

Results

During the four trapping seasons, 45 wolves (26 young and 19 adults) were captured, with a mean effort of 93 trap-nights per animal. Eight wolves were recaptured. We obtained 2462 locations from 43 collared wolves. As a result of trapping success, four packs were followed in 1980–1981, four in 1981–1982, eight in 1982–1983, and six in 1983–1984 (Fig. 2). Territories were exclusive and ranged in size from 85 to 324 km^2, with a mean of 199 $\pm$ 16 km^2 (SE) ($N = 21$). Perimeters were not stable from year to year, but activity centers remained generally the same. NDL, the most important pack in 1980–1981, could not be found in 1983–1984. Conversely, although we had no collared animals, some other packs could be identified on the basis of aerial observation of groups of wolves or their tracks on lakes and river systems. We conclude that 10 packs were present in PL reserve during 1982–1983, which was the best-documented year. Another pack was located north of Kiamika village, completely outside the reserve.

Mean pack size on 1 December was 5.6 $\pm$ 0.44 wolves ($N = 19$). The maximum pack size was 10, while half of the groups had 6 or more animals. There was a weak correlation between territory size and pack size ($r = 0.35$, $N = 0.19$, $P =$ 0.14). Mean density within territories was 2.8 wolves/100 km^2 over the years.

Territories were the same in winter and summer for most packs (13/17 pack-years). Ten of these (four different packs, LCH, NDL, LPN, and LHY) encompassed a large deer yard. Only NDL pack completely restricted its movements from December 1 to March 15 of each year, when it used exclusively that portion of its territory within a large deer yard. In most cases (8/10 pack-years), though, those packs whose territories included part of a large deer yard were located proportionately more often (χ^2-test, $P < 0.05$) in that portion of their territory (Fig. 3).

An excursion is a movement of a group of wolves for a short time towards an area not usually visited. Only two typical excursions were identified. From March 9 to 11, 1983, the whole LHY pack was seen 10 km SW of its territory, in the traditional area of NDL pack. One day later, it moved back 18 km to reach the center of its territory. Between March 13 and 14 of the same year, four wolves of LHY pack travelled 20 km E, more than 10 km outside their territory. They were back on March 16.

A dispersal is a definitive movement outside the pack territory. It can be accomplished by one or two wolves and may be preceded by trials. A total of 15 wolves (5 males and 10 females) dispersed. Most wolves (12/15) were 10–20 months old when they began to exhibit dispersal behavior. Out of 15 collared wolves that were periodically located between 10 and 20 months of age, only 3 did not disperse. One of those left its pack at 29 months. Some wolves disperse as early as March, but others wait until the next fall before leaving the pack definitely. Typically, most animals made a few 10-km trials outside their territory before dispersing. Most final movements exceeded 20 km and averaged 40 $\pm$ 11 km ($N = 15$). The longest distance was 190 km. Wolves generally dispersed outside PL reserve in all directions. Six wolves were located in large deer wintering areas distinct from the three areas at the periphery of PL reserve.

Figure 4 shows the known composition of each pack studied. Most wolves were observed with collared animals and are therefore of unknown status. The results regarding the social structure of the packs are limited. The basic unit probably contains a reproductive pair, a variable number of pups, and some young of previous years that have not yet dispersed.

During our study, 22 collared wolves were found dead and 21 carcasses of noncollared animals were also reported. Data were pooled because no difference was detected for age structure (χ^2-test, $P = 0.9$) and sex ratio ($P = 0.8$). The proportion of young was 28% ($N = 39$) and the sex ratio was 91 males : 100 females ($N = 42$). Identified causes of mortality were trapping (23), hunting (6), and road kill (6).

The annual survival rate of collared wolves averaged 64 $\pm$ 7% (Table 1). The young had a lower survival rate in summer than in winter, while the contrary prevailed for adults. No difference in annual rates was detected between age-classes (young, yearlings, and 24+ months) or sexes of adults (z-test, $P > 0.2$).

During 1982–1983, the eight documented packs contained 52 wolves (20 collared animals). Eleven noncollared wolf carcasses were reported inside those territories for the same year. The recorded mortality rate of noncollared wolves (11/32, 34%) was almost identical with the annual rate computed for collared animals.

At least 17 of 22 pack-years produced pups over the 4 years. No reproductive failure was evident because data were too limited to allow conclusions to be drawn in the other cases. Based on reproductive tracts ($N = 7$) and pairs of ovaries examined ($N = 3$), the number of young per female ranged between two and eight ($\bar{x} = 5.6 \pm 0.67$).

Discussion

The wolf is a social animal, living mainly in a pack. Each pack occupies a territory that is generally exclusive (Mech 1970, 1974; Peterson et al. 1984; Messier 1985*b*). The results from PL reserve follow this general trend. The size of territories in PL reserve (about 200 km^2) is comparable with those of wolf–deer ecosystems in central and eastern Minnesota and in Ontario (Kolenosky 1972; Mech 1974, 1975; Berg and Kuehn 1982). In western Minnesota, Fritts and Mech (1981) have described territories that are generally larger than 300 km^2, while Van Ballenberghe et al. (1975) found areas of about 110 km^2 near Lake Superior. Territories are larger than 300 km^2 in most wolf–moose ecosystems (Fuller and Keith 1980; Gasaway et al. 1983; Peterson et al. 1984; Messier 1985*b*).

The estimation of wolf numbers is directly related to visual observations. Wolves were seen during only 24% of locations in winter. Much higher rates were attained in Minnesota (58–78%) (Mech 1977; Fritts and Mech 1981) and La Vérendrye reserve, which is located some 70 km NW of PL reserve (75%) (Messier 1985*a*). The presence of closed coniferous canopy in my study area, mainly deer yards in winter, and possibly the use of a different fieldworking technique, might explain these differences. Only one observation of all pack members is needed to get a correct density value. But because some members may be temporarily dissociated from the group, especially at the end of winter (Messier 1985*a*), repeated observations are necessary. Fifteen estimates are based on two or more observations of a pack in winter, and five are based on fewer observations (LCH in 1981–1982, NDL, C27, and LAR in 1982–1983, and C27 in 1983– 1984). The density

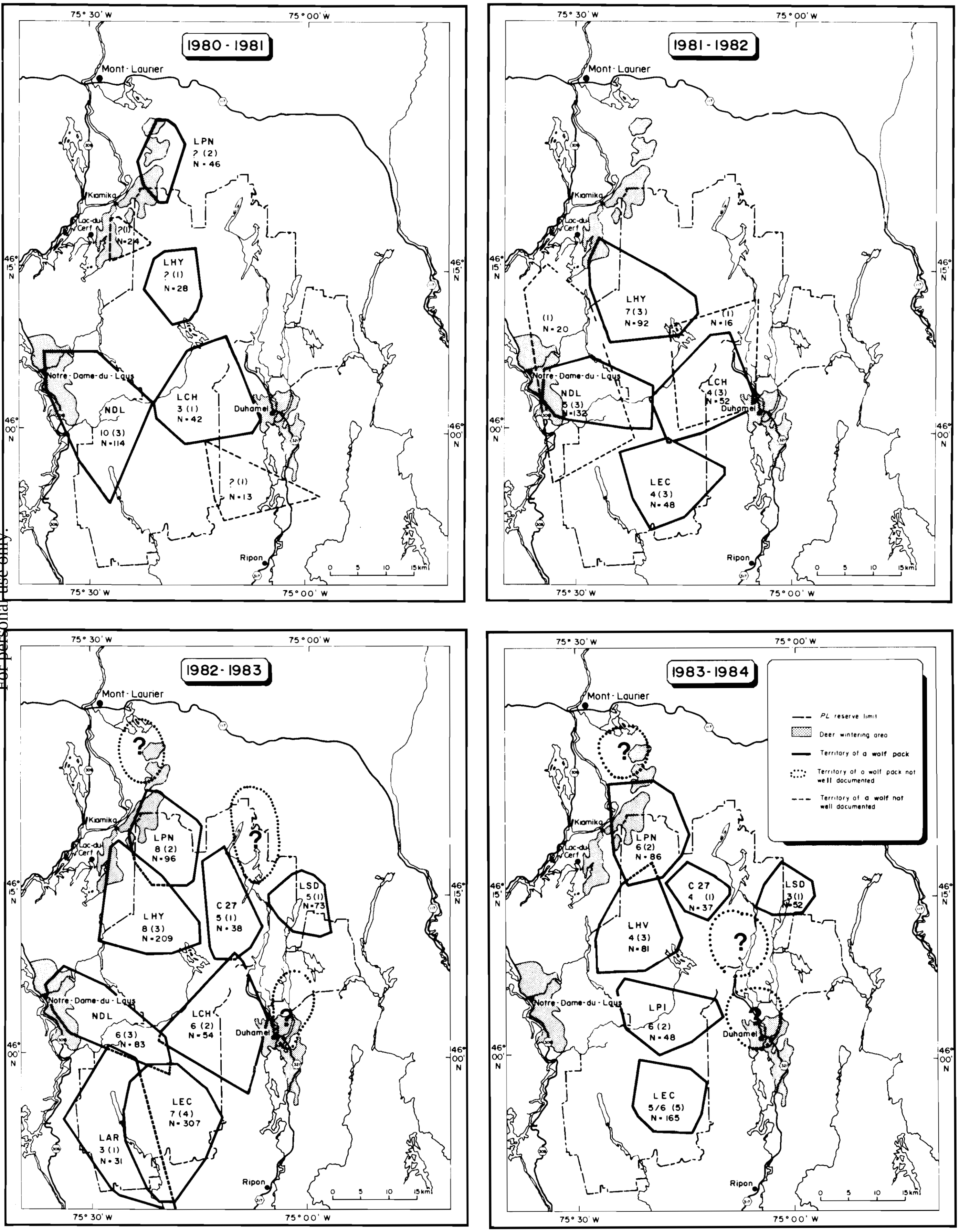

FIG. 2. Wolf territories in Papineau-Labelle reserve area, 1980–1984. LPN, LHY, C27, LSD, LCH, LEC, LPI, and LAR designate wolf packs. Number in each territory indicates number of wolves in pack, with number of collared wolves in parentheses. N, number of locations (95%).

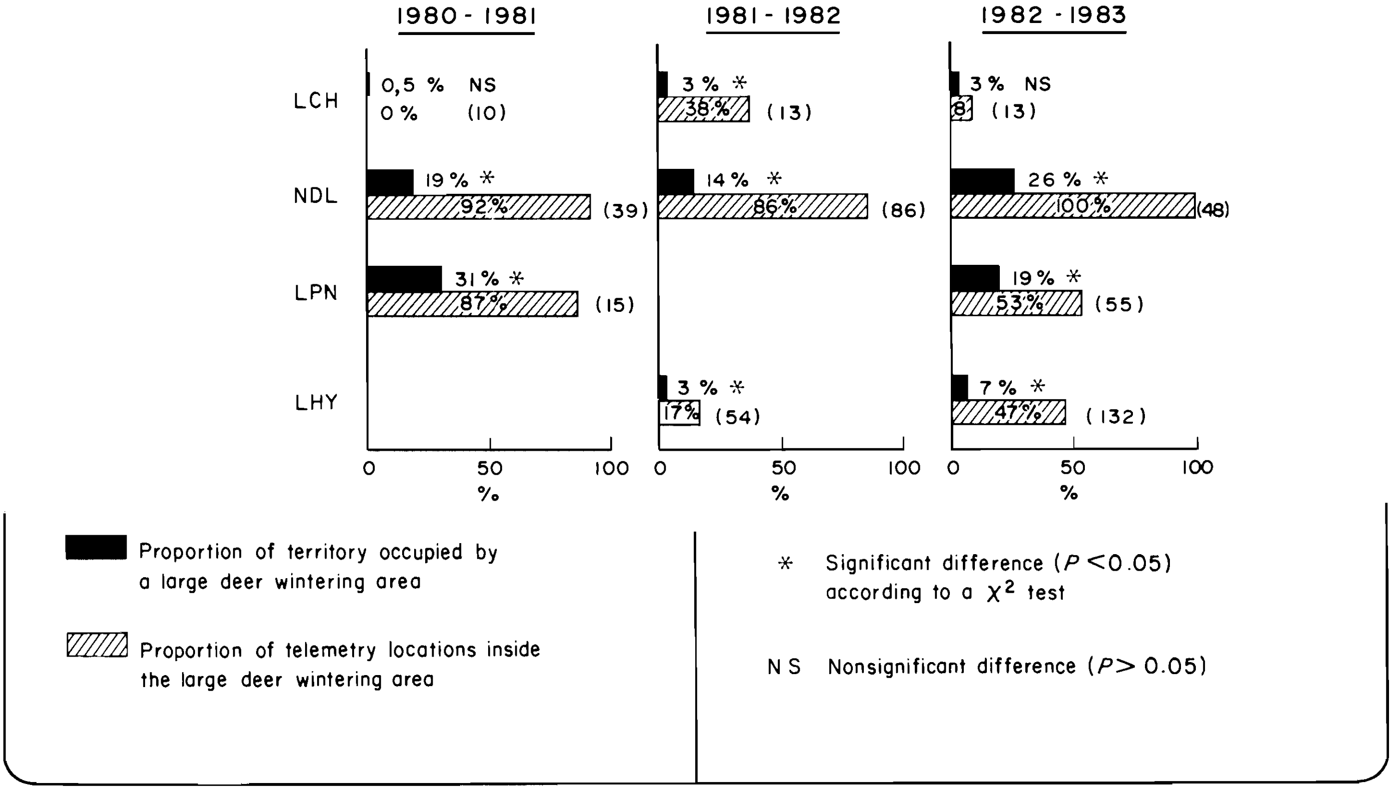

FIG. 3. Distribution of telemetry locations of wolf packs in Papineau-Labelle reserve in winter (December 1 – March 15), in relation to large deer wintering areas. LCH, NDL, LPN, and LHY designate wolf packs. Number of locations is in parentheses.

estimates presented are therefore minimum values.

Pack size in wolf–deer ecosystems generally ranges from two to eight members, with four as an overall mean (Mech and Frenzel 1971; Kolenosky 1972; Mech 1975, 1977; Van Ballenberghe et al. 1975; Fritts and Mech 1981; Scott and Shackleton 1982). With 5.6 wolves on average, PL reserve packs have a rather large size. Wolf–moose ecosystems have larger packs, usually with 4–10 members (Fuller and Keith 1980; Bergerud et al. 1983; Gasasway et al. 1983; Peterson et al. 1984). Pack size (5.7) in La Vérendrye reserve, a moose range, is identical with that of PL reserve (Messier 1985*b*).

Reported wolf densities in wolf–deer ecosystems are 1–4/100 km^2 (Pimlott et al. 1969; Mech 1974; Van Ballenberghe et al. 1975; Fritts and Mech 1981; Berg and Kuehn 1982). Densities are lower in wolf–moose ecosystems, ranging from 0.6 to 1.6/100 km^2 (Fuller and Keith 1980; Gasaway et al. 1983; Messier 1985*b*), except on Isle Royale, where 4–5/100 km^2 was maintained from 1959 to 1966 (Jordan et al. 1967). Pimlott (1967, 1975) has suggested that 4–5 wolves/100 km^2 was the maximum density tolerable by a natural wolf society. In his literature review, Keith (1983) indicated that the density of seven stable wolf populations ranged from 0.27 to 4.2/100 km^2. While not exceptional, the density in PL reserve (2.8/100 km^2) is rather high, considering that wolves could be trapped or hunted outside the reserve.

The concept of a stable territory from year to year seems overstated for the wolf. The perimeters of our wolf territories, as well as those defined by Fritts and Mech (1981), changed over the years. One pack (NDL) was not found, and probably disappeared, in 1983–1984, while a new one (LPI) was formed nearby in the center of the reserve. However, the role of human-related factors in these changes, such as trapping of the reproductive members, is unknown.

Most authors have noted that summer and winter territories are generally the same (Mech 1975; Van Ballenberghe et al. 1975; Fritts and Mech 1981). Although this was the case for all packs in our study except NDL, those in contact with large deer yards used that portion of their territory more intensely in winter. In Minnesota, Van Ballenberghe et al. (1975) also showed a greater use of areas with higher deer densities.

Group excursions have recently been described (Peterson et al. 1984; Van Ballenberghe 1983). Messier (1985*a*) observed 23 group excursions ranging in distance from 5 to 76 km. Two packs in La Vérendrye reserve extended their territory in winter to the SE, where deer were present (Messier 1985*b*). Our packs did not make similar shifts in range and none left its territory for long periods to get access to higher deer densities outside. This observation is probably related to the fact that even those packs not in contact with large deer yards had an adequate prey base, with small deer concentrations scattered throughout their territory. Pack excursions appear more prevalent in moose–wolf systems.

Dispersal was a more common behavior. Most young wolves (13/15) did disperse when 10–20 months old. In Minnesota, Fritts and Mech (1981) indicate that no collared juvenile, except possibly one, was still associated with its pack beyond sexual maturity, unless it had replaced a reproducing adult. The proportion of such juveniles was almost one-third for wolves studied by Berg and Kuehn (1982).Such behavior is also common in wolf–moose ecosystems (Van Ballenberghe 1983; Peterson et al. 1984; Messier 1985*a*). Dispersal is a gradual event, preceded by trials and completed when the animals are about 2 years of age (Peterson et al. 1984; Messier 1985*a*).

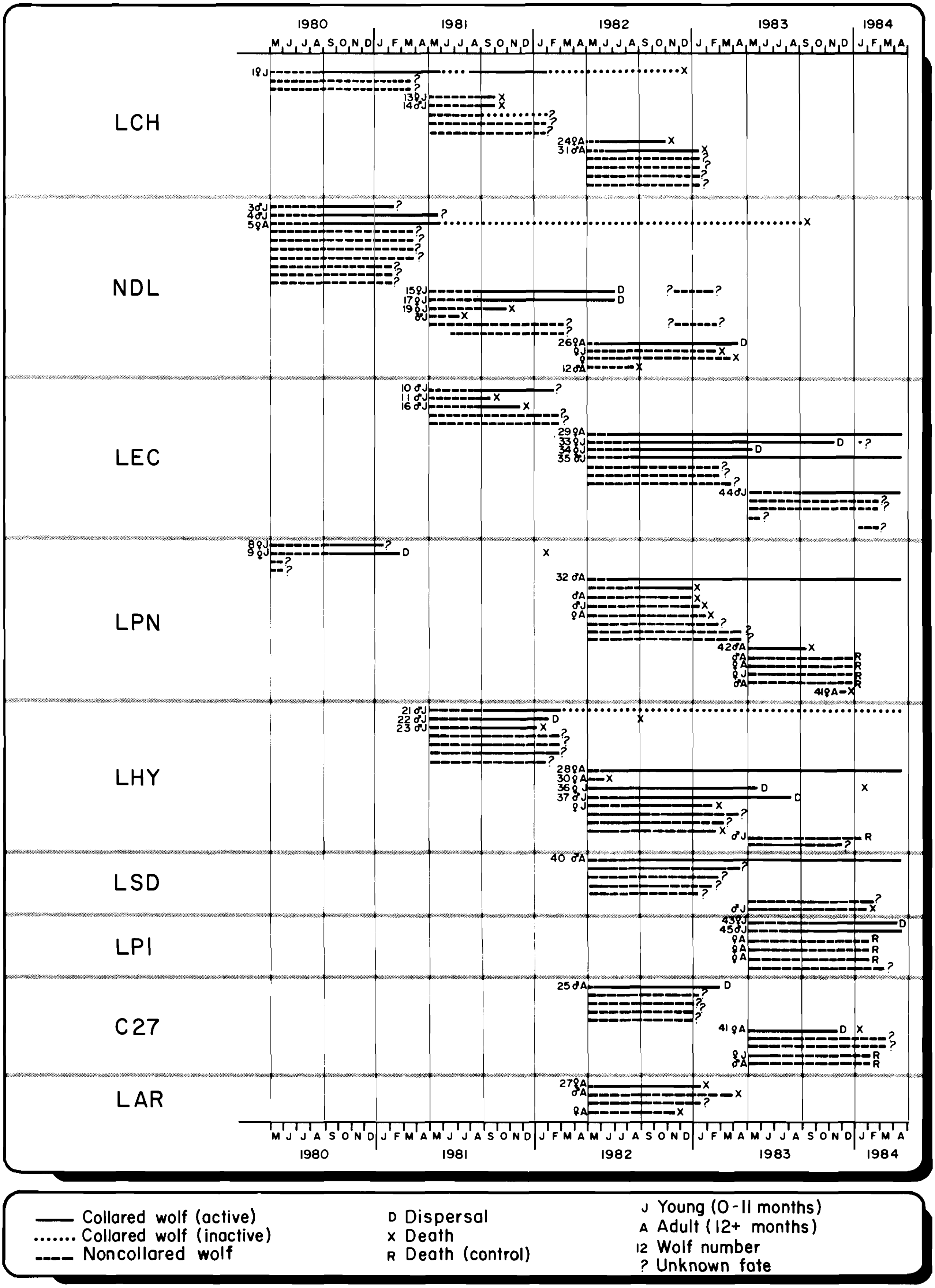

FIG. 4. Composition of wolf packs studied in Papineau-Labelle reserve area, 1980–1984.

TABLE 1. Survival rates of collared wolves in Papineau-Labelle reserve in summer (April 16 – October 15) and winter (October 16 – April 15), 1980–1984.

	No. of days surviving	No. of deaths	Survival rate (%) Summer ($\bar{x}$ ± SE)	Winter ($\bar{x}$ ± SE)	Annual ($\bar{x}$ ± SE)
Young					
(4–11 months)	4 401	6	58±17	* 84±8	49±16
Adults					
12–23 months	2 812	3	100±0	** 56±18	56±18
24 + months	3 013	3	89±10	75±14	67±16
Subtotal[a]	8 566	10	92±5	** 68±9	63±9
Total	12 967	16	85±6	76±6	64±7
Adults					
Male	3 339	3	89±10	79±13	72±14
Female	5 227	7	94±6	61±12	57±12

NOTE: Rates were computed with MICROMORT (Heisey and Fuller 1985). Summer and winter survival rates were compared within groups using the z-test. Statistically significant differences are indicated as follows: *, $P < 0.2$; **, $P < 0.05$.
[a] Includes adults of unknown age.

Food deprivation (Mech 1977; Messier 1985*a*), social stress (Packard and Mech 1980; Walters et al. 1981), and sexual maturity, at approximately 22 months (Mech 1970), are probably three associated stimuli for dispersal. Conversely, Fritts and Mech (1981) hypothesize that it would be advantageous for young to disperse when food is plentiful, even when wolf density is low. In PL reserve, high wolf density and an abundant prey base in all seasons suggest that dispersal is linked to the onset of sexual maturity and, possibly, to social stress.

Distances traveled by dispersing wolves in PL reserve are not exceptional. Mech (1970, 1974) noted movements of 47–300 km and indicated that wolves can disperse 200 km or more. Berg and Kuehn (1982) measured distances ranging from 37 to 432 km, with a mean of 148 km. Deer density was high in the area surrounding PL reserve where our wolves dispersed, while wolf densities were rather low, probably because of trapping. Therefore, dispersing animals did not have to travel far to find an unoccupied area with abundant prey.

The mortality rate of collared wolves (36%) appeared moderate. Capture stress and the presence of a collar apparently did not decrease survival rate, based on results for noncollared wolves in 1982–1983. Van Ballenberghe (1984) indicated that a high proportion (41%) of trapped wolves, in conditions similar to ours, showed injuries considered severe or very severe to feet, teeth, lips, and gums. He speculated that this could affect their adaptability and survival. Less severe effects were reported by Kuehn et al. (1986), especially with modified traps. We did not note the injury rate of wolves at capture during our study. None of the wolves examined at recapture or autopsy had injuries to the feet that were not completely healed. We believe that trapping and fitting with a collar may have short-term effects, but should not influence long-term survival.

Higher mortality rates than those in PL reserve have been commonly reported elsewhere: about 50% for adults in an area of Minnesota where the level of illegal killing was significant despite protected status for wolves (Fritts and Mech 1981); 38–65% in the Superior National Forest, Minnesota, when deer were plentiful, followed by a decline (Van Ballenberghe et al. 1975; Mech 1977); 55% in an area bordering La Vérendrye reserve (Messier 1985*b*). As reported elsewhere, most mortality was human related (trapping, hunting, road kills) (Berg and Kuehn 1982; Messier 1985*b*).

Food was plentiful for wolves in PL reserve. Keith (1983) reviewed seven studies related to stable wolf populations and expressed prey abundance in deer-equivalents (deer = 1, caribou = 2, moose = 6). In his review, the number of deer-equivalents ranged from 96 to 328 and was related to wolf density (0.27–4.2/100 km^2). Keith's (1983) data for wolf–deer systems were from Minnesota (224 deer-equivalents per wolf, 4.2 wolves/100 km^2) and Ontario (174 deer-equivalents per wolf and 3.9 wolves/100 km^2). At PL reserve, using the same approach, we have 115 deer/per wolf, 214 deer-equivalents per wolf if we include moose, and more than 240 deer-equivalents per wolf when we add beaver (4 beaver = 1 deer).

Based on prey availability, wolf density in PL reserve could probably exceed 3–4/100 km^2. What limits this population? Reproductive success, small territories, a high number of wolves per pack, frequent dispersals, and a low incidence of group excursions provide evidence that social factors rather than food are the main regulating mechanism (Packard and Mech 1980). Human-related mortality, especially trapping outside the reserve, was then only a major proximate factor.

Acknowledgements

We wish to thank especially L. Breton, R. Lemieux, and G. Mercier for field and laboratory work. The following regional personnel of the Ministère du Loisir, de la Chasse et de la Pêche also provided invaluable assistance: game wardens in Val-des-Bois and Papineauville, biologists and technicians of the Service de l'aménagement et l'exploitation de la faune, and personnel from the Papineau-Labelle reserve. Special thanks also to pilots of Air Mélançon and Express Air. M. Crête, J. Huot, H. Jolicoeur, and F. Messier kindly reviewed the manuscript.

BEKOFF, M., and MECH, L. D. 1984. Simulation analyses of space use: home range estimates, variability, and sample size. Behav. Res. Methods Instrum. **16**: 32–37.
BERG, W. E., and KUEHN, D. W. 1982. Ecology of wolves in north-central Minnesota. *In* Wolves of the world. *Edited by* F. H. Harrington and P. C. Paquet. Noyes Press, Park Ridge, NJ. pp. 4–11.
BERGERUD, A. T., WYETT, W., and SNIDER, B. 1983. The role of

wolf predation in limiting a moose population. J. Wildl. Manage. **47**: 977–988.
BOWEN, W. D. 1982*a*. Home range and spatial organization of coyotes in Jasper National Park, Alberta, J. Wildl. Manage. **46**: 201–216.
——— 1982*b*. Determining age of coyotes, *Canis latrans*, by tooth sections and tooth-wear patterns. Can. Field-Nat. **96**: 339–341.
FRITTS, S. H., and MECH, L. D. 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. Wildl. Monogr. No. 80.
FULLER, T. K., and KEITH, L. B. 1980. Wolf population dynamics and prey relationships in northeastern Alberta. J.Wildl. Manage. **44**: 583–602.
GASAWAY, W. C., STEPHENSON, R. O., DAVIS, J. L., SHEPHERD, P. E. K., and BURRIS, O. E. 1983. Interrelationships of wolves, prey and man in interior Alaska. Wildl. Monogr. No. 84.
GIER, H. T. 1968. Coyotes in Kansas. Kans. State Coll. Agric. Appl. Sci. Agric. Exp. Stn. Bull. No. 393.
GILMER, D. S., COWARDIN, L. M., DUVAL, R. L., MECHLIN, L. M., SHAIFFER, C. W., and KUECHLE, V. B. 1981. Procedures for the use of aircraft in wildlife biotelemetry studies. U.S. Fish Wildl. Serv. Resour. Publ. No. 140.
GOODWIN, E. A., and BALLARD, W. B. 1985. Use of tooth cementum for age determination of gray wolves. J. Wildl. Manage. **49**: 313–316.
HEISEY, D. M., and FULLER, T. K. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. J. Wildl. Manage. **49**: 668–674.
JEAN, Y., and BERGERON, J.-M. 1984. Productivity of coyotes (*Canis latrans*) from southern Québec. Can. J. Zool. **62**: 2240–2243.
JORDAN, P. A., SHELTON, P. C., and ALLEN, D. L. 1967. Numbers, turnover and social structure of Isle Royale wolf population. Am. Zool. **7**: 233–252.
KEITH, L. B. 1983. Population dynamics of wolves. *In* Wolves in Canada and Alaska. *Edited* by L. N. Carbyn. Can. Wildl. Serv. Rep. Ser. No. 45. pp. 66–77.
KOLENOSKY, G. B. 1972. Wolf predation on wintering deer in east-central Ontario. J. Wildl. Manage. **36**: 357–369.
KUEHN, D. W., FULLER, T. K., MECH, L. D., PAUL, W. J., FRITTS, S. H., and BERG, W. E. 1986. Trap-related injuries to gray wolves in Minnesota. J.Wildl. Manage. **50**: 90–91.
LAUNDRÉ, J. W., and KELLER, B. L. 1984. Home-range size of coyotes: a critical review. J. Wildl. Manage. **48**: 127–139.
LINHART, S. B., and KNOWLTON, F. F. 1967. Determining age of coyotes by tooth cementum layers. J. Wildl. Manage. **31**: 362–365.
MECH, L. D. 1970. The wolf: the ecology and behaviour of an endangered species. American Museum of Natural History, New York.
——— 1974. Current techniques in the study of elusive wilderness carnivores. Proceedings of the 11th International Congress of Game Biologists, Stockholm, September 3–7, 1973. *Edited by* I. Kjerner and P. Bjurholmt. National Swedish Environment Protection Board, Stockholm. pp. 315–322.
——— 1975. Population trends and winter deer consumption in a Minnesota wolf pack. *In* Proceedings of the 1975 Predator Symposium. *Edited by* R. L. Phillips and C. Jonkel. Montana Forest and Conservation Experiment Station, University of Montana. pp. 55–83.
——— 1977. Productivity, mortality, and population trends of wolves in northeastern Minnesota. J. Mammal. **58**: 559–574.
——— 1983. Handbook of animal radio-tracking. University of Minnesota Press, Minneapolis.
MECH, L. D., and FRENZEL, L. D., JR. (*Editors*). 1971. Ecological studies of the timber wolf in northeastern Minnesota. U.S. For. Serv. Res. Pap. NC-52.
MECH, L. D., and KARNS, P. D. 1978. Role of the wolf in a deer decline in the Superior National Forest. U.S. For. Serv. Res. Rep. NC-148.
MESSIER, F. 1985*a*. Solitary living and extraterritorial movements of wolves in relation to social status and prey abundance. Can. J. Zool. **63**: 239–245.
——— 1985*b*. Social organization, spatial distribution, and population density of wolves in relation to moose density. Can. J. Zool. **63**: 1068–1077.
MOHR, C. O. 1947. Table of equivalent populations in North American small mammals. Am. Midl. Nat. **37**: 223–249.
NELSON, M. E., and MECH, L. D. 1986. Deer population in the central Superior National Forest, 1967–1985. U.S. For. Serv. Res. Pap. NC-271.
PACKARD, J. M., and MECH, L. D. 1980. Population regulation in wolves. *In* Bio-social mechanisms of population regulation. *Edited by* M. N. Cohen, R. S. Malpass, and H. G. Klein. Yale University Press, New Haven, CT. pp. 135–150.
PETERSON, R. O., WOOLINGTON, J. D., and BAILEY, T. N. 1984. Wolves of the Kenai peninsula, Alaska. Wildl. Monogr. No. 88.
PIMLOTT, D. H. 1967. Wolf predation and ungulate populations. Am. Zool. **7**: 267–278.
——— 1975. The ecology of the wolf in North America. *In* The wild canids: their systematics, behavioral ecology and evolution. *Edited by* M. W. Fox. Van Nostrand-Reinhold, New York. pp. 280–285.
PIMLOTT, D. H., SHANNON, J. A., and KOLENOSKY, G. B. 1969. The ecology of the timber wolf in Algonquin Provincial Park. Ont. Dep. Lands. For. Res. Rep. Wildl. No. 87.
POTVIN, F., and BRETON, L. 1986. Sommaire des conditions d'enneigement pour le cerf au Québec de 1973 à 1985. Qué. Min. Loisir Chasse Pêche, Dir. gén. faune, Publ. 1208.
POTVIN, F., JOLICOEUR, H., and HUOT, J. 1988. Wolf diet and prey selectivity during two periods for deer in Quebec: decline versus expansion. Can. J. Zool. **66**. This issue.
RAUSCH, R. A. 1967. Some aspects of the population ecology of wolves, Alaska. Am. Zool. **7**: 253–265.
SCOTT, B. M. V., and SHACKLETON, D. M. 1982. A preliminary study of the social organisation of the Vancouver Island wolf (*Canis lupus crassodon* Hall, 1932). *In* Wolves of the world. *Edited by* F. H. Harrington and P. C. Paquet. Noyes Press, Park Ridge, NJ. pp. 12–25.
VAN BALLENBERGHE, V. 1983. Extraterritorial movements and dispersal of wolves in southcentral Alaska. J. Mammal. **64**: 168–170.
——— 1984. Injuries to wolves sustained during live-capture. J. Wildl. Manage. **48**: 1425–1429.
VAN BALLENBERGHE, V., ERIKSON, A. W., and BYMAN, D. 1975. Ecology of the timber wolf in northeastern Minnesota. Wildl. Monogr. No. 43.
WALTERS, C. J., STOCKER, M., and HABER G. C. 1981. Simulation and optimization models for a wolf–ungulate system. *In* Dynamics of large mammal populations. *Edited by* C. W. Fowler and T. D. Smith. John Wiley and Sons, New York. pp. 317–337.