

MOOSE-WOLF DYNAMICS AND THE NATURAL REGULATION
OF MOOSE POPULATIONS

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ABSTRACT

Long term data indicate that naturally regulated moose populations in southwestern Québec stabilize at a density of ≈ 0.40 animal \cdot km $^{-2}$. To test population regulation by forage competition, moose body condition was investigated near this equilibrium density ($0.37=H$) and at 2 lower densities ($\approx 0.23=M$, $0.17=L$). Measurements of head length, cranial breadth, heart weight, and kidney weight were collected from 443 moose killed during the autumn harvesting seasons of 1981 and 1982. There was no indication that body condition was poorer at the high moose density, and hence no evidence that competition for forage explains the regulatory process.

To test population regulation by predators, moose-wolf dynamics were studied at the same 3 moose densities (partial data in area L). In areas H and M, packs averaged 5.7 and 3.7 individuals, year-long territory sizes averaged 390 and 255 km 2 , and interstices between territories represented $\approx 0\%$ and 30% of the available area, respectively. The wolf population in area M, as compared to area H, suffered from a higher mortality rate due to malnutrition and lethal intraspecific combat, and from a lower success in producing pups. Analysis of summer scats and winter feeding observations indicated a greater use of alternative food resources at lower moose densities. Each pack killed on average 5.3, 1.8, and 1.1 moose \cdot 100 days in areas H, M, and L, respectively. January

wolf densities were respectively 1.38, 0.82, and 0.36 animals·100 km⁻². Year-long predation rates proved to be density-dependent, increasing with moose density from 6.1 to 19.3% of the postnatal populations.

I conclude that moose populations in southwestern Québec are regulated by predators at a density where competition for forage offers no detrimental effect. Preliminary results of a wolf removal experiment in area H support this hypothesis.

A review of the natural regulation of moose populations is presented. I support the concept that wolf predation can have an important regulatory effect at low moose densities (<0.5-1.0 animal·km⁻²) but also a compensatory (inversely density-dependent) effect at higher densities. Moose populations that are regulated by predators appear to be more stable than those regulated at high densities by forage competition.

RESUME

Les données obtenues au cours d'une étude de longue durée démontrent que les populations d'orignaux habitant le sud-ouest du Québec atteignent un équilibre lorsque leurs densités approchent $0.40 \text{ animal} \cdot \text{km}^{-2}$. Afin de vérifier si la compétition pour la nourriture disponible peut expliquer ce phénomène, la condition physique des orignaux a été étudiée à des densités de 0.37 (H) , $\approx 0.23 \text{ (M)}$, et $0.17 \text{ animal} \cdot \text{km}^{-2} \text{ (L)}$. Les mesures de longueur de tête, largeur du crâne, poids du coeur, et poids des reins, furent recueillies sur 443 orignaux abattus à la chasse sportive en 1981 et 1982. Les résultats n'indiquent pas une dégradation de la condition physique des animaux à la plus forte densité d'orignaux. La compétition pour la nourriture n'expliquerait donc pas le processus de régulation.

Afin de vérifier la régulation des populations par les prédateurs, les interactions loups-orignaux ont été étudiées aux 3 mêmes densités d'orignaux. Dans les aires d'études H et M, les meutes ont regroupé 5.7 et 3.7 loups en moyenne. Les territoires annuels ont couvert une superficie moyenne de 390 et 255 km^2 , et les espaces entre les territoires ont représenté respectivement ≈ 0 et 30% de l'aire disponible. La population de loups de l'aire M a accusé un plus haut taux de mortalité par malnutrition et combats léthaux intra-spécifiques, et un plus faible succès à produire des

louveteaux que la population de l'aire H. L'analyse des excréments d'été et des observations d'alimentation des loups en hiver a indiqué une exploitation accrue des sources alternatives de nourriture à des densités moindres d'orignaux. Chaque meute de loups a tué en moyenne 5.3, 1.8, et 1.1 orignaux·100 jours dans les aires H, M, et L, respectivement. En Janvier, les densités de loups ont été estimées à 1.38, 0.82, et 0.36 animaux·100 km⁻², respectivement. Le taux de prédation annuel s'est accru avec la densité d'orignaux, passant de 6.1 à 19.3% de la population estimée après la parturition. J'en conclus que les populations d'orignaux dans le sud-ouest du Québec sont maintenues à des faibles densités par l'action régulatrice des prédateurs. Les résultats préliminaires d'un contrôle expérimental de loups à l'intérieur de l'aire H supportent cette hypothèse.

Une revue des mécanismes de régulation chez l'orignal est présentée. Je supporte le concept que la prédation par le loup peut avoir un effet régulateur à des faibles densités d'orignaux (<0.5-1.0 animal·km⁻²), mais un effet inverse (non-régulateur) à des densités plus élevées. Les populations d'orignaux étant régularisées par les prédateurs apparaissent plus stables que celles régularisées à des densités élevées par l'abondance de nourriture.

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GENERAL INTRODUCTION

It has been commonly claimed that predators strongly interact with ungulate populations (e.g., Keith 1974; Smuts 1978; Bergerud 1980; Bergerud et al. 1983; Gasaway et al. 1983; Peterson and Page 1983). Yet, no study has demonstrated the regulatory effect of predation upon ungulates, i.e., that predation rate increases with ungulate density. Here, I report on such a study. The natural regulation of moose is analysed among 3 populations, 1 near an equilibrium density and 2 others disrupted from this equilibrium by intensive harvesting. It was felt that only by "manipulation" would a clear comprehension of the population process emerge.

As an entry into the intricate interactions between predators, moose, and forage availability, I first address the question of population regulation by food resources via a study of moose body condition (Chapter I). Subsequently (Chapter II), I present information on the social organization of wolves because of its potential importance in determining changes in wolf numbers. In Chapter III, I elaborate on moose-wolf dynamics, discussing the regulatory effect of wolf predation. The preliminary results of an on-going wolf removal experiment are reported in Chapter IV. In the concluding Chapter V, I review the natural regulation of moose populations, with summary statements designed to provoke thought and to inspire new lines of research.

Chapter 1

BODY CONDITION AND POPULATION REGULATION BY FOOD RESOURCES IN MOOSE

INTRODUCTION

Two factors are commonly invoked to explain population regulation in ungulates: availability of food resources (e.g., Caughley 1970, 1976; Sinclair 1977; Sinclair and Norton-Griffiths 1982; Houston 1982), and predation (e.g., Pimlott 1967; Keith 1974; Bergerud 1980; Gasaway et al. 1983). Studies testing these explanations have been notably scarce, mainly because they are difficult to conduct in the field (but see Macnab 1983).

When facing food limitation, individuals in an ungulate population compete for preferred, higher quality forage (Klein 1970; Kie et al. 1980). As a result, many important life-history events are adversely affected: growth, fat accumulation, and, ultimately, reproduction and survival (reviews in Hanks 1981; Huot 1982). Among the Cervidae, there is both circumstantial and experimental evidence that intraspecific size differences exist due to variations in food quality, food quantity, and population density (Verme 1963; Klein 1964, 1968; Klein and Strandgaard 1972; Verme and Ozoga

1980a; Suttie 1980; Leader-Williams and Ricketts 1982; Reimers et al. 1983; Skogland 1983). There is similar evidence that fat accumulations and their seasonal variations are largely governed by the summer and the winter foraging conditions (Dauphiné 1976; Mitchell et al. 1976; Verme and Ozoga 1980b; Huot 1982). In short, the lower fecundity rate, the retardation in prenatal and postnatal development, the delay in the calving time (which results in a shorter period of growth before the winter), and the increase of perinatal mortality, appear to be the most critical consequences of a poor nutritional plane (Verme 1963, 1969, 1979; Thorne et al. 1976; Peterson and Harper 1978; Robbins and Robbins 1979; Blaxter and Hamilton 1980). Initial growth retardation has a permanent effect which can result in a size difference for all age classes (Peterson 1977; Suttie 1980; Skogland 1983). This permanent effect is an important premise in the present study. Many of the authors listed above concluded that the assessment of body condition is a more appropriate approach with which to evaluate habitat condition than the direct evaluation of habitat, because body condition represents an 'in vivo' evaluation of habitat quality.

This study attempted to test whether or not moose (Alces alces) are regulated by available food resources. In southwestern Québec, non-harvested moose populations appear to stabilize at a density of ≈ 0.40 animal \cdot km $^{-2}$ (Crête et al. 1981; data herein). Elsewhere in North America, where

predation does not occur, moose populations can reach densities of 2 to 4 animals·km⁻² and still have a calf production in early winter of 15 to 25% of the total population (Bergerud and Manuel 1969; Blood 1973). The approach was to study moose body condition near the expected equilibrium density (0.37 animal·km⁻²) and at 2 lower densities (0.22 and 0.17 animal·km⁻²) for comparison. The 3 populations differed in density because they were manipulated by different harvest intensity rather than by a radical change in habitat quality (Crête et al. 1981).

I predicted that moose in the high density area would exhibit body growth retardation and poorer body condition, compared to moose in the 2 lower density areas where food competition should be reduced and habitat quality should be higher. If our prediction proves to be correct, population regulation by food resources would be suggested.

STUDY AREA

The 3 study areas (Fig. 1) are located within the most productive moose habitat in Québec (Brassard et al. 1974). Area H, the game reserve La Vérendrye (13,615 km²), had a relatively high moose density (0.37 animal·km⁻²). Sport hunting was not allowed in the reserve from its establishment in 1939 until 1964. Since 1964 harvest has been restricted by a limited entry system. Area M (2390 km²) had a moderate

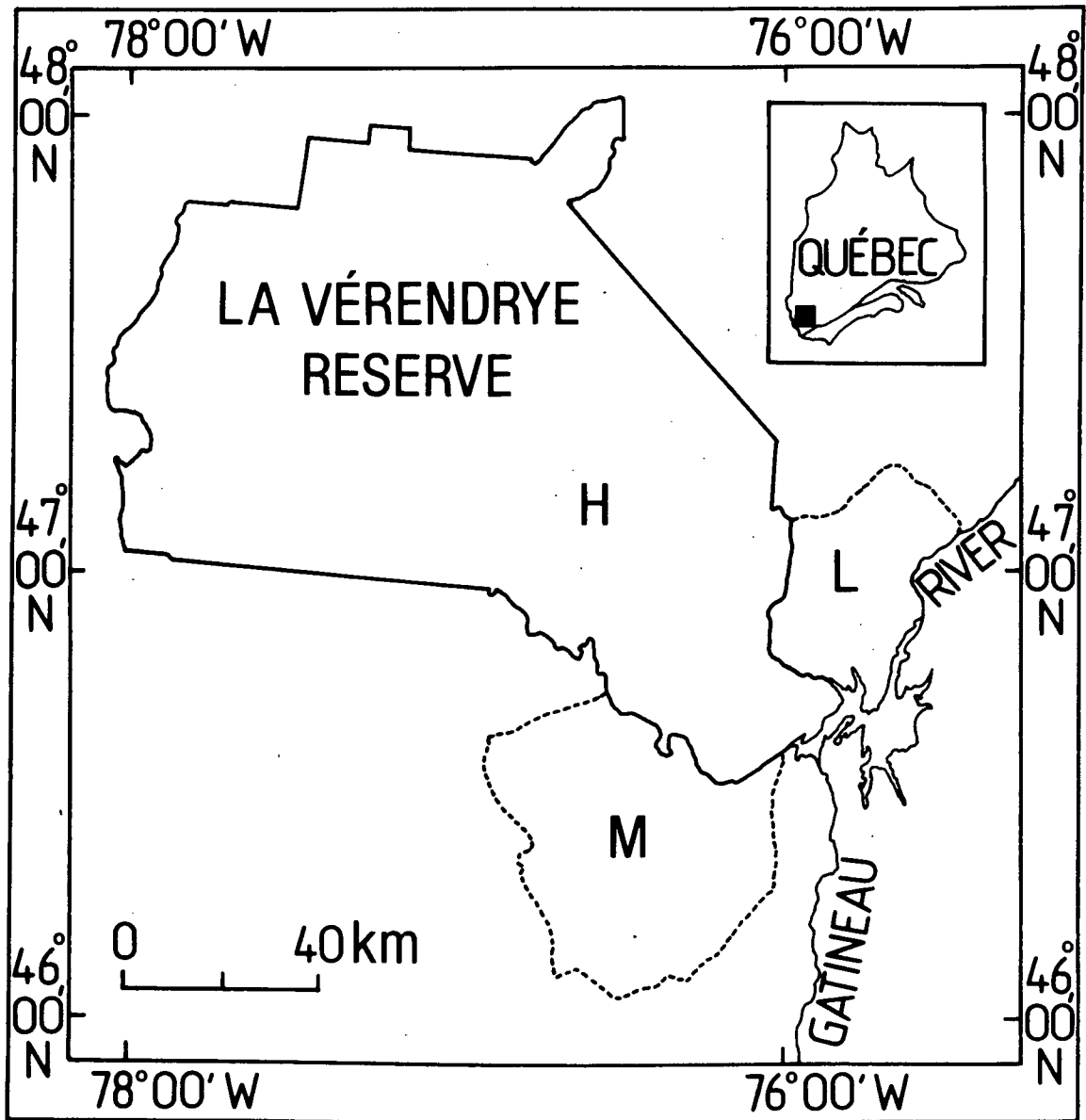


Fig. 1. Locations of areas H, M, and L, where the study was conducted.

moose density ($0.22 \text{ animal} \cdot \text{km}^{-2}$), and encompasses the former game reserve Pontiac (1205 km^2) abolished in 1978. Hunting has been unrestricted and high throughout area M since 1978. Area L (1185 km^2) had a relatively low moose density ($0.17 \text{ animal} \cdot \text{km}^{-2}$). During the 15-year period preceding the present study, area L had been intensively harvested under an unlimited entry system.

The relief is rolling hills with elevations ranging from 200 to 600 m above sea level. Snow accumulation averages 75 cm in February, and is comparable among the 3 study areas (Soucy 1971; Messier unpubl.). Lakes, ponds, and creeks are common and well distributed.

The forest consists of mixed coniferous and deciduous stands (Rowe 1972). The dominant tree species in the lower sites are balsam fir (Abies balsamea), white spruce (Picea glauca), black spruce (P. mariana), trembling aspen (Populus tremuloides), and paper birch (Betula papyrifera). Shade-tolerant hardwoods, mainly sugar maple (Acer saccharum) and yellow birch (B. alleghaniensis), cover tops and sides of the hills. Mountain maple (A. spicatum) and beaked hazelnut (Corylus cornuta) comprise most of the shrub strata. Crête and Jordan (1982a, b) provided additional information on availability, quality, and use of moose forage.

Two large predator species are present in the study area. Wolf (Canis lupus) densities range from approximately 0.4 to $1.4 \text{ animals} \cdot 100 \text{ km}^{-2}$, depending on the moose density (Messier

and Crête in press). Black bear (Ursus americanus) densities are unknown, but tracks and droppings are common in the 3 areas; area H appears to support the highest density (a minimum of $0.25 \text{ bear} \cdot \text{km}^{-2}$; Lachapelle et al. 1984).

METHODS

Data were collected during autumn 1981 and 1982 at compulsory hunter-kill registration stations. Moose were killed from 18 September to 18 October in area H, and from 16 to 24 October in areas M and L. Age was determined by a combination of tooth eruption patterns and counts of incisor cementum annuli.

Most moose densities were estimated from partial aerial surveys (minimum 500 km^2) initiated for other projects. Moose inventory techniques are described by Crête and St-Hilaire (1979) and Crête et al. (1981). Results were corrected for visibility bias (Crête et al. submitted). When aerial survey data were not available, moose densities were calculated from the predictive relationship between the number of hunting-days per kill (hunting-effort) and moose density (Crête al. 1981). Confidence intervals of density figures are not available and can be as wide as 20-30% of the estimate (Crête et al. submitted). I do not consider this imprecision to be a major weakness of the study because the analysis relies on long term data in which year-specific errors may compensate. Changes over a single year period exceed the accuracy of these

data.

To provide additional past information for area H, the 1967-82 trend of moose population was estimated by the hunting success (i.e., % of hunting parties who killed 1 moose, the bag limit). The number of hunting parties and the number of moose killed were known exactly. Harvest regulations remained comparable throughout this period. Between 1967 and 1978, parties of two hunters and a guide were allowed to hunt 4 days (same for all years) within a predetermined area. From 1979 the guide was no longer required and a third hunter could be included in the party. Harvest rates were computed by dividing the harvest by the sum of the January moose population and the harvest.

Four body condition indices, easily measured at harvest registration stations, were chosen. Two skeletal measures, head length (Haigh et al. 1980) and cranial breadth (minimum inter-orbital breadth with skin), were used as indicators of the environmental conditions during the body development phase (i.e., long-term effects). Two organs, heart weight (without fat deposit, surplus blood, and atria), and kidney weight (without fat deposit; average of the right and the left) were selected as proximate indicators of body condition (i.e., short-term effects) at the end of the plant growing season. These two organs appear sensitive to either energy or protein intake (Verme and Ozoga 1980a). I assumed that the 4 indices, interpreted together, would be effective to detect poor body

condition.

Data were treated by analysis of variance (UBC GENLIN). ANOVA tables were interpreted at 0.05 probability level. The homogeneity of variances was tested by the Layard chi-square technique with a probability level of 0.01. The predicted means of each index (i.e., after the age effect had been removed) were compared by the Scheffé method. Because this method is conservative, (Neter and Wasserman 1974:479), the probability level was set at 0.10. Six age classes were used for males and 4 for females.

RESULTS

Evidence of population regulation

From 1939 until 1964 (25 years), sport harvesting was not allowed in area H and moose likely were at an equilibrium density. The initiation of limited harvesting in 1964 may have induced a slight decline of the moose population, but since 1967 the population appears to be stable at 0.37 moose·km⁻². Population stability was indicated by the lack of trend in the hunting success ($\underline{r}^2=0.35$, $\underline{P}>0.10$, $n=16$, Fig. 2) and in the density estimates ($\underline{r}^2=0.36$, $\underline{P}>0.10$, $n=8$, Table 1). The critical point here is that the data do not show any population increment whatsoever. Assuming a density of 0.37, the annual harvest between 1964 and 1983 averaged 3.6% (186 ± (SD)25 moose). This rate was sustainable.

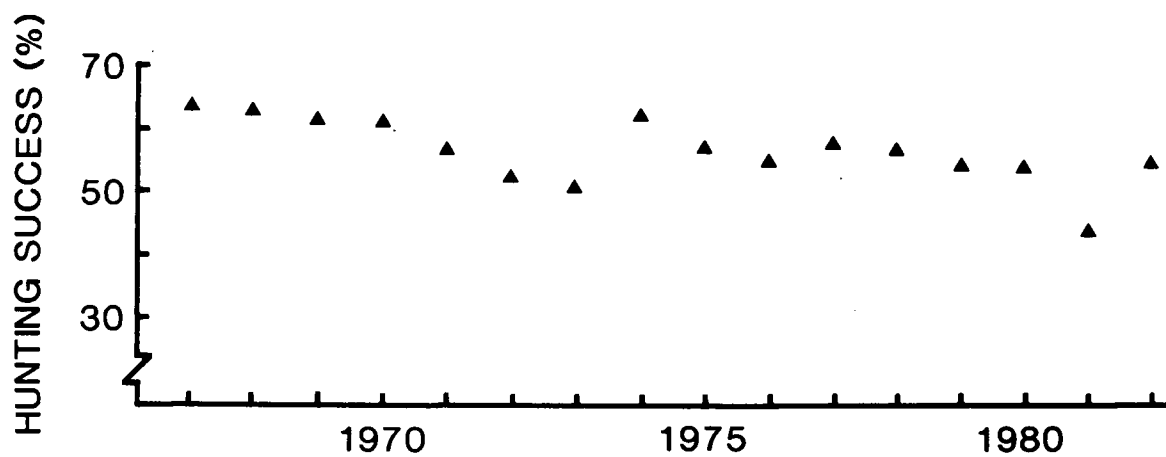


Fig. 2. Percent success of hunting parties (3 persons) to kill 1 moose (the bag limit) in area H from 1967 to 1982. The lack of trend ($P > 0.10$) suggests a stable population.

Table 1. Estimates of moose density and annual hunting rate in the 3 study areas from 1976 to 1983. Males represented 66%, 47%, and 53% of the harvest in areas H, M, and L, respectively. No data = n.d.

	Area H		Area M		Area L	
	Moose N / km ²	Hunting %	Moose N / km ²	Hunting %	Moose N / km ²	Hunting %
1976	0.41 _c	3	0.30 _a	n.d.	n.d.	
1977	0.36 _b	4	n.d.		n.d.	
1978	0.37 _b	4	0.29 _c	22	0.15 _b	26
1979	0.39 _c	3	0.26 _c	25	0.22 _c	20
1980	0.36 _c	4	0.19 _c	27	0.18	21
1981	0.36	4	0.25	21	0.16	23
1982	0.32	3	0.19	25	0.16	23
1983	0.37	4	0.22 _c	22	0.16	31
mean	0.37	3.6	declining	23	0.17	24

a Crête and St-Hilaire, unpubl.

b Crête et al. 1981

c estimated from the hunting-effort per kill (Crête et al. 1981);
results from Tremblay, unpubl.)

Crête et al. (1981) estimated that, without harvesting, the moose population in area H would stabilize at a density of $0.40 \text{ animal} \cdot \text{km}^{-2}$. Original values given by Crête et al. (1981) were 0.28 and 0.30 but were divided by 0.73 to correct for the now-known visibility bias in aerial surveys (Crête et al. submitted). From retro-calculation, the equilibrium density is evaluated at a maximum of $0.41 \text{ animal} \cdot \text{km}^{-2}$ (i.e., the 1967-82 density, 0.37, plus a maximum loss of 10% for the 1964-67 harvest or 3 to 4% annually). Both evaluations suggested that the moose density in area H during the present study was not substantially lower than the equilibrium density ($0.37 \text{ vs } \approx 0.40 \text{ animal} \cdot \text{km}^{-2}$).

In area M, the moose population was at $0.30 \text{ animal} \cdot \text{km}^{-2}$ in 1976 and declined at an annual rate of $\approx 5\%$ until 1983 ($r^2=0.62$, slope= -0.0145 or 5% , $P<0.05$, Table 1). This population received an average annual harvest rate of 23% (Table 1), so the sustainable harvest rate was evaluated at $\approx 18\%$ (i.e., the harvest rate, 23% , minus the population decrement, 5%). In area L, the moose population was apparently stable and at a density of $0.17 \text{ animal} \cdot \text{km}^{-2}$ ($r^2=0.10$, $P>0.10$, $n=6$, Table 1). This population sustained a harvest rate of 24% (Table 1).

Considering the 3 study areas, results indicate that the population growth rate, as evaluated by the sustainable harvest (Caughley 1976), declined from 24% to a maximum of 4% as moose density increased from 0.17 to $0.37 \text{ animal} \cdot \text{km}^{-2}$.

Clearly, a density-dependent factor underlies these population responses. Moreover, these results imply that the 3 populations were certainly at different levels below their respective equilibrium density. Note that I am not assuming that these 3 equilibrium densities were necessarily equal, only that the 3 populations were at different levels below their equilibrium density because of the differences in population growth rate (Caughley 1976).

Body condition vs moose density

A total of 443 moose were measured in the autumn 1981 and 1982; 232 in area H, 118 in area M, and 93 in area L. Observations in both years were combined because year had no significant effect on either head length, heart weight, or kidney weight. The difference between years in cranial breadth was the result of an unexplained difference in area L only.

Age interacted significantly with sex in regard to head length, cranial breadth, and heart weight. These observations indicate that males and females grow differently which obliged me to treat them separately. Body development continued at least until 5 1/2 years of age in males and until 3 1/2 years in females (Tables 2 and 3).

No interaction was present between moose density and age for the 4 indices (Table 4). This lack of response demonstrates that the age-specific increments (i.e., growth

Table 2. Age-specific head length (cm), cranial breadth (cm), heart weight (kg), and kidney weight (kg) for male moose, given as mean values \pm SE(n), in relation to 3 levels of moose density in southwestern Québec: area L, 0.17 / km²; area M, 0.22 / km²; area H, 0.37 / km². No data = n.d.

	Calf	1½ yr.	2½ yr.	3½ yr.	4½ yr.	≥ 5½ yr.
Head length						
Area L	40.12 \pm 1.29 (8)	57.74 \pm 0.72(26)	60.89 \pm 1.29 (8)	63.82 \pm 1.63 (5)	64.14 \pm 1.38 (7)	64.50 (1)
Area M	43.77 \pm 1.22 (9)	58.01 \pm 0.94(15)	61.61 \pm 1.10(11)	64.83 \pm 2.11 (3)	63.63 \pm 2.11 (3)	65.25 \pm 1.82 (4)
Area H	40.50 \pm 2.58 (2)	57.99 \pm 0.57(41)	62.73 \pm 0.62(35)	64.35 \pm 0.76(23)	64.54 \pm 0.86(18)	66.87 \pm 0.58(40)
Cranial breadth						
Area L	15.62 \pm 0.47 (8)	19.11 \pm 0.26(26)	19.14 \pm 0.47 (8)	20.10 \pm 0.59 (5)	22.22 \pm 0.54 (6)	21.00 (1)
Area M	16.08 \pm 0.42(10)	19.14 \pm 0.33(16)	20.72 \pm 0.38(12)	22.50 \pm 0.76 (3)	21.40 \pm 0.76 (3)	21.87 \pm 0.66 (4)
Area H	16.25 \pm 0.94 (2)	20.78 \pm 0.21(41)	22.06 \pm 0.22(36)	22.56 \pm 0.28(23)	22.75 \pm 0.31(18)	23.46 \pm 0.21(41)
Heart weight						
Area L	n.d.	1.49 \pm 0.07(10)	1.73 \pm 0.12 (3)	1.97 (1)	2.12 \pm 0.15 (2)	n.d.
Area M	0.98 \pm 0.12 (3)	1.37 \pm 0.08 (7)	1.75 \pm 0.07 (8)	2.01 \pm 0.12 (3)	2.03 (1)	1.97 \pm 0.12 (3)
Area H	0.74 \pm 0.15 (2)	1.66 \pm 0.03(37)	1.94 \pm 0.04(33)	2.10 \pm 0.05(20)	2.30 \pm 0.06(14)	2.28 \pm 0.04(33)
Kidney weight						
Area L	n.d.	0.46 \pm 0.03 (7)	n.d.	0.51 \pm 0.06 (2)	0.59 \pm 0.06 (2)	n.d.
Area M	0.31 (1)	0.49 \pm 0.04 (5)	0.51 \pm 0.05 (4)	n.d.	n.d.	n.d.
Area H	0.30 (1)	0.52 \pm 0.01(38)	0.61 \pm 0.02(29)	0.63 \pm 0.02(18)	0.78 \pm 0.03 (9)	0.84 \pm 0.02(28)

Table 3. Age-specific head length (cm), cranial breadth (cm), heart weight (kg), and kidney weight (kg) for female moose, given as mean values \pm SE(n), in relation to 3 levels of moose density in southwestern Québec: area L, 0.17/km²; area M, 0.22/km²; area H, 0.37/km². No data=n.d.

	Calf	1½ yr.	2½ yr.	≥ 3½ yr.
Head length				
Area L	42.31 ± 1.14 (8)	55.24 ± 0.81 (16)	60.93 ± 1.87 (3)	61.94 ± 0.88 (13)
Area M	44.65 ± 1.02 (10)	57.45 ± 0.66 (24)	62.73 ± 1.08 (9)	63.35 ± 0.71 (21)
Area H	n.d.	56.87 ± 0.62 (27)	63.11 ± 1.08 (9)	62.89 ± 0.58 (31)
Cranial breadth				
Area L	14.94 ± 0.42 (8)	17.77 ± 0.31 (15)	20.33 ± 0.69 (3)	19.17 ± 0.33 (13)
Area M	15.06 ± 0.35 (12)	17.52 ± 0.27 (28)	19.50 ± 0.42 (8)	19.19 ± 0.26 (22)
Area H	n.d.	18.77 ± 0.23 (27)	20.33 ± 0.40 (9)	20.55 ± 0.20 (35)
Heart weight				
Area L	0.87 (1)	1.45 ± 0.09 (5)	1.86 ± 0.14 (2)	1.83 ± 0.09 (5)
Area M	0.88 ± 0.08 (6)	1.59 ± 0.05 (15)	1.68 ± 0.08 (6)	1.97 ± 0.06 (12)
Area H	n.d.	1.70 ± 0.04 (26)	2.06 ± 0.07 (8)	2.05 ± 0.04 (29)
Kidney weight				
Area L	0.30 (1)	0.44 ± 0.03 (5)	n.d.	0.67 ± 0.05 (2)
Area M	0.26 (1)	0.47 ± 0.02 (8)	0.51 ± 0.03 (4)	0.54 ± 0.03 (6)
Area H	n.d.	0.53 ± 0.02 (19)	0.61 ± 0.03 (5)	0.68 ± 0.01 (30)

Table 4. Analysis of variance treating moose density and age effects on head length, cranial breadth, heart weight, and kidney weight of hunter-killed moose in southwestern Québec, data of 1981 and 1982 combined. Moose density = 3 levels (area L, area M, and area H). Age = 6 levels for males (calf, 1½ yr., 2½ yr., 3½ yr., 4½ yr., ≥ 5½ yr.), and 4 levels for females (calf, 1½ yr., 2½ yr., ≥ 3½ yr.).

	Head length		Cranial breadth		Heart weight		Kidney weight	
	df	<u>P</u> *	df	<u>P</u>	df	<u>P</u>	df	<u>P</u>
Males								
Moose density	2	0.296	2	0.000	2	0.000	2	0.003
Age	5	0.000	5	0.000	5	0.000	5	0.000
Moose d. X age	10	0.840	10	0.103	8	0.439	4	0.359
Error	241		245		164		132	
Females								
Moose density	2	0.014	2	0.000	2	0.000	2	0.000
Age	3	0.000	3	0.000	3	0.000	3	0.000
Moose d. X age	5	0.981	5	0.732	5	0.230	4	0.230
Error	160		169		104		71	

* probability of F-ratio MS : MS error

rate) of head length, cranial breadth, heart weight, and kidney weight were not affected by moose density. My interpretation here implies that the possible effect of food competition was uniform during the 6 years or so preceding the study. This assumption is most likely correct in area L and H where moose populations appeared to be stable.

Significant effects of moose density on the 4 indices were found in both sexes, with the exception of male head length (Table 4). These results indicate that, although individual growth rates of the various morphological parameters followed the same pattern in the different populations, the levels achieved within age classes differed between populations (i.e., a carry over effect). (The analogy in regression analysis would be that the slopes of regression lines were equal, but their elevations differed.) Such differences normally are analysed by the comparisons of the predicted means; i.e., the means computed after the age effect has been removed from the measures (from the ANOVA, Table 4). None of the 4 indices had a significantly lower value in area H as predicted. Cranial breadth in males and females, and heart and kidney weight in females were significantly higher in area H (Table 5).

Table 5. Head length (cm), cranial breadth (cm), heart weight (kg), and kidney weight (kg) for hunter-killed moose, given as the predicted mean values \pm SE(n), in relation to 3 levels of moose density in southwestern Québec: area L, 0.17 / km²; area M, 0.22 / km²; area H, 0.37 / km². Predicted mean values are the means obtained after the age effect has been removed from the measures following the variance analysis presented in Table 4. Means were compared by Scheffé test, $\alpha = 0.10$.

	Area L	Area M	Area H	Homogeneous means	Differing means
Males					
Head length	59.91 \pm 0.51(55)	60.69 \pm 0.56(45)	60.85 \pm 0.30(159)	L,M,H	none
Cranial breadth	19.84 \pm 0.19(54)	20.33 \pm 0.20(48)	21.66 \pm 0.11(161)	L,M	H
Heart weight	1.78 \pm 0.05(16)	1.75 \pm 0.04(25)	1.95 \pm 0.02(139)	L,M ; L,H	none
Kidney weight	0.54 \pm 0.03(11)	0.58 \pm 0.03(10)	0.63 \pm 0.01(123)	L,M,H	none
Females					
Head length	57.09 \pm 0.52(40)	59.00 \pm 0.41(64)	58.57 \pm 0.41 (67)	M,H	L
Cranial breadth	18.25 \pm 0.19(39)	18.12 \pm 0.14(70)	19.36 \pm 0.15 (71)	L,M	H
Heart weight	1.63 \pm 0.05(13)	1.61 \pm 0.03(39)	1.85 \pm 0.03 (63)	L,M	H
Kidney weight	0.54 \pm 0.02 (8)	0.51 \pm 0.02(19)	0.61 \pm 0.01 (54)	L,M	H

DISCUSSION

The understanding of population regulation is relevant to 3 important aspects of ungulate management: conservation, sustained yield, and population control. Caughley (1976) presented a model of ungulate population dynamics with respect to the ungulate-vegetation system. In Caughley's model, an ungulate population with a growth rate at or near zero (i.e., at equilibrium) will be food stressed compared to a population reduced much below the equilibrium density. The present results on moose population dynamics in southwestern Québec are contrary to Caughley's model, specifically to the regulatory mechanism implied rather than the general approach.

In La Vérendrye game reserve, area H, long-term data on population density and harvest rate suggested that: a) the population was fairly stable, b) its annual surplus was less than 4%, and c) its density was not substantially lower than the estimated non-harvested population density. This study tested whether animals in area H were nutritionally stressed compared to the 2 other populations at lower densities with less food competition and a higher population growth rate. I did not detect any differences in body development rate as assessed by the growth of head length, cranial breadth, heart weight, and kidney weight. Differences in the measurements were found within age classes, but contrary to the predictions, none of them was lower in area H. In 4 cases the

values were slightly but significantly higher in area H ; a fact I cannot explain readily. One explanation is that moose experienced more favourable foraging conditions in area H, but this benefit was outweighed by another population process that prevented population growth.

There are two alternative explanations for the lack of evidence of poorer body condition as the population growth rate approaches zero (i.e., food resource regulation). The first is that I may have selected the wrong indices. From food trial experiments, Verme and Ozoga (1980a) demonstrated that cranial breadth and kidney weight of white-tailed deer fawns (Odocoileus virginianus) are correlated to protein intake, whereas heart weight is affected by energy intake. Verme and Ozoga's findings were used for the justification of these 3 body condition indices. In addition, head length provided a measure specifically related to the skeletal growth, and moreover this measure is well related to carcass weight (Haigh et al. 1980). Among the 3 areas, the 2 structural and the 2 organ-indices lead to a common trend (Table 5). From this consistency between indices, I believe that the combined information from the 4 indices was sufficient to detect possible degradation of animal body condition. In a parallel study using the same indices, Crête (unpubl.) found that the duration of the vegetative season significantly affected body growth of moose from different Québec populations.

Egress may have confounded the results. This possibility is unlikely for the following reasons. Moose in eastern Canada do not exhibit seasonal directional migrations (Goddard 1970; Roussel et al. 1975; Addison et al. 1980; Crête unpubl.). During radio-tracking of over 60 moose within the 3 study areas, only 5 animals (3 marked near a border) moved between areas (Crête unpubl.). From these observations, and considering the large size of the study areas, I assumed that the 3 moose populations were discrete. Even if the discreteness is suspect, this would not have vitiated results for calves and most yearlings which are not yet at an age to disperse (Gasaway et al. 1980). The conclusions would have been similar relying exclusively on these data (see Table 2 and 3).

Fertility of Cervidae has been related to the level of malnutrition of females at the time of breeding, and at the time they give birth (Blaxter and Hamilton 1980; Thomas 1982; Saether and Haagenrud 1983). In area H, there was no evidence of a low pregnancy rate or low postnatal calf production. From 1964 to 1966 (i.e., following 25 years without sport harvesting), the number of corpora lutea present was 35 per 100 yearling cows ($n=23$), and 128 per 100 cows $\geq 2 \frac{1}{2}$ yr. of age ($n=132$; Gauthier 1978). With the aid of radio-collared females, Crête (unpubl.) observed a minimum post-partum productivity of 96 calves per 100 cows ≥ 2 yr. of age (i.e., yearling and older cows at breeding time combined, $n=26$).

These indices of productivity are equal or superior to the values reported for other North American moose populations (Pimlott 1959; Schladweiler and Stevens 1973; Blood 1973; Simkin 1974; Hauge and Keith 1981).

Crête and Jordan (1982a) investigated production and quality of both summer and winter moose forage in areas H and L. They maintained that the population growth of moose in area H was not limited by habitat quality. They also showed that in area H the proportion of in-yard winter forage removed by moose rarely exceeded 10% (Crête and Jordan 1982b).

Peek et al. (1976), and Peek and Eastman (1983) argued that an increase in moose population is the likely response to an amelioration of habitat quality following disturbance. Spruce budworm (Choristoneura fumiferama) had caused extensive mortality to conifers in the study areas during the early 1970's. This episodic infestation enriched markedly the shrub strata in coniferous stands (Crête and Jordan 1982a). Despite that, moose in area H did not respond by higher recruitment and an increase in density (Fig. 2, Table 1). This observation supports the assertion that habitat quality was not limiting moose populations.

I conclude that, in southwestern Québec, low moose population growth rate does not necessarily reflect deterioration of foraging conditions. Availability of food resources is not sufficient to explain natural regulation of moose populations when density approaches $0.40 \text{ animal} \cdot \text{km}^{-2}$.

This density appears to be the equilibrium density of moose in eastern Canada (i.e., boreal forest) where predation occurs (Crête et al. 1981; Bergerud et al. 1983; this study). I showed that the population growth rate diminished from 24% to 4% when different harvesting regimes allowed moose populations to stabilize at densities ranging from 0.17 to 0.37 animal·km⁻². Along with this decline in the population growth rate, there was no indication that moose body condition deteriorated. I would suggest that, under these conditions, management policy should not be centered on improving moose habitat when densities are below 0.40 animal·km⁻².

Because I could not falsify the null hypothesis, the study does not provide a definitive proof that availability of food resources does not regulate moose in southwestern Québec. The food regulation hypothesis is still viable, but, considering all the evidence, this hypothesis certainly is not very healthy. I continue to feel the need for some controlled studies where the necessary criterion is to relate a population process to the population growth rate.

As an alternative to food regulation, I suggest that predation by wolves and/or black bears may be density-dependent between 0.0 and 0.4 moose per km², and thus has a regulating capability. This is a testable hypothesis, and already proposed by Crête et al. (1981) and Bergerud et al. (1983).

Chapter II

SOCIAL ORGANIZATION, SPATIAL DISTRIBUTION, AND POPULATION DENSITY OF WOLVES IN RELATION TO MOOSE DENSITY

INTRODUCTION

The effect of wolf predation on moose remains a question of substantial theoretical and applied interest. Much of the previous research has focussed primarily on a descriptive approach: e.g., estimation of wolf numbers and their basic social structure, wolf food habits, prey selectivity, food intake rate, and a general evaluation of predation rate (Mech 1966; Haber 1977; Peterson 1977; Fuller and Keith 1980; Peterson et al. 1984b). Relatively little work has been done toward understanding certain underlying processes and functional relationships by means of manipulative experiments (Gasaway et al. 1983; Crête and Messier 1984; see also Macnab 1983). In particular, solid information is lacking on the functional and numerical responses of wolves to different moose densities.

Here, I present data on social organization, spatial distribution, and population density of 2 wolf populations relying primarily on moose as prey. The study documents the wolf numerical response and the important behavioural

attributes associated with this process. One wolf population experienced relatively high moose abundance due to low human exploitation, whereas the second inhabited a contiguous area where the moose population had been reduced (manipulated) to about half its naturally regulated density by harvesting.

STUDY AREA AND METHODS

The ecology of wolves was investigated in a 6400-km² area of southwestern Québec, Canada (47°N, 77°W; Fig. 3) from June 1980 to February 1984. This area was selected because it covered a 3000-km² area of high prey density (HP) in La Vérendrye reserve, and a 3400-km² area of low prey density (LP) south of the reserve (Fig. 3). The boundary of La Vérendrye reserve delineated the HP area. Moose, the predominant prey species of the wolf, was at a stable density of 0.37 animal·km⁻² in HP, and declined during the study from ≈0.25 animal·km⁻² to ≈0.21 animal·km⁻² in LP (Messier and Crête 1984). The natural equilibrium density (i.e., non-harvested) was estimated at 0.4 moose·km⁻² in HP (Messier and Crête 1984). Crête et al. (1981) presented evidence that moose density decreased abruptly (within a few km) from the HP to the LP area. Beaver (Castor canadensis) density was estimated at 3.5 colonies·10 km⁻² in HP, and at 1 colony·10 km⁻² in LP (Crête and Samson unpubl.; in 1981). Moose represented approximately 70% and beaver 15% of the annual

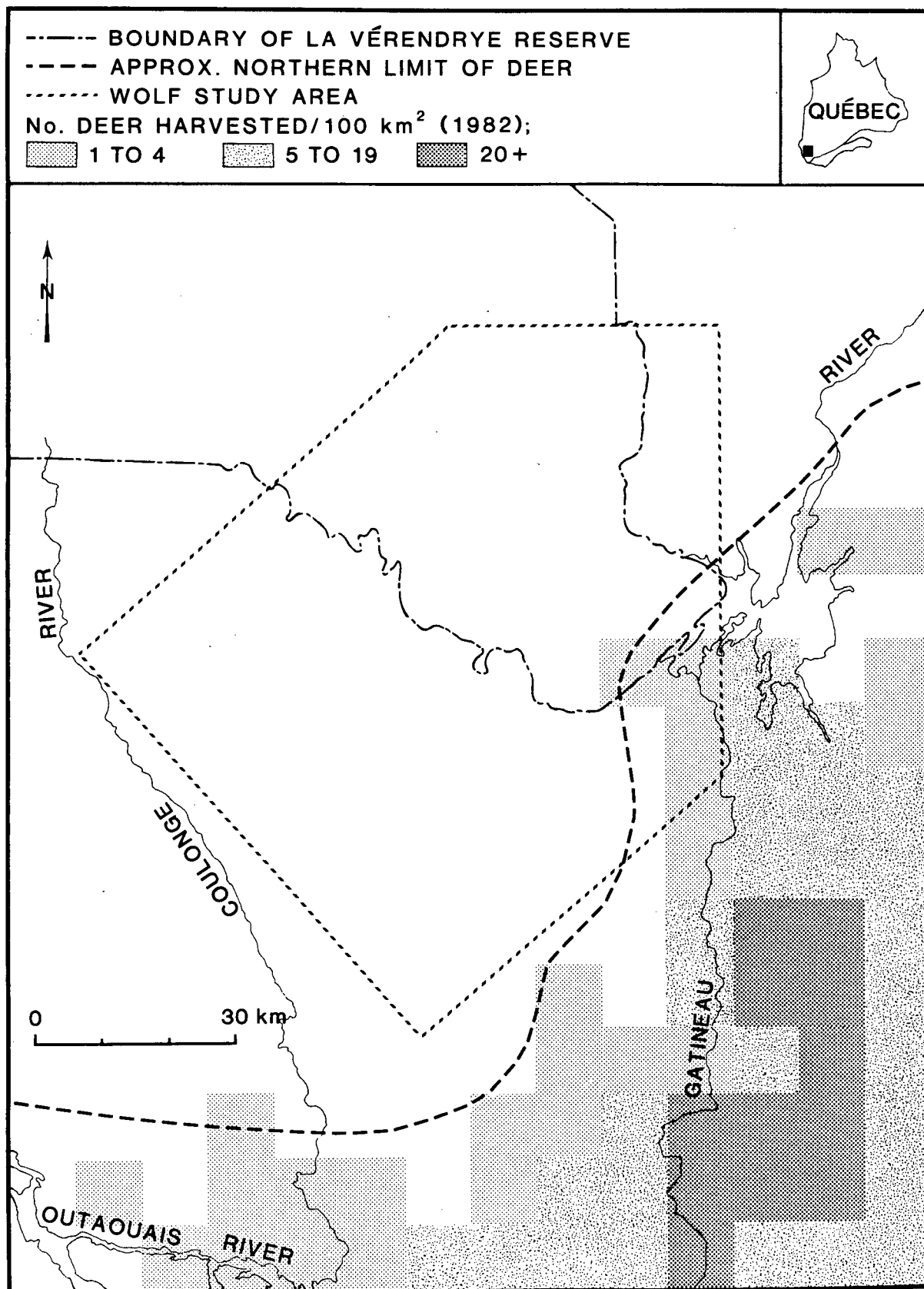


Fig. 3. Location of the area where most of the radio tracking of wolves was conducted. The number of deer harvested per 100 km² in 1982 are presented to illustrate the deer distribution.

prey biomass ingested by wolves (Messier and Crête in press). Deer, the only alternative ungulate species, were present southeast of the study area (Fig. 3). Messier and Crête (1984) have presented information on other features of the study area.

Fifty-four wolves from 14 contiguous packs were radio-tracked from an airplane (methodology in Mech 1974). Some 4700 wolf locations were accumulated during 2000 h of flying time. Each year the frequencies of tracking flights were 3-4 per week from 15 May to 1 November, almost daily from 15 December to 1 April, and occasionally during the remaining periods. Wolves were observed visually in 75% of the winter locations, but rarely in other periods. Each observation included group size, whether or not all animals were seen (i.e., in open habitat), and the identity of marked individuals.

Mortality rate of wolves was calculated from the cumulative radio-tracking times and the interim deaths. Successful year-specific reproduction was ascertained when: 1) a pack increased in size from March to the following December providing that focal activity sites (pup resting areas) were observed in the intervening time, or 2) when at least one pup was captured after August. Unsuccessful reproduction (i.e., no or failed reproduction) was ascertained when: 1) a pack did not demonstrate focal activity sites in summer, or 2) when a pair remained as a pair from March to the following December.

I excepted 2 instances for which the assertion on reproduction was uncertain, 1 in HP and 1 in LP. Packs that had a territory overlapping HP and LP areas, were assigned to the area in which the pups had been reared.

Wolf grouping was analysed from 3 perspectives with specific meanings. In all cases, I used those winter observations (December to April) for which all wolves were counted reliably. This condition occurred frequently in winter ($\approx 70\%$ of the visual observations) because wolves tended to travel and rest in open areas such as lake shores, streams, clearcut stands, and forest openings. Moreover, about 40% of the forest stands in the area were deciduous with good visibility in winter. Travelling group size represented the number of individuals within a group when they moved about their territory. Travelling group size is particularly important in encounters with prey. Pack size represented the number of socially interacting wolves within a pack, and included members temporarily dissociated from the pack. The assessment of pack size relied on each pack's history (i.e., prolonged observation). Pack cohesiveness refers to the proportion of pack members present in the pack core (i.e., the group including the reproductive pair) at any given time. For this index, all observations of a pack within a 15-day period were considered as one sample. This restriction was imposed to avoid bias among periods.

The year-long (1 May to 30 April) territories were

delineated by the minimum-convex-polygon method using 95% of the closest locations of instrumented pack member(s). Territories were assumed to be defined when the observation-area-curve formed an asymptote (Messier and Barrette 1982; Bowen 1982; Bekoff and Mech 1984). Normally this condition was satisfied after 40 to 80 daily locations, depending on the pack's reproductive status and season. Radio fixes more than 5 km from the border of established territory, were interpreted as excursions (Messier in press b) and were excluded from the analysis. It was evident that wolves engaged in excursions of less than 5 km, but I could not discard these excursions objectively because the circumscription of a territory was, to some extent, arbitrary (i.e., determined by the computational procedure). This consideration justified the use of the 95% convex-polygon method. On average, the areas of the 95% convex-polygons corresponded to 84% ($\pm 8\%$ SD) of the 100% convex-polygons.

Values of territory size were regressed in relation to pack size and moose density. Moose density estimates for the entire LP area, HP area, and for a third area east of HP (used for pack L8) have been presented and discussed elsewhere (Messier and Crête 1984). Moose densities were derived from regression analyses of yearly estimates between 1976 and 1983 to minimize the year-specific error. Moose density estimates of territories encompassing 2 areas were weighted by the area contributed and the respective density. I could not evaluate

moose density within each territory directly. Thus, the analysis contains an undefined variance linked with the heterogeneity of moose dispersion.

Wolf density in January was estimated each year in the LP and the HP areas. I used the total-area-approach because it allows inclusion in the census area of interstices between territories. The possibility of undetected pairs or packs in the census area was believed to be minimal. During the intense ground patrolling and scanning during flights, signs of known resident packs were frequently noticed. I presume that the same would have been true for untracked packs. For territories partially within a census area, I multiplied the pack size by the percentage of locations in the census area (i.e., relative presence) to assess the number of wolves to be used in the density estimates.

Space-use patterns were illustrated by typical sets of wolf locations. For this type of behavior, it was felt that a visual representation is the simplest way to convey the information. More quantitatively, daily distances (i.e., the distance between 2 consecutive locations separated by 20 to 28 hours) were treated by cumulative frequency analyses (Kolmogorov-Smirnov test). It was assumed that the daily distances reflected the actual distances travelled by wolves. I divided data into 2 periods: summer, 1 May to 30 November, and winter. In summer, because wolves were rarely observed, I considered each pack member independently. If 2 instrumented

animals had travelled together (same locations) only 1 movement was included in the analyses. In winter, daily distances of packs were quantified exclusively from the pack cores.

Nonparametric statistical tests were used if the assumptions of parametric tests were violated (Siegel 1956; Sokal and Rohlf 1981). All tests except F-tests were two-tailed if not otherwise specified. Tests leading to a probability of rejection greater than 0.05 were judged to be not significant.

RESULTS

Mortality and reproduction

Wolf social organization relies on an extended family system. Thus, the in-group mortality and recruitment represent 2 important attributes of the pack size dynamics. Observations of deaths (only animals older than 3 months) indicate that the annual mortality rate was higher in LP (55%) than in HP (35%; Table 6). These estimates are likely high because more tracking took place from October to February (54%) when wolves experienced a higher mortality risk, i.e., the exploitation exerted by man (trapping and shooting) was distributed exclusively during this period. Human-caused mortality was comparable in both study areas (30% in HP and 25% in LP annually, but was likely over-estimated due to the

Table 6. Mortality observations from 54 wolves (>3 months of age) tracked during the study. Radio-tracking time when wolves were inside their territory is referred to as "home", and when they were outside as "foray".

Area	Tracking time (in wolf-year)		Mortality						
			Natural		Human-caused			Overall	
	Home	Foray	Malnutrition	Strife	Car	Trap	Gun	Home	Foray
HP	20.2	2.2	1	0	3	4	0	6	2
LP	19.2	2.4	5	2	1	3	1	7	5
Total	39.4	4.6	6 ϕ	2 †	4	7	1	13	7
			8		12				

ϕ 2 pups, 1 yearling, 3 adults

† 2 adults

yearly distribution of tracking effort). Thus, the LP population suffered from a higher mortality rate because of the higher occurrence of natural mortalities such as malnutrition and lethal combat (Table 6).

Wolves had a higher mortality rate when travelling over unfamiliar ground (Table 6). Of 20 mortalities, 7 occurred during extra-territorial movements (3 from trapping, 2 from malnutrition, 1 car-killed, and 1 from intraspecific strife). Considering the respective tracking time, the distribution of mortalities was not homogeneous ($X^2[1] = 12.7$, $P < 0.01$; Table 6).

Direct counts of pups could not be conducted in this study due to the secretive nature of the wolves. In December, when most wolves were observed for the first time, pups could not be distinguished from adults reliably. Nonetheless, a difference in reproduction was apparent between HP and LP area. In the HP area, packs produced at least some pups in 14 of the 15 possible occasions (93%). This proportion differs significantly from the 62% observed in the LP area ($n=21$; one-tailed Z-test = 2.1, $P=0.02$). During 3 unsuccessful occasions in LP, movements typical of a den attendance were initially observed, but wolves subsequently resumed movements characteristic of non-reproductive packs.

Social organization

Travelling group size in winter averaged 2.7 individuals in HP and 2.3 in LP. Grouping of wolves differed significantly between the HP and the LP areas ($\chi^2[3] = 37.5$, $P < 0.01$; from original frequency distribution of wolf individuals; Fig. 4). Single wolves represented as much as 46% of the groups encountered (18% of the wolves; Fig. 4), and were as frequent in the LP area as in the HP area. More groups of 6 to 8 wolves were observed in the HP area.

In January, pack size averaged 5.7 ± 0.5 (SE, $n=12$) individuals in the HP area. This estimate was significantly larger than the average of 3.7 ± 0.4 ($n=20$) observed in the LP area (t -test = 3.9, $P < 0.01$). From December to the end of March, average pack size decreased by 6% in HP and 12% in LP. Prey abundance did not influence significantly the decrement of pack size through the winter (one-tailed Z -test = 1.2, $P > 0.10$).

Pack cohesiveness, or the proportion of the pack members in the pack core, declined through the winter from about 0.90 to 0.75 (Fig. 5). The decline appeared to be related to the higher aggressiveness within packs during the breeding season (Messier in press b; Peterson et al. 1984b). No difference in pack cohesiveness was detected between LP and HP area (Mann-Whitney U -test[7,7] = 25, $P > 0.20$; Fig. 5).

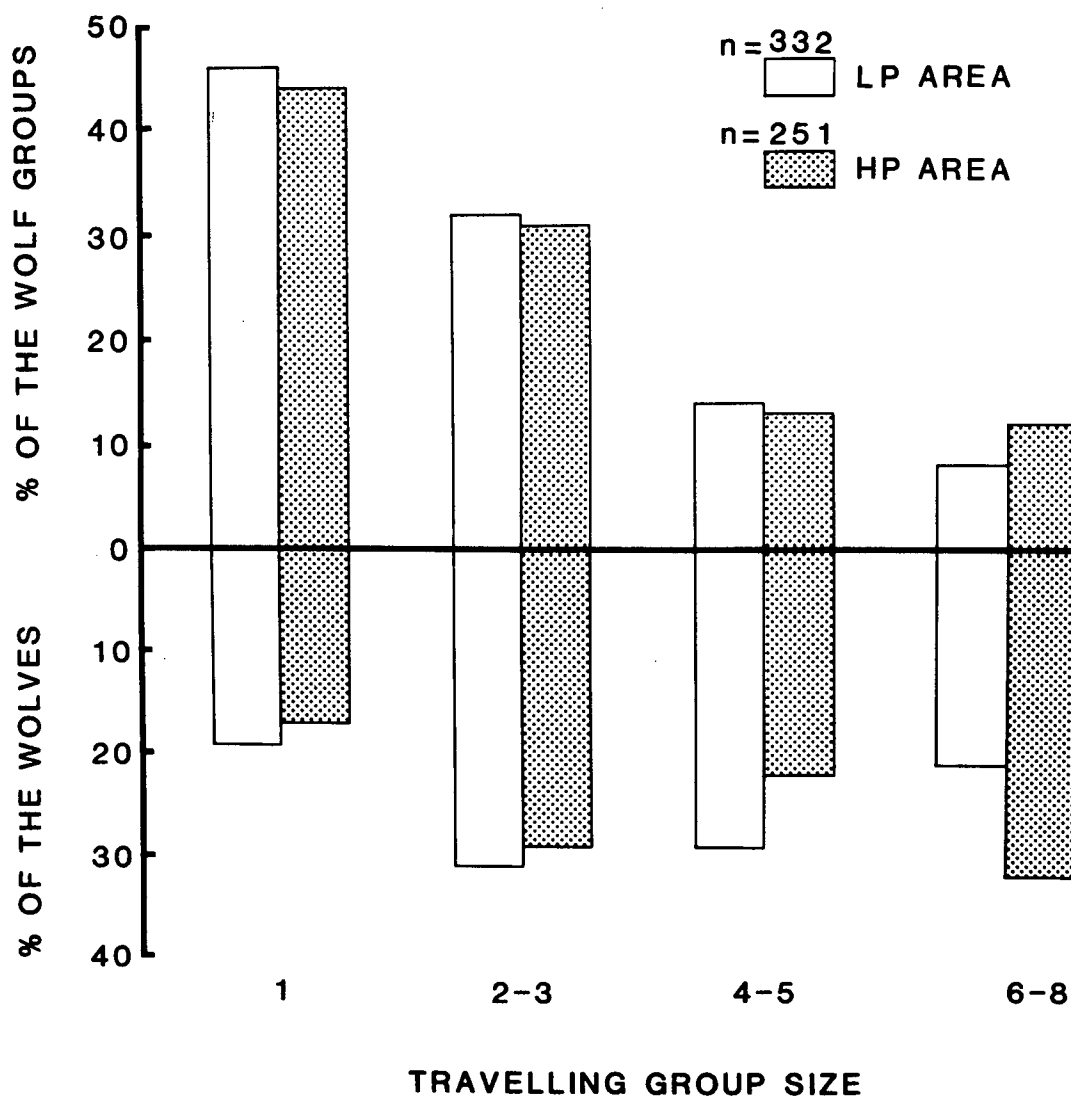


Fig. 4. Grouping of wolves when they travelled in the LP or in the HP area. Sample sizes refer to the number of groups observed in winter.

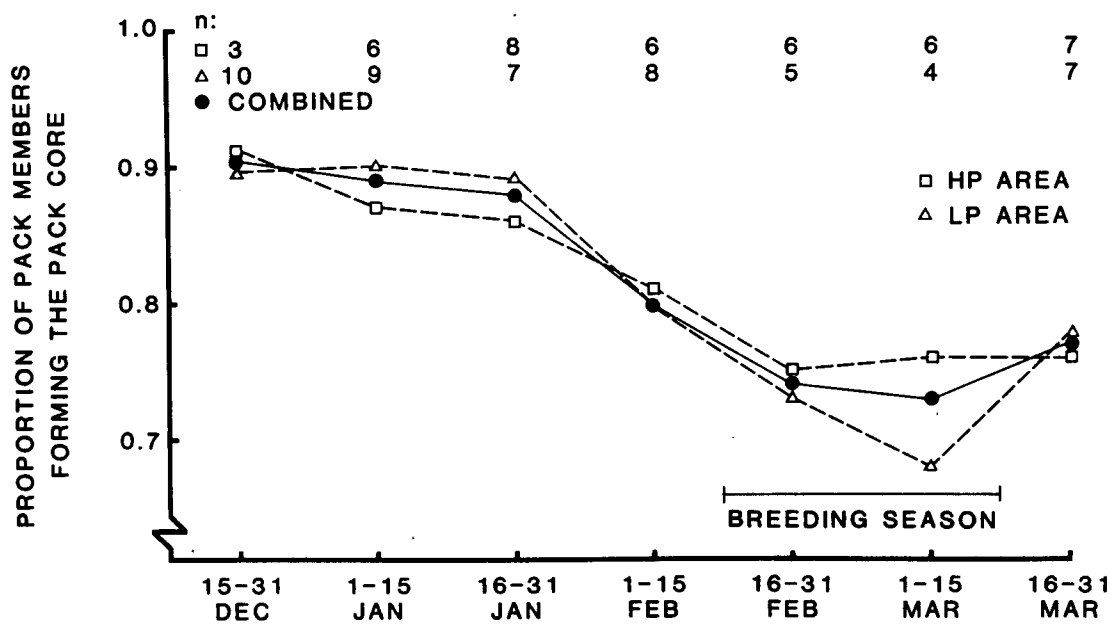


Fig. 5. December to March changes in the proportion of members forming the pack core (i.e., group cohesiveness) when packs were observed in the LP or in the HP area.

Spatial distribution

Thirty year-long territories were adequately defined in this study (i.e., only territories for which the observation-area-curve asymptoted; Table 7). They ranged from 110 to 625 km², and had a mean of 320 ± 25 (SE) km². Territory size averaged 390 ± 40 (SE) km² in HP (excluding pack H1 due to its substantial overlap between LP and HP), as compared to 255 ± 20 (SE) km² in LP. This difference in territory size may have been caused by either the difference in pack size or moose density. The territory-area per wolf (territory size \div pack size) was not correlated to moose density ($r=0.14$, $n=27$, $P>0.50$; data in Table 7) and averaged $83 \pm (SE)7$ km²·wolf. In the other hand, pack size was correlated to moose density ($r=0.49$, $n=27$, $P=0.01$). Therefore, the larger territories in the HP area was apparently related to the difference in pack size.

Each HP pack appeared to occupy the same general area throughout the study. In the LP area, 2 new pairs established territories (Fig. 6), but the fate of 4 pairs was hazardous when I terminated the study in January 1984. Probably, some of these pairs vanished due to the death of 1 or both members. The territory mosaic in the LP area was probably more dynamic (higher turnover) as a result of low pack size and marginal moose density.

Maximum extent of interstices between territories from 1981 to 1984 represented 25%, 20%, 5%, and 5% of the HP area

Table 7. Summary of data regarding wolf territories adequately defined, and the respective pack size and moose density (see methods).

Pack I.D.	Year	Territory (km ²)	Pack size	Moose (No./km ²)	No. fixes
H1	1980-81	305	2	0.29	53
H1	1981-82	340	6	0.27	222
H1	1982-83	575	5	0.28	245
H1	1983-84	475	6	0.27	117
H2	1980-81	425	7	0.37	163
H2	1981-82	500	6	0.34	340
H2	1982-83	625	7	0.34	409
H2	1983-84	350	3	0.37	112
H4	1981-82	215	4	0.37	87
H4	1982-83	210	?	0.37	68
H5	1983-84	285	?	0.37	109
H6	1982-83	430	8	0.34	166
H6	1983-84	380	7	0.34	120
H8	1982-83	440	?	0.37	37
L1	1981-82	275	3	0.24	74
L2	1980-81	300	4	0.25	45
L2	1981-82	225	4	0.24	81
L2	1982-83	295	3	0.23	96
L2	1983-84	250	2	0.21	58
L3	1982-83	285	2	0.23	68
L4	1980-81	130	2	0.25	32
L4	1981-82	145	5	0.24	103
L4	1982-83	185	6	0.23	256
L4	1983-84	165	6	0.21	98
L5	1982-83	400	6	0.23	114
L5	1983-84	330	3	0.21	54
L6	1983-84	190	2	0.21	55
L7	1982-83	245	4	0.23	45
L8	1981-82	365	3	0.22	84
L8	1982-83	300	2	0.22	60

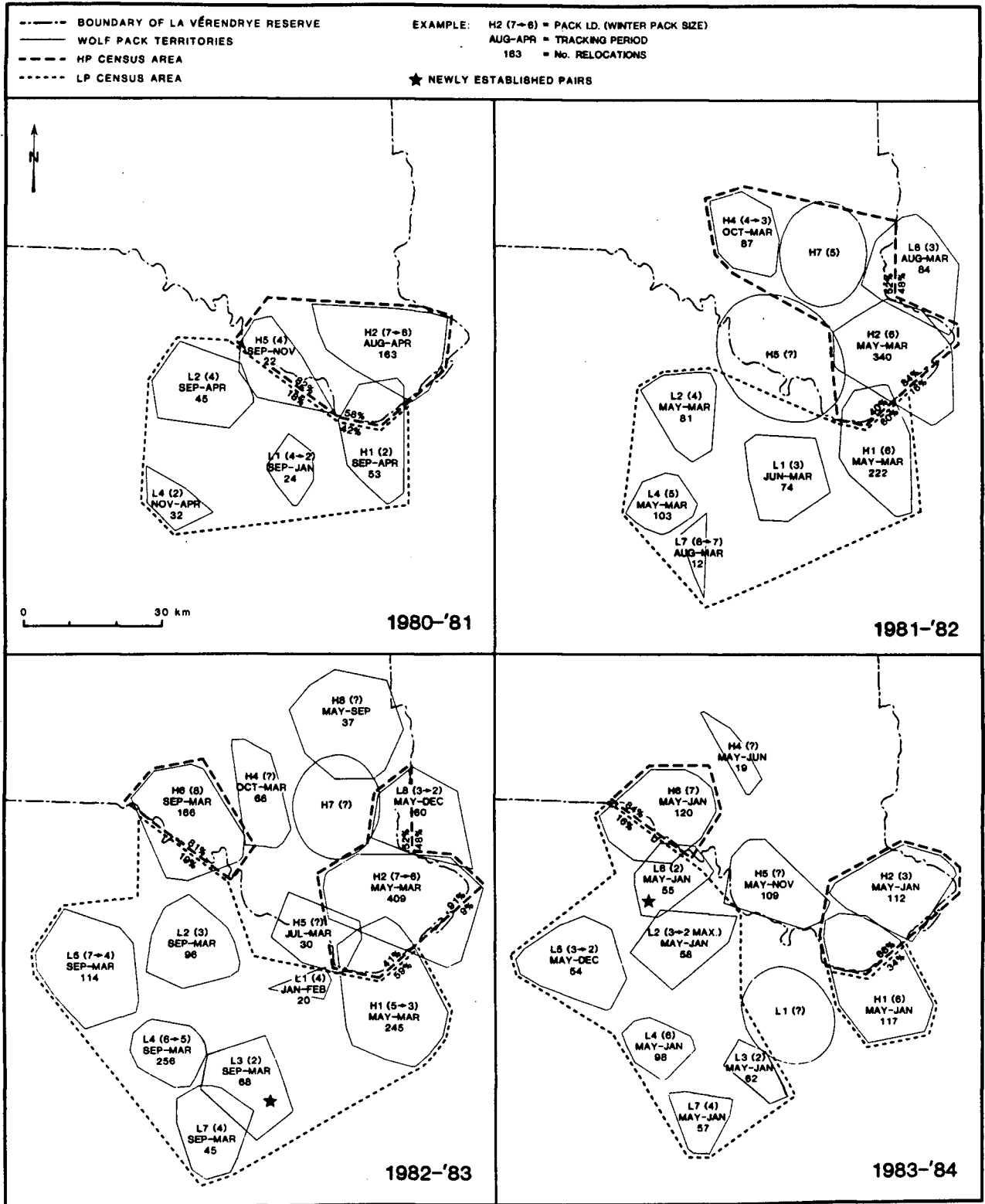


Fig. 6. Depiction of the areas used annually (May to April) by individual packs during the study period. Ellipses represent the approximate location of packs known to be present but not radio-tracked. The percentages along the border of a census area correspond to the proportion of pack locations within the census area.

(average = 15%), and 55%, 55%, 45%, and 30% of the LP area (average = 45%; Fig. 6). These percentages are somewhat overestimated because not all territories were defined adequately each year. The multi-year territory mosaic (Fig. 7) provides a better illustration of the actual territory settlement. Some territory sectors were used infrequently which means that, within a 1-year period, some of these sectors could have been missed by chance. Overall, the territory mosaic appeared to be saturated in the HP area, whereas interstices still accounted for $\approx 30\%$ of the LP area (Fig. 7).

Wolf density in the HP area was estimated at 1.2, 1.3, 1.5, and 1.5 animals $\cdot 100 \text{ km}^{-2}$ in January of 1981, '82, '83, '84, respectively (average = 1.4). Corresponding values in LP area were 0.6, 1.0, 0.8, 0.9 wolf $\cdot 100 \text{ km}^{-2}$ (average = 0.8). Inevitably, there was some subjectivity on how to delineate the census areas (see Fig. 6). The main criteria were to enclose only territories of known pack size, and to be confident that the census area did not contain resident and untracked packs. Considering the limited number of packs monitored each year, only the average density values are retained for discussion. In summer, wolf density was estimated at 2.1 animals $\cdot 100 \text{ km}^{-2}$ in area HP, and at 1.2 animals $\cdot 100 \text{ km}^{-2}$ in area LP. Summer densities were derived from the observed January-July mortality (9% in area H, 17% in area M) and an assumed recruitment of 4 pups for every packs

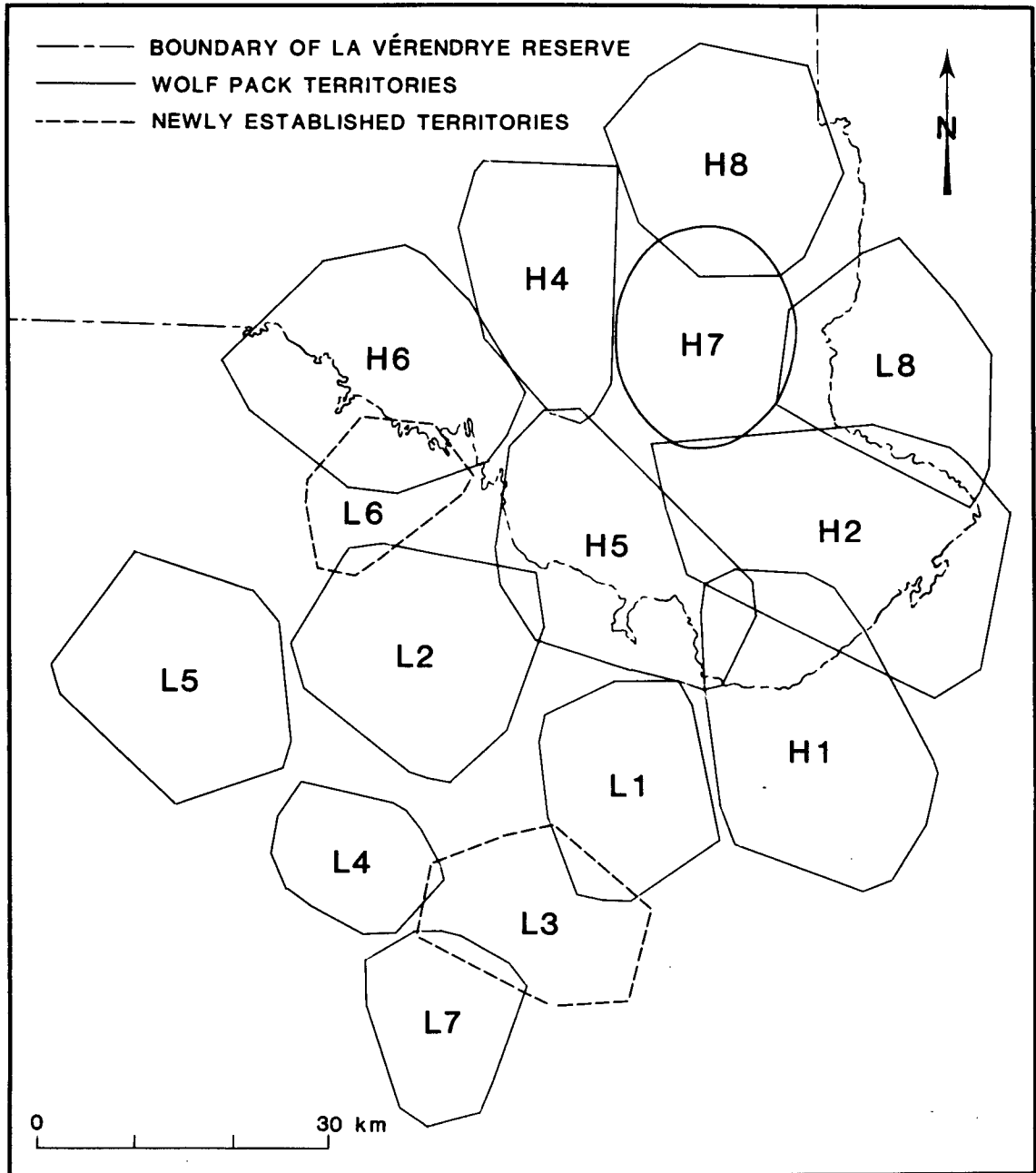


Fig. 7. Depiction of the territory settlement in the LP and the HP areas from the pooled data between 1980 and 1984. The approximate ellipsoidal territory (H7) was held by a non-radio-collared pack (limited ground accessibility) for which the presence was certified many times by aerial observations.

which reproduced successfully (93% of packs in area H, 62% in area M). Two wolves were constantly observed alone (Messier in press b) and they both travelled over the LP and HP areas. The density estimates did not include lone wolves.

Space-use patterns of pack members differed markedly with the pack's reproductive status and the season. In summer, pups were generally found either at the natal den or at a rendezvous site. The sedentariness of pups forced adults to forage radially, and this effect was quite obvious when monitoring reproductive packs (Fig. 8a, c). In some packs, pups were moved occasionally during summer. These changes produced a sudden and quite noticeable shift in movements of adult wolves (Fig. 9c). Yearlings and young non-reproductive adults were less affected by the presence of pups. They travelled extensively throughout the pack's territory, and occasionally without any apparent visits to the pups (Messier in press b). Non-reproductive packs patrolled their territory freely and used it more homogeneously (Fig. 9a, b).

In winter, presence of moose carcasses markedly influenced pack movements (Fig. 8b, c). When wolves used a moose carcass, resulting either from predation or other natural mortality, they tended to stay in its vicinity (often sleeping beside it) for up to 3 weeks (Messier and Crête 1984). The relatively low pack size in the study area permitted prolonged consumption of a moose carcass. These typical movements created a clumped distribution of winter

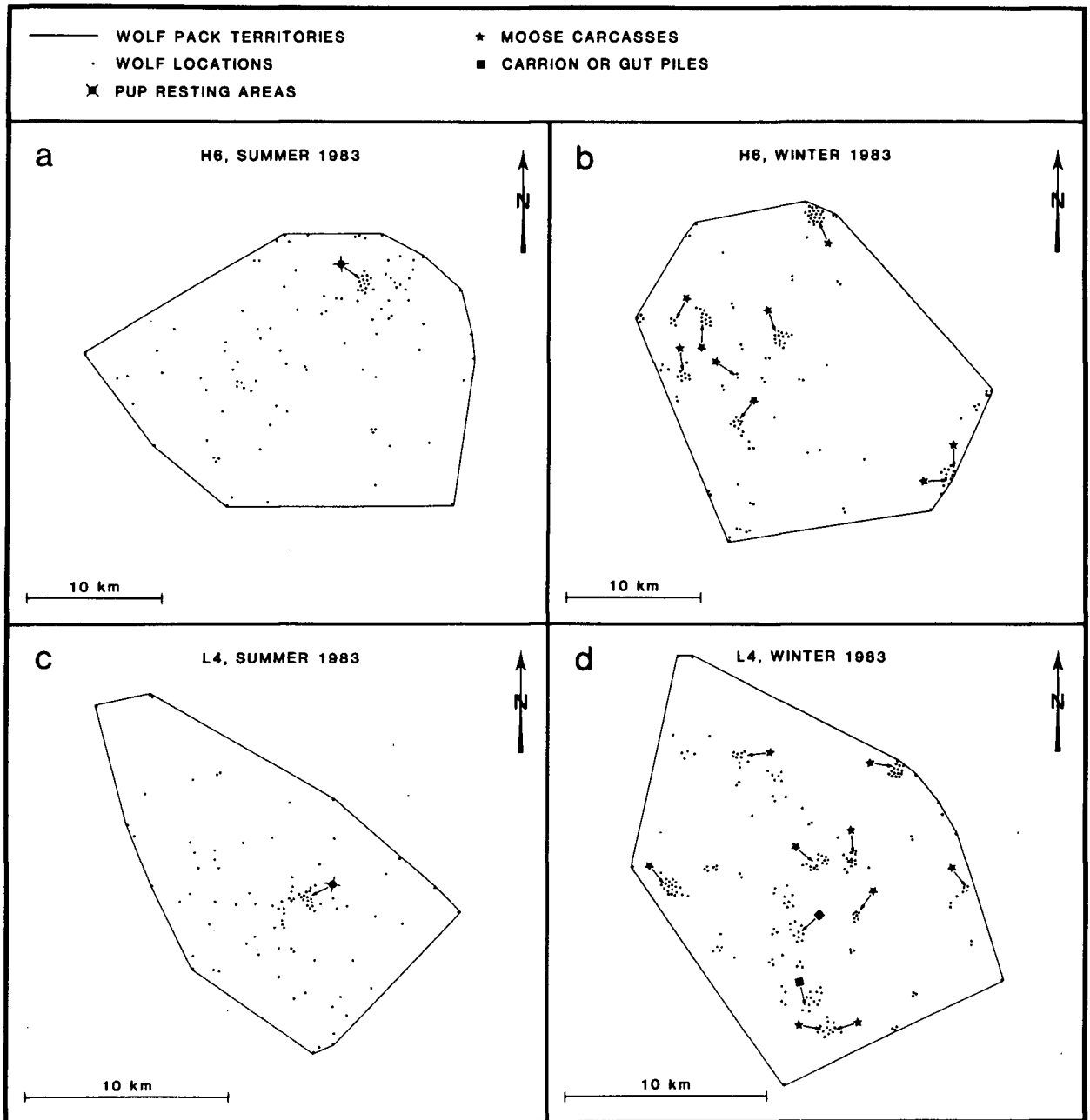


Fig. 8. Space-use patterns of packs H6 and L4 during the summer period (May to November), as compared to the winter period (December to April).

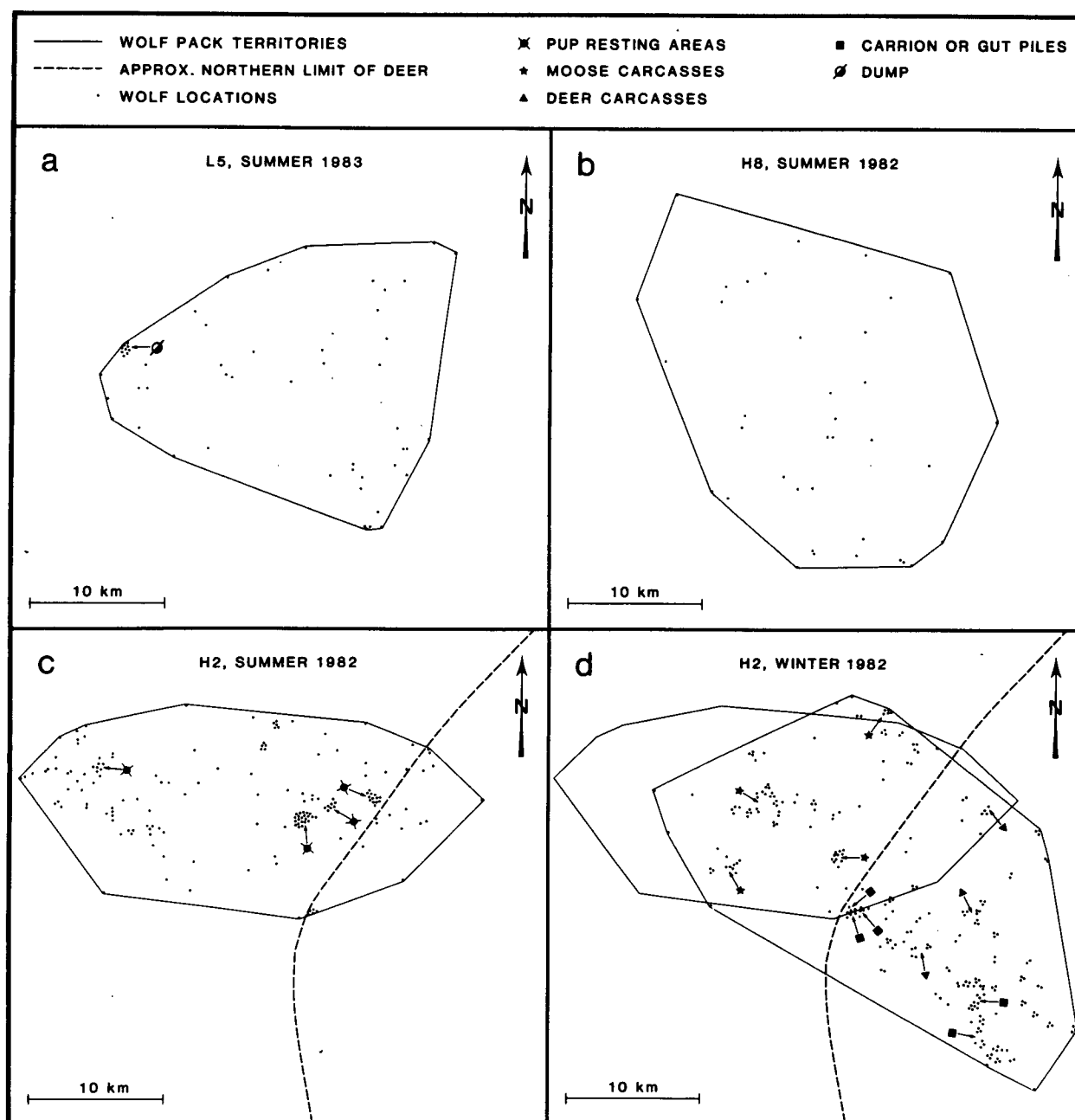


Fig. 9. Space-use patterns of 2 non-reproductive packs (L5 and H8) during the summer period, and the representation of the seasonal territory shift demonstrated by the pack H2.

locations.

Two packs, H1 and H2, repeated a traditional pattern of movements which can be described as a seasonal territory extension (Fig. 9c, d). Typically, pack H2 moved southeast at the onset of winter and exploited an area where at least 3 small concentrations of deer were situated. The trip normally lasted 1 or 2 weeks, and was repeated a few times during the winter. A similar southeastern territory extension was observed for pack H1, but in this case, farm and butchery offal were used in addition to 1 deer wintering area. In both packs, deer kills were observed periodically. Deer exploitation likely represented the principal motivation for these territory extensions. Packs H1 and H2 always reared their pups within the portion of their range inhabited by very few, if any, deer.

The analysis of daily distances (Fig. 10) revealed that, during the summer, reproductive packs travelled more extensively in the LP area than in the HP area (Kolmogorov-Smirnov (K-S) one-tailed test, $D[421,202] = 0.10$, $\underline{P}=0.05$). Likewise, non-reproductive packs moved greater distances in the LP area (K-S test, $D[26,89] = 0.28$, $\underline{P}=0.04$). Summer appears to be the critical season to acquire an adequate quantity of food (Peterson et al. 1984b). Non-reproductive packs wandered more freely than reproductive packs (K-S test, $D[623,115] = 0.18$, $\underline{P}<0.01$; combined data of LP and HP).

In winter, the analysis of daily distances revealed no

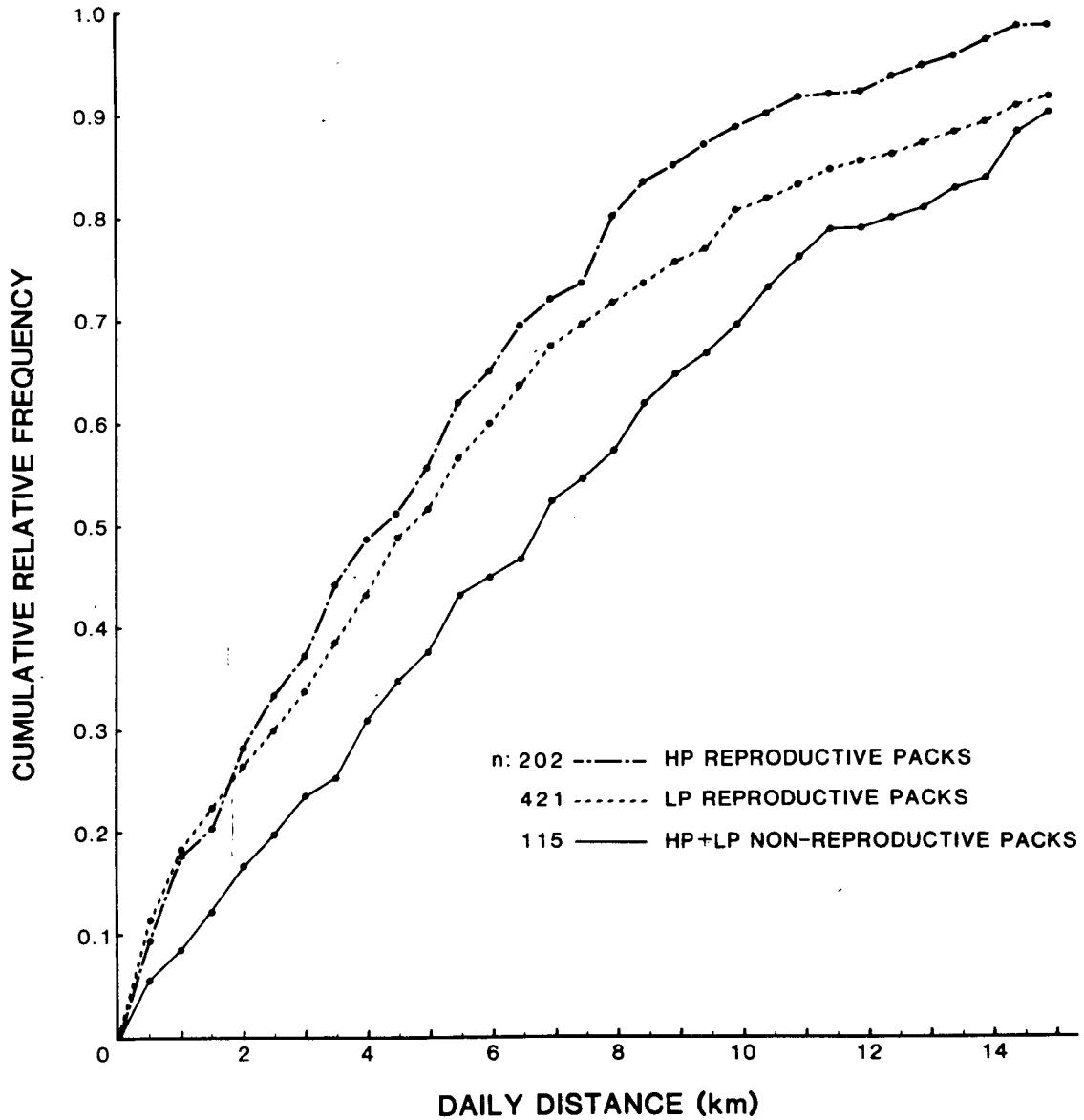


Fig. 10. Cumulative relative frequencies for the in-territory daily distances of reproductive and non-reproductive packs during the summer period. In this analysis, the area of affiliation of each pack was the one in which pups had been reared.

difference between LP and HP packs (K-S test, $D[451,296] = 0.04$, $P > 0.20$; Fig. 11). Dissociated, single pack members travelled similar distances inside or outside the pack's territory (K-S test, $D[120,130] = 0.04$, $P > 0.20$; combined data of LP and HP). Packs and single animals (i.e., lone wolves and solitary pack members) did not differ in their travelling (K-S test, $D[747,566] = 0.04$, $P > 0.20$; combined data of LP and HP).

DISCUSSION

Recently, changes in wolf density have been linked to nutritional status (Packard and Mech 1980; Keith 1983). Present results, where wolf ecology has been investigated at 2 levels of prey abundance, corroborate this view. Low moose density in the LP area resulted in a wolf density approximately 40% lower than in the HP area. This density difference resulted from natural population processes, i.e., the LP wolves suffered from a higher mortality rate due to deaths from malnutrition and intraspecific combat. Further, and probably of greater importance, LP packs had a much lower success in reproduction. Human-caused mortality was similar in both study areas and cannot explain the disparity in wolf densities.

Extra-territorial excursions were commonly witnessed in this study, particularly in the LP area (Messier in press b,

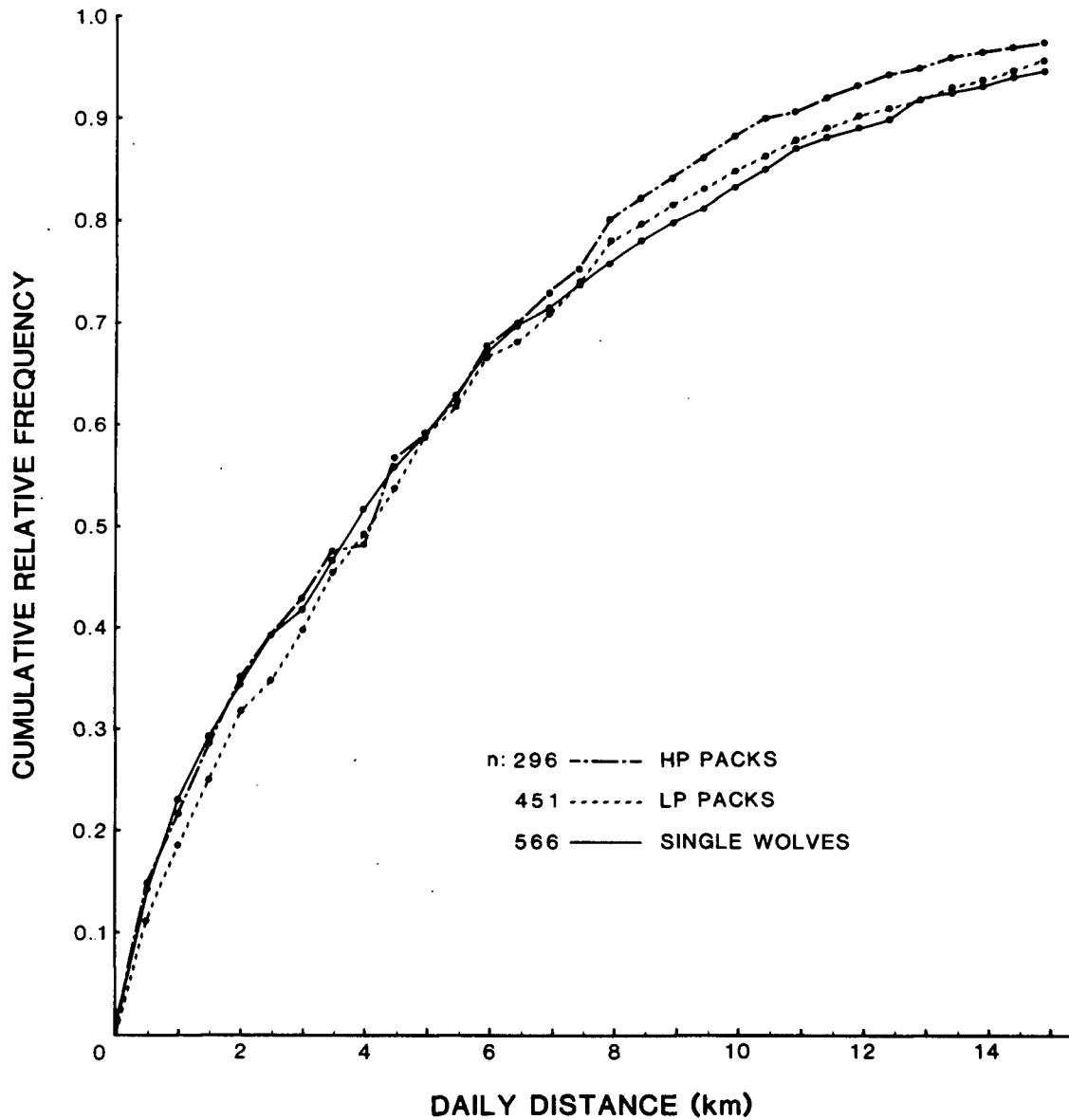


Fig. 11. Cumulative relative frequencies for the in-territory daily distances of packs during the winter period. Also presented is the daily distance frequency of single wolves (lone animals or pack members dissociated from the pack more than 5 days) during the same period.

or Appendix). Food stress upon packs entailed hazardous extra-territorial movements and may have caused some human-related deaths (i.e., concealed natural mortality). Possibly, human-caused mortality altered group dynamics of some packs, but not sufficiently to invalidate the preceding description of pack social organisation. Natural mortality (including the non-measured pup mortality) and failure in reproduction had a far-reaching effect on pack dynamics.

Pack size, year-long territory size, and interstices between territories potentially influence wolf density. From a broad examination of wolf populations across North America, pack size appears to be intimately related to moose density (Table 8). The mechanism underlying the regulation of pack size is complex and imperfectly understood (Zimen 1976, 1982; Packard and Mech 1980). An increase in prey abundance seems to produce a direct increment in the in-group recruitment and survival rates (Keith 1983). Moreover, pack size may be related to the dispersal strategy of pack members. As prey abundance increases, the territory mosaic becomes progressively saturated (lower territory vacancy; Fig. 7) which could provoke delayed dispersal (Packard and Mech 1980; also Messier and Barrette 1982). Thus, given the rarity of vacant areas, a maturing wolf might benefit more by trying to obtain reproductive status within its pack than by dispersing; i.e., a non-disperser could take advantage of the ability of the entire pack to defend a space in which it may eventually

Table 8. Early winter pack size, wolf and moose densities reported for different boreal ecosystems in North America. Only studies for which moose constituted the major prey species of wolves are included.

Area	Wolf/100 km ²	Pack size	Moose/km ²	Source
S.W. Québec (LP area)	0.8	3.7	0.2	This study
N.E. Alberta (Athabasca River)	0.8	4.4 #	0.3	Fuller and Keith 1980
N.W. Ontario (Pukaskwa)	1.5	4.0 #	0.4	Bergerud et al. 1983 from Table 1
S.W. Québec (HP area)	1.4	5.7	0.4	This study
S. Alaska (Kenai Peninsula)	1.1-2.0	11.2	0.8	Peterson et al. 1984
Isle Royale, MI (1971-'84)	2.0-9.5	8.6	1.0-2.2	Peterson et al. unpubl.
Isle Royale, MI (1959-'70)	3.1-5.1	11.1	1.5-2.6	Peterson 1977

Minimum estimate based on cursory observations of non-radio-collared packs.

breed. This advantage could be crucial in a highly saturated condition.

Territory size appears to be governed largely by pack size and prey abundance. Peterson et al. (1984b) found a significant exponential relationship between pack size (≥ 3) and territory size. I showed that territories were larger in the HP area because pack size was greater. Bowen (1982) found that territory size in coyotes (Canis latrans) was positively related to family size. Thus, modelling the adjustment of wolf territory size to changing moose density, without considering the concurrent influence of pack size (e.g., Walters et al. 1981), should not be expected to reflect reality.

Walters et al. (1981) suggested that territory size should be inversely related to prey density so as to prevent depletion of prey within each territory. I would recommend use of the territory-area per wolf in such a relation, because of the confounding effect of pack size. Data here indicate that between 0.2 and 0.4 moose \cdot km $^{-2}$, territory-area per wolf is independent of moose abundance. When wolves are facing low moose densities as here, without the presence of alternative ungulate species, they seem to maintain a constant area per individual but they intensify the exploitation of their territory if moose density decreases. Wolves can achieve this goal: 1) by persevering in each moose attack (many exceeding 1 day and up to 5 days), 2) by using each carcass thoroughly, 3)

by feeding on alternative and possibly second choice food resources (Messier and Crête in press for statements 1, 2, and 3), and 4) by patrolling their territory more intensely. In regard to the last statement, daily distances of LP packs were on average either greater (summer) or equal (winter) to daily distances of HP packs. However, territory size was approximately 35% smaller in the LP area which supports the fact that wolves were searching each unit area at greater intensity. Across a large range of moose densities, territory-area per wolf appears to be inversely related to moose density. At $0.2-0.4 \text{ moose} \cdot \text{km}^{-2}$, each wolf occupied approximately 85 km^2 (this study). At $0.8 \text{ moose} \cdot \text{km}^{-2}$ (Kenai Peninsula, Alaska), Peterson et al. (1984) found an average figure of $55 \text{ km}^2 \cdot \text{wolf}$. At $1.0-2.6 \text{ moose} \cdot \text{km}^{-2}$ (Isle Royale, Michigan), Peterson et al. (1977 and unpubl.) reported a range of $10-90 \text{ km}^2 \cdot \text{wolf}$. Thus, the inverse relationship proposed by Walters et al. (1981) is tenable when the effect of pack size is considered.

Present results indicate that a density of $0.2 \text{ moose} \cdot \text{km}^{-2}$ may represent the density threshold below which a pack cannot subsist and/or reproduce successfully. In the LP area ($\approx 0.23 \text{ moose} \cdot \text{km}^{-2}$), wolves older than 1 year of age tend to: 1) perish from malnutrition, 2) reproduce poorly, 3) dissociate from their pack commonly (Messier in press b), and 4) engage in extra-territorial excursions frequently (Messier in press b). All of which lead to an unstable social organization. In

winter, LP packs used an average of 3.2 moose per 100 days which is far below the average found in the HP area (6.2) and that of 15 to 20 moose per 100 days observed in other studies conducted at higher moose densities (Peterson 1977; Fuller and Keith 1980; Peterson et al. 1984b; moose density in Table 8). As a general consequence of the marginal pack size in the LP area (3.7), the territory mosaic appeared to be relatively less stable than in the HP area, presumably with the occasional formation and disappearance of certain packs.

At a density of ≈ 0.23 moose \cdot km $^{-2}$ (LP area), interstices between territories were present ($\approx 30\%$ of the total area; Fig. 7), and did not prevent the enlargement of territories. The habitat within interstices was not noticeably different from that of surrounding areas. At a density of 0.37 moose \cdot km $^{-2}$ (HP area), the territory mosaic appeared to be saturated; interstices being filled from larger rather than additional territories. The greater abundance of the HP moose population facilitated the use of more extensive territories by larger (less food-constrained) packs.

HP wolf density accounted for 1.4 animals \cdot 100 km $^{-2}$, a low density compared to the possible density of 1 to 10 wolves \cdot 100 km $^{-2}$ reported in many other wolf-ungulate studies (Table 8; review in Keith 1983). The HP moose population was stable and very close to the estimated natural equilibrium density of 0.4 animal \cdot km $^{-2}$ (Messier and Crête 1984; from analysis of long-term data); again, a relatively low density compared to the 2

to 4 moose·km⁻² observed where predation does not occur (Bergerud and Manuel 1969; Blood 1973). Therefore, I concur with Pimlott (1967) who was one of the first to propose that wolf-ungulate systems, if naturally regulated, may stabilize at low prey and low predator densities (also Keith 1974; Bergerud 1980; Bergerud et al. 1983; Gasaway et al. 1983).

Chapter III

MOOSE-WOLF DYNAMICS

INTRODUCTION

Present theory on the natural regulation of North American moose populations is ambiguous. Peek and Eastman (1983) hypothesized that moose populations fluctuate with forage availability. They rejected the notion that predation may represent a basic regulating factor of moose numbers, although they recognized that predation diminishes moose productivity and survival. Walters et al. (1981), and Gasaway et al. (1983) suggested that predation may become an increasingly important (i.e., compensatory) mortality agent as a moose population decreases. Both groups of authors argued that this inversely density-dependent effect may prevent a moose population from increasing if, previously, an extrinsic mortality factor (e.g., extra hunting) caused this population to decline; otherwise, they predicted that food resources would constitute the ultimate regulatory agent. Peterson and Page (1983) reported an example where a wolf population apparently induced instability in a moose population. They maintained that such a system would be characterized by long term predator-prey cycles. Crête et al. (1981), Bergerud et

al. (1983), and Messier and Crête (1984) proposed that predation by wolves may be density-dependent and regulate moose populations well below the density which could be sustained by available food resources.

To resolve these competing hypotheses, the problem is best approached by means of manipulative or natural experiments (e.g., Gasaway et al. 1983; Crête and Messier 1984; Messier and Crête 1984; see also Macnab 1983). In particular, the concept of moose population dynamics may lose much of its present complexity and mystique when the functional and numerical responses of wolves to changing moose density will be better understood.

This study attempted to test whether or not moose were naturally regulated by predators. In southwestern Québec, non-harvested moose populations stabilize at a density of ≈ 0.40 animal \cdot km $^{-2}$ (Messier and Crête 1984). Body condition of moose was investigated near this equilibrium density (0.37 animal \cdot km $^{-2}$) and at 2 lower densities (0.22 and 0.17 animal \cdot km $^{-2}$) created by more intensive harvesting. Based on the body condition data and related evidence, Messier and Crête (1984) concluded that availability of food resources was not sufficient to explain natural regulation of moose populations when density approaches 0.40 animal \cdot km $^{-2}$. Here, using the same 3 populations, I analyse predation by wolves. I show that this mortality factor is density-dependent and thus has a regulatory capability. Information presented

includes: wolf feeding ecology, prey selectivity, killing rates, handling times, moose:wolf ratios, and predation rates on moose.

STUDY AREAS AND METHODS

The 3 study areas are located within the most productive moose habitat in Québec (Brassard et al. 1974; Fig. 1; 47°N, 77°W). Area H, the game reserve La Vérendrye (13,615 km²), had a stable density of 0.37 animal·km⁻². Moose density in area M (2390 km²) declined from ≈ 0.25 to ≈ 0.21 animal·km⁻² during the study. Area L (1185 km²) had a relatively low and stable moose density of 0.17 animal·km⁻² (Messier and Crête 1984). Moose densities should be reasonably accurate because they were corrected for visibility bias (Crête et al. submitted; with aid of radio-collared moose). However, the year-specific imprecision is still unknown. Moose densities were derived by regressing yearly estimates from 1976 to 1983 to reduce the annual variability.

Wolf ecology was studied from June 1980 to February 1984 in a 6400-km² sector overlapping the 3 study areas (Fig. 1 and 3). The scarcity of wolves in area L did not permit us to obtain complete information there. Food habits of wolves were determined from scat analysis in summer (May to November) and direct observations in winter (December to April). Scat analysis was not used in winter because scats were usually

found during autopsies of kills. In summer, scat sampling was independent of wolf activities. Fresh scats (<1 week old) were collected along forest roads while trapping and during weekly scat surveys.

Prey remains in scats were identified by macroscopic examination, comparison with a reference collection of the major food items, and hair-scale impressions (Adorjan and Kolenosky 1969). The proportion of each food item within a scat was visually estimated to the nearest 0.10, and a value of 0.05 was assigned to items occurring in trace amounts. No estimation was necessary in 71% of the samples, where only 1 food item was present. The estimation took place after scats were washed in a 1-mm mesh screen. Non-food elements such as stones, conifer needles, dry twigs, and grass (4% of scat content) were not included in the analysis. The sum of all proportions for a given item refers to the frequency of occurrence expressed in whole scat units. Such data presentation is required to evaluate the biomass originally ingested using the technique described by Floyd et al. (1978).

Winter feeding ecology was studied from direct observations during telemetry flights. Each time a wolf was located, the observer circled the area, attempted to count the animals present (successful in 70% of observations), and recorded the presence of food sources. The majority ($\approx 90\%$) of feeding sites (except obvious instances of beaver kills) were ground-investigated within a few days. The investigator then

determined the nature of the food source, assessed prey characteristics, the cause of death, and collected morphological samples such as incisors (age) and bone marrow (general physical condition; following Neiland 1970). A feeding-day was defined as 1 wolf daily-location at a food source or within 1 km if it was apparent that the animal had frequented the site (from track interpretation). For example, I recorded 35 feeding-days when a pack of 5 wolves was located at a moose carcass during 7 days. Evaluation of the number of wolves involved was quite reliable because wolves commonly used a food source for many consecutive days and were easily observed.

Moose killing rate was calculated from the cumulative radio-tracking periods and the interim kills. In this analysis, I considered only those winter tracking sessions (23 ± 7 SD days) in which none of the pack relocations were separated by more than 52 h (≈ 2 days). I attempted to fly every day but weather conditions occasionally interrupted wolf tracking. Pack excursions outside the study areas were excluded.

Dead moose were classified as: 1) wolf kills if there was positive evidence of attack (large bloody area, blood-soaked hair on the inside thighs or on the lower rear legs, and broken vegetation around the site), or 2) as natural death in absence of struggling (typically with signs such as carcass on sternum with folded legs, rumen frozen whole in the body, low

bone marrow fat, and aged carcass on bare ground emitting strong smell).

Wolf densities were assessed in both areas M and H from the number of wolves per pack, the size of pack territories, and the area between territories (Messier in press a). To provide additional information among areas H, M, and L, I present 3 population indices: 1) weekly scat counts along a permanent circuit (48 km) of randomly selected road segments, 2) frequencies of wolf observations by moose hunters, and 3) percentages of hunting-days for which hunters heard wolves howling. The methodologies associated with these indices will be presented in Chapter IV.

RESULTS

Feeding ecology

Summer food habits were determined by analysis of 628 scats collected in areas H and M (Table 9). Moose occurrence in scats ranged from 24 to 56%, and was consistently higher in area H (summer average = 52% in area H and 26% in area M). In area M, wolves partly compensated for the lower use of moose by a greater exploitation of secondary prey species such as beaver, woodchuck (Marmota monax), snowshoe hare (Lepus americanus), and raccoon (Procyon lotor). For example, beaver density was estimated at 3.5 colonies·10 km⁻² in area H, and at 1.0 colony·10 km⁻² in area M (Crête and Samson unpubl.),

Table 9. Comparative prey use by wolves during summer in areas M and H. Number of scats analysed are presented in parentheses (years combined).

Species or food items	May & Jun		Jul & Aug		Sep to Nov		Weighted \bar{X}	
	M (33)	H (109)	M (152)	H (228)	M (35)	H (71)	M (220)	H (408)
Percent prey occurrence in scats								
Adult moose	7	17	10	17	10	21	9	19
Calf moose ^a	24	36	15	28	14	35	17	33
Beaver	31	28	41	26	62	33	47	30
Woodchuck	31	14	18	16	2	T ^e	15	9
Snowshoe hare	3	1	4	6	T	0	2	2
Fruits	0	T	8	5	6	8	5	5
Other items ^b	4	3	4	2	6	3	5	3
Percent biomass originally ingested ^c								
Adult moose	46	66	50	61	43	51	46	58
Calf moose	20	19	17	23	26	37	21	28
Beaver	18	9	18	8	23	7	21	8
Woodchuck	12	3	5	3	T	T	5	2
Snowshoe hare	1	T	1	1	T	0	1	T
Fruits	0	T	4	3	3	4	2	3
Other items	3	2	5	1	4	1	4	1
Relative number of prey ingested ^d								
Adult moose	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Calf moose	5.1	3.4	2.0	2.2	1.6	2.0	2.7	2.5
Beaver	9.2	3.3	8.5	3.1	12.5	3.1	10.4	3.2
Woodchuck	29.7	4.9	12.0	5.0	1.1	0.5	12.4	3.0
Snowshoe hare	6.2	2.9	6.3	3.5	5.0	0	5.7	1.8

^a By late August calves acquired a darker coat that resembled adult pelage. Thus, total moose in Sep to Nov was apportioned on the basis of the adult-calf ratio in Jul & Aug.

^b All scats totaled: 1.5% small rodent, 1.0% white-tailed deer, 0.5% raccoon, and 1.0% diverse items.

^c Estimation technique for mammals as described by Floyd et al. 1978. Assumed whole prey weights (kg) were: adult moose (350), calf moose (30, 60, and 130, respectively), beaver (12.5), woodchuck (2.5), snowshoe hare (1.2), other mammals as Crête et al. 1981a. Fruit percentages were halved after Andelt and Andelt 1984.

^d Consumable prey weight was estimated at 90% of whole weight for all prey except moose (75%) as in Peterson et al. 1984.

^e Traces (<1%).

yet, beaver occurrence in scats was 30% in area H and 47% in area M. Relative density estimates of other secondary prey species were not available. Moose represented respectively 84% and 65% of the biomass originally ingested in areas H and M; corresponding values for alternative prey species were 10% and 27%. In terms of the relative number of prey ingested, ratios of calf:adult moose were comparable in both areas, but the ratios of secondary prey:adult moose differed markedly between areas (8.1:1 and 28.4:1 in areas H and M, respectively).

In winter, moose predominated as prey species, but more so in the area H than in the area M (85% of feeding-days in area H as compared to 60% in area M; Table 10). Human-related foods (baits, offal, and gut piles) were used more frequently in area M (Table 10). I suspect that wolves in area M deliberately searched for these types of food even though such actions entailed hazardous approaches to human habitations (farms, logging and trapper camps). Limited information did not permit a description of the wolf food habits in area L. However, the few wolves inhabiting this area were possibly more dependent on secondary food items than in the 2 other areas.

Table 10. Comparative prey use by wolves during winter in areas M and H. Number of feeding-days (see methods) are presented in parentheses (years combined).

Species or food items	Percent feeding-days	
	Area M (728)	Area H (693)
Moose (calves & adults)	60	85
White-tailed deer	4	6
Beaver	3	2
Trapper baits ^a	21	0
Offal ^b	4	11
Gut piles	1	3
	25	14

^a Included carcasses of furbearer animals; trapping was permitted in both areas.

^b Included dump, farm and butchery offal.

Age, sex, and condition of dead moose^a

Carcasses of 62 moose were consumed by wolves during winter periods. Ground-examination revealed that 38 were victims of wolves, 16 died from chronic mortality (i.e., senescence, malnutrition, disease, natural injuries), 3 succumbed from wounds inflicted during hunting, 1 was killed by a car, and 1 was poached but not retrieved (Table 11). The cause of mortality was uncertain in 3 instances. Chronic mortality included 7 prime-aged males (i.e., 1 to 9 years of age; included 2 pairs with locked antlers) and 9 senile (>12 years) females. Calves dead from malnutrition were not observed in this study. Malnutrition mortality occurred from November to February (Fig. 12) with no period of chronic starvation in late winter.

Calves, prime-aged adults, and older animals, comprised 16%, 50%, and 34% of wolf-killed moose (Table 11). The age structure of kills did not differ between areas ($\chi^2[2] = 0.78$, $P > 0.20$), but deviated significantly from the assumed age structure of living animals (respectively, 21, 70, and 9% of combined H and M data; Table 12; $\chi^2[2] = 22.7$, $P < 0.01$). Wolves selected old individuals, but still, the majority (66%) of the kills were either calves or prime-aged, reproductive moose.

Bone marrow fat reserves were depleted (<20% of marrow content) in 27% of wolf-killed moose ($n=33$; Fig. 12). These cases included 2 calves, 3 prime males, and 6 senile females.

Table 11. Age, sex, and mortality distribution of 62 moose consumed by wolves in areas M and H.

Observations were recorded from 15 December to 30 March of each winter of the study.

	Area M				Area H			
	Calf	1-9 yr.	10 ⁺ yr.	? (>1 yr.)	Calf	1-9 yr.	10 ⁺ yr.	? (>1 yr.)
		♀ ♂ ?	♀ ♂ ?			♀ ♂ ?	♀ ♂ ?	
Predation	1	4, 2, 0	3, 0, 0	2	5	7, 4, 0	7, 1, 0	2
Natural mortality ^a	0	0, 2, 0	5, 0, 0	0	0	0, 5, 0	4, 0, 0	0
Other causes ^b	0	0, 2, 0	0, 0, 0	2	0	0, 0, 1	0, 0, 0	0
Uncertain	1	0, 0, 0	1, 0, 0	0	0	0, 0, 0	0, 1, 0	0

^a A minimum of 4 prime males perished from combat injuries in area H.

^b Included 4 deaths related to hunting, and 1 road-kill in area H.

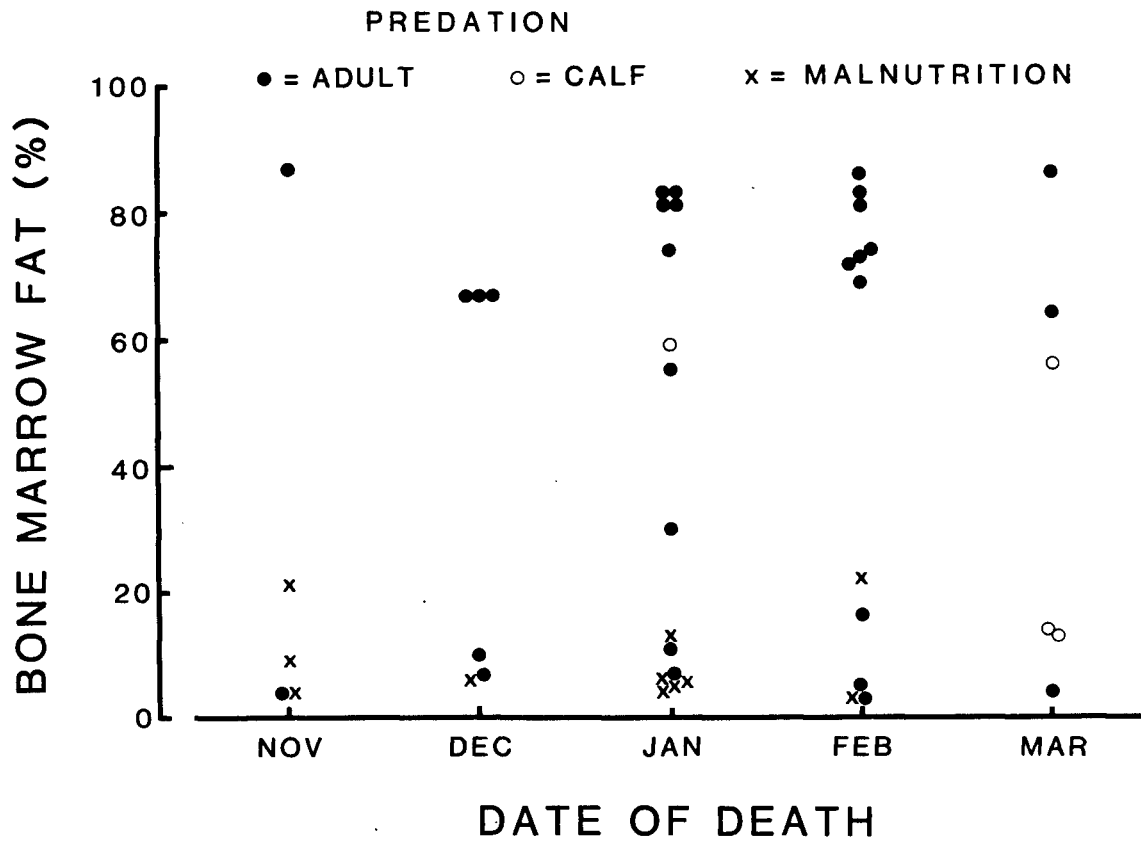


Fig. 12. Bone marrow fat content by month for moose which died of wolf predation or malnutrition.

Table 12. Sex and age structures of moose inhabiting areas H, M, and L, as obtained from January aerial surveys and autumn hunter-killed animals. Pooled data were from 1981 to 1984 for aerial surveys, and from 1978 to 1983 for hunting samples.

	From aerial surveys			From hunter-killed animals	
	No. cows per 100 adults	No. calves per 100 cows	% calves (N=100%)	% 1-9 years ^a (N)	% 10 ⁺ years ^a (N)
Area H	63	37	19 (334)	71 (592)	10 (81)
Area M	70	41	22 (224)	69 (163)	9 (22)
Area L	63	65	29 (196)	65 (132)	6 (13)

^a Calculated as the % of all hunter-killed adults X (100 - % calves observed in surveys) = the assumed % in living populations.

Animals that died from old age or malnourishment consistently had a bone marrow fat level of $\leq 20\%$ (Fig. 12). Three prime, naturally dead males exhibited fat depletion (2 in January and 1 in February). This occasional phenomenon may reflect a cost associated with a high reproductive effort the previous autumn (see Clutton-Brock et al. 1982).

Killing rates, food intake rates, and handling time

Killing rates were 5.3, 1.8, and 1.1 moose per 100 pack-days in areas H, M, and L, respectively (Table 13). These rates correspond respectively to 1.1, 0.5, and 0.4 moose per 100 wolf-days. I am confident that most, if not all, moose killed during tracking sessions were located because a pack location was recorded every 28 hours on average, and by the fact that wolves remained at their kills from 8 to 23 days for adult moose and from 2 to 4 days for calves. Large packs (5-8 individuals) in areas H and M succeeded more frequently in killing moose than small packs (2-4 individuals; Table 13). Wolves in areas M and L partly compensated for their lower killing rate by scavenging moose carcasses. The ratio of killed:scavenged moose was 18:3, 12:9, and 1:1 in areas H, M, and L, respectively. Overall, approximately 1.3, 0.8, and 0.7 moose were consumed per 100 wolf-days in the 3 areas, respectively (Table 13). These moose intakes represent 2.8, 1.7, and 1.6 kg/wolf/day (assuming whole weight = 150 kg for a calf and 350 for an adult moose; consumable fraction = 0.75 of

Table 13. Summary of data used to estimate moose killing rate by wolves, and the total moose consumption rate (December to April) in areas H, M, and L. The analysis was based on data collected during intensive tracking sessions (1 pack location every 28 hours on average, from 14 packs). Tracking-effort is expressed in wolf-days (w.-d) and pack-days (p.-d).

	Tracking-effort		No. moose consumed		Moose killing rate		Total moose consumed	
	N w.-d	N p.-d	Predation	Others	N /100 w.-d	N /100 p.-d	N /100 w.-d	N / 100 p.-d
Area H								
Packs 2-4 ^a	577	193	6	1	1.04	3.11	1.21	3.63
Packs 5-8	1033	146	12	2	1.16	8.22	1.36	9.59
All	1610	339	18	3	1.12	5.31	1.30	6.19
Area M								
Packs 2-4	1283	413	5	5	0.39	1.21	0.78	2.42
Packs 5-8	1293	242	7	4	0.54	2.89	0.85	4.55
All	2576	655	12	9	0.47	1.83	0.82	3.21
Area L								
Packs 2-4	270	90	1	1	0.37	1.11	0.74	2.22

^a Pack size

whole weight; 20% of the sample consisting of calves, Table 11). If it is accepted that moose comprised 85%, 60%, and 60% of the prey biomass ingested (as indicated in Table 2 for areas H and M; 60% for area L is a conservative estimate), total intake rate is best evaluated at 3.3, 2.8, and 2.6 kg of food/wolf/day (or 0.11, 0.09, 0.08 kg/kg wolf/day). Total intake rates are likely underestimated due to the possibility of missing small prey items.

The time spent at moose kills (handling time) decreased significantly with pack size ($P < 0.01$, Fig. 13). The number of feeding-days per carcass was not related to pack size ($r = 0.32$, $P > 0.10$) and averaged $48.7 \pm (SE)3.5$ wolf-days for adult moose ($n=25$), and $12.5 \pm (SE)2.4$ for calves ($n=4$). These results suggest that a kill provides a fixed number of wolf-meals, so smaller the pack, longer the time spent at a kill. Handling time here did not include the time required to surround and kill a moose (as in Walters et al. 1981). Including this time would have obliged us to consider the respective time associated with failed attacks (up to 90% of the total attempts in moose; Mech 1966; Haber 1977; Peterson et al. 1984b) but such information was not available.

Haber (1977) reported that the time spent to pursue and kill a moose is generally less than 2 hours. Of the 38 fresh kills observed, 29 had been made in less than 1 day (the minimum time interval), 5 between 1 and 2 days, 3 between 2 and 3 days, and 1 record of 5 days. Seven of the 9 prolonged

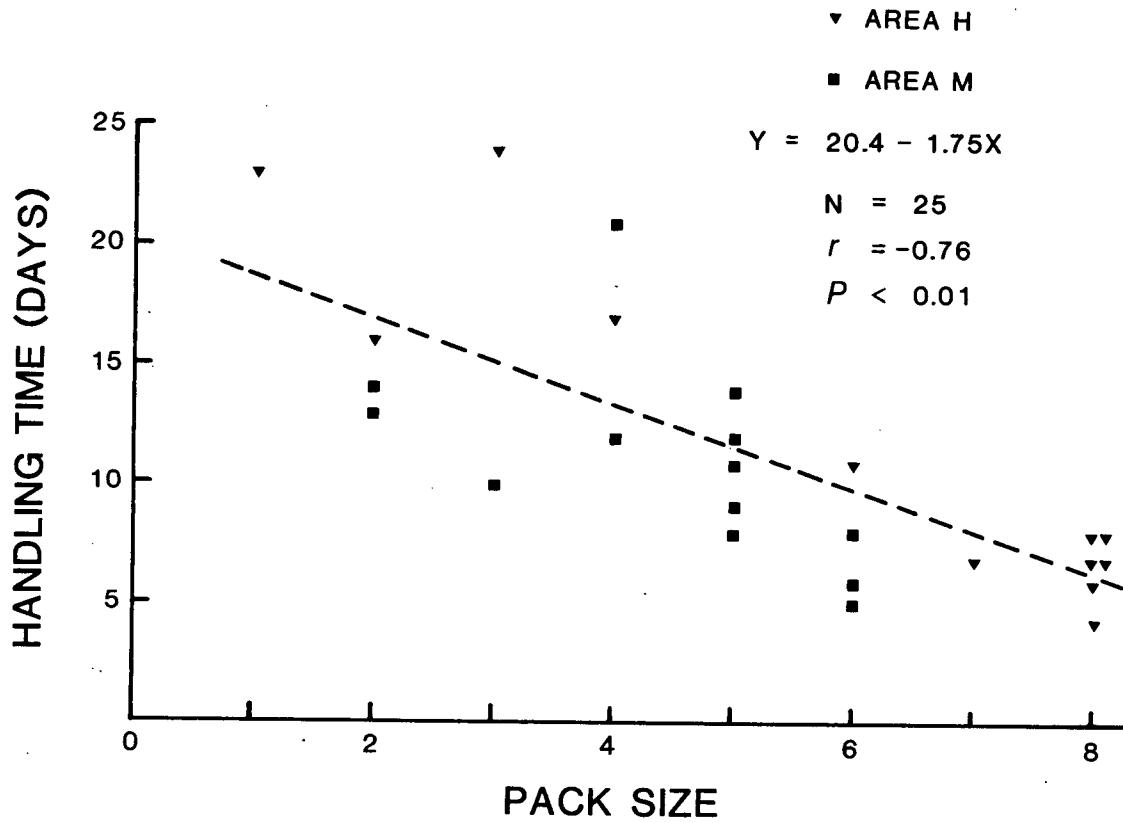


Fig. 13. Time spent at adult moose kills (handling time) as a function of the number of wolves present (pack size).

attacks were conducted by small packs of 2 to 5 wolves. These results clearly indicate that wolves were persevering in many attacks.

Wolf densities and moose:wolf ratios

Wolf density in January averaged $1.38 \text{ animals} \cdot 100 \text{ km}^{-2}$ in area H and 0.82 in area M (Messier in press a, or Chapter II). From 3 population indices, wolf density in area L was extrapolated at $0.36 \text{ animal} \cdot 100 \text{ km}^{-2}$ (Table 14). Moose:wolf ratios were almost equal in the areas H and M (27:1 and 28:1 respectively) but higher in area L (47:1). In summer, wolf density was estimated at $2.07 \text{ animals} \cdot 100 \text{ km}^{-2}$ in area H, and 1.16 in area M (Messier in press a). The relative population indices in area L suggest a summer density of $0.51 \text{ wolf} \cdot 100 \text{ km}^{-2}$.

Year-long predation rates and population balances

To estimate the year-long predation rate, I calculated the number of adult moose ($\geq 1 \text{ yr}$) and calves alive on 1 June, and the total number killed by wolves over the ensuing biological year. The basic reference point for all mortality estimates are the postnatal populations, i.e., adults plus the recruitment as evaluated after the perinatal mortality (stillborn, malformation, nutritional deprivation, etc.). Perinatal mortality is believed to be restricted largely to

Table 14. Indices, relative indices (RI), and best estimates of wolf density (January) in areas H, M, and L. Weekly scat counts were conducted in July and August 1980-'81-'82-'83, and data used in the 2 other indices were collected in September and October 1981-'82.

	No. scats per 100 km • week		No. wolves seen per 100 hunting-days		No. days with howling per 100 hunting-days		\bar{X} of RI	Wolf density
	\bar{X} (No. km • week)	RI	\bar{X} (No. h.-d)	RI	\bar{X} (No. h.-d)	RI		No./ 100 km ²
Area H	5.6 (1440)	1.00	5.1 (1172)	1.00	11.2 (1145)	1.00	1.00	1.38 ^a
Area M	4.6 (1440)	0.82	2.5 (483)	0.49	4.9 (510)	0.44	0.58	0.82 ^a
Area L	1.4 (1392)	0.25	1.1 (631)	0.22	3.6 (631)	0.32	0.26	0.36 ^b

^a Average density in January 1980-'81-'82-'83 established from an intensive telemetry study of pack size, number packs, and territory size (Messier submitted a).

^b Estimated from the average RI in area L and the observed wolf density in area H ($0.26 \times 1.38 = 0.36$).

the few days following parturition (Verme 1974) and, consequently, its importance is often difficult to quantify.

The computation of predation rates and the associated assumptions are summarized in Tables 15 and 16. Regarding the assumptions, I am certain that other authors may have chosen somewhat different values, but I stress that the same assumptions were applied for the 3 areas, thus validating the comparison. Year-long predation rates proved to be density dependent, increasing from 6.1 to 19.3% as moose density differed from 0.17 to 0.37 animal.km⁻². Summer predation, mostly oriented toward calves, represented 75 to 85% of the year-long predation. I estimated that 10, 5, and 2% of adults perished annually from wolf predation in areas H, M, and L, respectively. The corresponding values among calves were 38, 22, and 14%.

The full implication of a mortality factor is revealed only after being juxtaposed to the other limiting factors on reproduction and survival. In Table 17, I present the natality-mortality balances for the 3 moose populations. Recruitment on 1 June accounted for 100 calves per 100 females aged ≥ 2 years of age and did not differ among areas (note d of Table 15; Crête unpubl.). The importance of wolf predation, hunting, and road kills could be assessed with some confidence. The importance of black bear predation and chronic mortality are not known reliably and merit specific comments.

Table 15. Derivation of the density (No./km²) of calf and adult (≥ 1 yr) moose in areas H, M, and L, on 1 June (i.e., post-natal density).

	Area H	Area M	Area L
(A) Overall density on 15 Jan ^a	0.37	0.23	0.17
(B) Proportion of moose surviving until 1 Jun ^b	0.91	0.94	0.97
(C) Density of adults on 1 Jun, (A) X (B)	0.337	0.216	0.165
(D) Density of females aged ≥ 2 yr ^c	0.172	0.118	0.074
(E) No. calves/female ≥ 2 yr after perinatal mortality ^d	1.00	1.00	1.00
(F) Density of calves, (D) X (E)	0.172	0.118	0.074
(H) Overall density, (C) + (F)	0.51	0.33	0.24

^a From Messier and Crête in press.

^b These figures were derived from the wolf killing rates (Table 13), wolf densities (Table 14), and a baseline mortality of 4% per yr (see text).

^c Calculated as (C) X (1 - % of calves in Jan) X (% of females among adults); data from Table 12. I inferred that the % of calves in Jan equalled the % of yearlings on 1 Jun, i.e., a proportional mortality.

^d A composite sample of 45 radio-tracked females were associated with a minimum of 46 calves on 1 Jun (5-10 days after parturition); calf production did not differ among areas ($\chi^2 [2] = 0.87$, $P > 0.50$).

Table 16. Estimation of the number of moose killed by wolves and the year-long predation rate in a 1000-km² area H, M, and L. The calculation was made independently in the summer (S = May to Nov) and winter period (W = Dec to Apr).

	Area H		Area M		Area L	
	S	W	S	W	S	W
(A) Wolf numbers ^a	20.7	13.8	11.6	8.2	5.1	3.6
(B) Food intake (kg/wolf/day) ^b	2.6	---	2.2	---	2.1	---
(C) Moose consumed (kg) ^c						
Calf	3200	---	1180	---	500	---
Adult	6700	---	2510	---	1050	---
(D) Number moose killed ^d						
Calf	57.0	8.2	23.4	2.0	9.8	0.7
Adult	17.9	15.2	6.7	3.8	2.8	1.3
(E) Year-long predation rate (%) ^e	19.3		10.7		6.1	

^a See text.

^b Calculated as the observed winter food intake (3.3, 2.8, and 2.6 kg/wolf/day in areas H, M, and L, respectively) for adults, and half these amounts for pups (= 40% of wolves); only the weighted food intakes are presented.

^c Calculated as (A) X (B) X (the proportion of adult or calf moose in the biomass originally ingested; Table 9). Profile of wolf diet in area L was assumed to be similar to that in area M.

^d In summer, we assume that 10% of the calf biomass (after consideration of Franzmann et al. 1980, Ballard et al. 1981) and 30% of the adult biomass represented scavenging; see also notes ^c and ^d of Table 9 for the calculation. In winter, the estimations were derived directly from the observed killing rate per 100 wolf-days (Table 13), assuming that calves count for 35% of kills.

^e Calculated as (D) ÷ [(H) in Table 15 X 1000].

Table 17. Summarization of the recruitment and mortality data in areas H, M, and L, given as the percentages of the post-natal populations. Values in parentheses are not known reliably (see text).

	Area H	Area M	Area L
Recruitment, $(F) \div (H)$ in Table 15	33.8	35.3	31.0
Mortality			
Hunting ^a	3.1	22.2	23.7
Wolf predation, (E) in Table 16	19.3	10.7	6.1
Road kills ^b	1.0	0.0	0.0
Black bear predation ^c	(5.0)	(2.0)	(1.5)
Other natural mortalities ^d	(4.0)	(4.0)	(4.0)
Net balance	(+1.3)	(-3.6)	(-4.3)
Population trend, 1976-1983 ^e	Stable	Declining at ~5% per yr	Stable
Comments	Possible egress	Possible ingress from area H	Possible ingress from area H Recruitment likely underestimated by 2-3% ^f

^a From 1980 to 1984, annual hunting averaged 15.9, 73.3, and 59.2 moose/1000 km² in areas H, M, and L, respectively; hunter-killed registration was compulsory and poaching appeared negligible.

^b Each year, 50-70 moose (4.4/1000 km²) were killed by accident along the 117 Highway traversing area H.

^c Assuming that 15%, 10%, and 5% of the calves were killed by black bears in areas H, M, and L, respectively.

^d Assuming a baseline mortality of 4% for all areas (see text).

^e From the analysis presented by Messier and Crête (in press).

^f We suspect an over-representation of males in area L (Table 12); assuming that males comprised 30% of adults as in area M (similar rate of harvesting), the recruitment rate is 34.3%.

Black bear predation is inherently difficult to quantify because moose consumption per individual bear is presumably small. The possible importance of bear predation originates from the high population density of this facultative carnivore compared to a obligatory carnivore such as the wolf. Analysis of 375 black bear scats collected in area H during months of May, June, and July, revealed that remains of calf moose (the only members presumably killed) occurred only in trace amounts (Lachapelle et al. 1984). Bear predation may be estimated crudely from the premise that calf mortality between ≈ 10 days of age and the following winter is mostly ($\approx 80\%$) attributable to predation (Franzmann et al. 1980; Ballard et al. 1981; Larsen 1984). Beginning with 100 calves:100 females on 1 June and subtracting losses from wolf predation until 1 January, a ratio of 60-65 calves:100 females would be expected in area H. The observed ratio was 37:100 (Table 12) which indicates an additional loss of 20-25% of the recruitment. In areas M and L, bear predation was likely lower due to the apparent difference in bear density. Weekly scat counts in July and August 1980 to 1983 resulted in 9.6, 3.3, and 2.4 bear scats $\cdot 100$ week-km in areas H, M, and L, respectively (same methodology in all areas; efforts = 2880, 1440, and 1440 week-km, respectively). From these considerations, I evaluated that 15%, 5%, and 5% of the calves were killed each summer by black bears in the 3 respective areas (Table 17).

Limited data from radio-collared female moose suggest a

chronic mortality of 2-3% (Crête unpubl.; 2 cases during 84 moose-yr). I suspect that such mortality was relatively uncommon because either predation (area H) or human exploitation (areas M and L) curtailed the occurrence of chronic mortality. Considering that males may be subjected to higher natural mortality, I tentatively estimated chronic mortality at 4% for all areas. This figure conforms with other values found at comparable moose densities (Rolley and Keith 1980; Hauge and Keith 1981; Gasaway et al. 1983).

From the 1976-83 density estimates, moose populations appeared stable in area H, slightly declining ($\approx 5\%$ per year) in area M, and stable in area L (Messier and Crête 1984). The natality-mortality balances matched reasonably well with these population trends (Table 17). These correspondences strengthen the realism of the underlying estimates, although many possible sources of imprecision remain.

DISCUSSION

In southwestern Québec, the plasticity of prey selection by wolves in response to moose density represented an important aspect of the moose-wolf dynamics. Both the analysis of summer scats and winter feeding observations indicated a greater use of alternative, probably less profitable, food resources with a lower moose density. Prey switching has been documented in other wolf studies (Voigt et al. 1976; Peterson

1977; Shelton and Peterson 1983).

Killing rate reflects the amount of time a predator is engaged in consuming prey (handling time) and the amount of time searching for prey (Holling 1959). Walters et al. (1981) reported that the time spent at a moose kill was nearly independent of pack size. They argued that it is not the number of wolves that is critical in determining predation rate, rather, it is the number of packs. This notion may prove to be dangerously deceptive for 2 reasons: 1) the paucity of the data presented did not warrant such a conclusion, and 2) the variation in the amount of time searching between 2 kills in relation to pack size was not addressed. In the present study, handling time (sensu time at kill) was negatively correlated with pack size. For an average pack size of 5.7, 3.7, and 3.0 wolves in areas H, M, and L (n=12, 20, and 2, respectively; Messier in press a), I calculated a handling time of 11, 13, and 15 days (Fig. 13). Considering the average time between kills (19, 55, and 90 days respectively; from Table 13), the amount of time between consuming 2 kills was approximately 8, 42, 75 days. Therefore, a major determinant of the killing rates was the time searching for prey. Wolves survived through these protracted periods without kills by scavenging on already dead moose and by exploiting alternative food resources. Apparently, locating these food-sources was enhanced by the fact that wolves were searching each unit area at greater

intensity where moose were less numerous (Messier in press a).

Killing rates in winter ranged from 5.3 (area H) to 1.1 (area L) moose·100 pack-days. These rates are quite low compared to the 15-20 moose·100 pack-days observed in other studies (Mech 1966; Peterson 1977; Fuller and Keith 1980; Peterson et al. 1984b). It was apparent that wolves were not able to kill at will, even in area H. It was also remarkable how complete every kill was utilized (disarticulated skeleton, leg bones skinned down to the hooves). As a consequence, moose consumption in area H (0.09 kg/kg wolf/day), and especially in areas M and L, was low compared to the range determined for wolves preying on moose in other studies (0.10-0.19 kg/kg wolf/day; Peterson 1977 and unpubl.; Fuller and Keith 1980; Peterson et al. 1984b). Therefore, it is likely that wolves in this study would have increased their killing rate given a moose density higher than 0.4 animal·km⁻². The relatively low body weight of wolves (\approx 26 kg for adult females and 30 kg for adult males) and the small size of packs (i.e., longer refractory period after a kill) were 2 other factors involved in the markedly lower killing rates in this study.

Wolf densities in areas H and M were determined reliably with the aid of radio-collared animals. The density in area L was extrapolated from 3 indices to increase precision. Thus, the possible error associated with the wolf density estimates is believed to be minimal. Wolf densities in areas H and M paralleled the change in moose density. Therefore, the nearly

2-fold difference in the predation rates (19.3 and 10.7%) was attributable to changes in prey selection and killing rates (functional response) rather than a relative difference in wolf density. I suggest that moose-wolf ratios may reflect predation rate across a large range of moose densities, but so imperfectly that their utility in a management perspective remain questionable (see Gasaway et al. 1983 for a different advocacy). In area L, wolf density was much lower, resulting in a higher moose:wolf ratio. Messier (in press a) suggested that a density of $0.2 \text{ moose} \cdot \text{km}^{-2}$ approximated the density threshold below which a pack cannot subsist and/or reproduce successfully in the absence of other ungulate species. In area L ($0.17 \text{ moose} \cdot \text{km}^{-2}$), a food intake of $\approx 0.08 \text{ kg meat/kg wolf/day}$ was observed, which is far below the food requirement of $0.13 \text{ kg meat/kg wolf/day}$ to reproduce successfully, as proposed by Mech (1977). During 4 summers that the area L was intensively patrolled, I found evidence of only 1 pack that produced a litter of pups, and a portion (25%) of its territory was in area H.

Estimated predation rates increased from 6.1% at $0.17 \text{ moose} \cdot \text{km}^{-2}$ to 19.3% at $0.37 \text{ moose} \cdot \text{km}^{-2}$. Confidence intervals of predation rates cannot be computed due to the complexity of the analysis, and the presence of assumptions. The error associated with predation rates may easily be in the range of 15-30% of the estimates. Even with such an error, the study provides solid evidence that wolf predation was density-

dependent. Empirical justifications for this assertion are: 1) the sharp decline in killing rate with decreasing moose density, 2) the tendency to consume alternative food resources at lower moose density, and 3) the disruption of the wolf population at moose densities below $\approx 0.2 \text{ animal} \cdot \text{km}^{-2}$.

In southwestern Québec, non-harvested moose populations plateau at a density of $\approx 0.4 \text{ animal} \cdot \text{km}^{-2}$ (Messier and Crête 1984). Wolf predation appears to represent the dominant density-dependent mechanism but the entire regulatory process may involve other depressive factors. For example, wolf predation alone cannot explain the low ratio of 37 calves:100 females observed in area H during January surveys. Black bears were found to prey on calves in Alaska (Franzmann et al. 1980) and probably they inflicted a further reduction of calves in our situation. Whether or not bear predation is also density-dependent remains unknown. If it is, bear predation will reinforce the regulatory effect of predation on moose populations.

In regards to food resource limitation, there is no indication that foraging conditions deteriorate when a moose population reaches the equilibrium density of $0.40 \text{ animal} \cdot \text{km}^{-2}$ (Messier and Crête 1984; Crête et al. 1981; Crête and Jordan 1982a, b). Overall, wolf predation, in combination with the other limiting factors on recruitment and mortality, appears capable of regulating a moose population well below the density sustainable by available food resources. I conclude

that naturally regulated moose populations in southwestern Québec are heavily constrained by predators, but at the same time wolves are nutritionally stressed due to their own action on the abundance of moose.

Chapter IV

MOOSE RESPONSE TO EXPERIMENTAL WOLF REMOVAL

INTRODUCTION

In southwestern Québec, as in some other places in boreal ecosystems, non-harvested moose populations appear to stabilize at a density of ≈ 0.4 animal \cdot km $^{-2}$ (Crête et al. 1981; Bergerud et al. 1983; Messier and Crête 1984; Crête submitted). Habitat production and its use by moose have been investigated near this natural equilibrium and at lower moose densities for comparison (i.e., populations reduced by harvesting; Crête and Jordan 1982a, b). Body condition of moose was also studied in an effort to assess habitat quality from an animal perspective (Crête et al. 1982; Messier and Crête 1984). The general conclusion was that availability of food resources was not sufficient to explain the observed natural regulation of moose populations.

This ongoing study attempts to test whether or not wolf predation, combined with other limiting factors on reproduction and survival, can hold a moose population well below the density that can be sustained by available food resources. I postulated that wolf predation is density-dependent between 0.0 and 0.4 moose \cdot km $^{-2}$ (Crête et al. 1981;

Messier and Crête 1984, in press). This mortality may depress recruitment and increase adult mortality to a point where population growth is reduced to zero before food competition substantially impairs moose productivity (i.e., presence of a low density equilibrium). However, I recognize the possibility that at higher moose densities (i.e., >0.5 moose \cdot km $^{-2}$) wolf predation may decrease and act as a compensatory mortality factor (Walters et al. 1981; Gasaway et al. 1983). Therefore I am also attempting to verify if the wolf-moose system is characterized by a lower and an upper stable equilibrium (Clark 1976:236; Van Ballenberghe 1980).

The experimental design was to reduce wolves in an area where the moose population was naturally regulated and near a stable equilibrium. An increase in the moose population (higher recruitment, higher population growth rate) would support the hypothesis that moose are maintained at low densities by wolf predation. In order to test the multiple equilibria hypothesis, wolf removal will be stopped when the moose density has at least doubled (i.e., ≈ 1.0 animal \cdot km $^{-2}$). If in subsequent years the moose population declines to its former level, a single low density equilibrium will be suggested. Alternatively, if the moose population continues to increase, a second higher density equilibrium created by food competition will be indicated. Obviously, these responses will be quantifiable only in a long-term study (>10 years). In this paper, the preliminary results accumulated

during the first four years of the ongoing wolf reduction programme is presented.

STUDY AREA AND METHODS

The study was conducted in La Vérendrye game reserve, southwestern Québec (Fig. 14), from June 1980 to March 1984. The moose population has been lightly harvested for the past 15 years (3-4% annually) but its stable density was basically determined by natural regulation (Crête et al. 1981a; Messier and Crête 1984).

Two study areas were selected: a wolf removal area of 700 km² bounded by a 10-km buffer zone, and a non-removal area of 900 km² (Fig. 14). Wolf population status was determined by scat counts and hunter interviews. Weekly scat counts on forest roads began on 1 July and lasted 10, 8, 8, and 6 weeks respectively from 1980 to 1983. Within each area, I recorded all forest roads for which human use was sufficiently low to insure that scats remained noticeable for a 1-week period. Suitable road segments had an average length of $6.9 \pm (\text{SD})3.0$ km. They were randomly selected to form a permanent 48-km circuit in each study site. Counts were made by two observers on motorcycles patrolling at a maximum speed of 20 km·h. All scats were collected during each patrol.

Moose hunters were interviewed at the compulsory registration office of the reserve from 15 September to 20

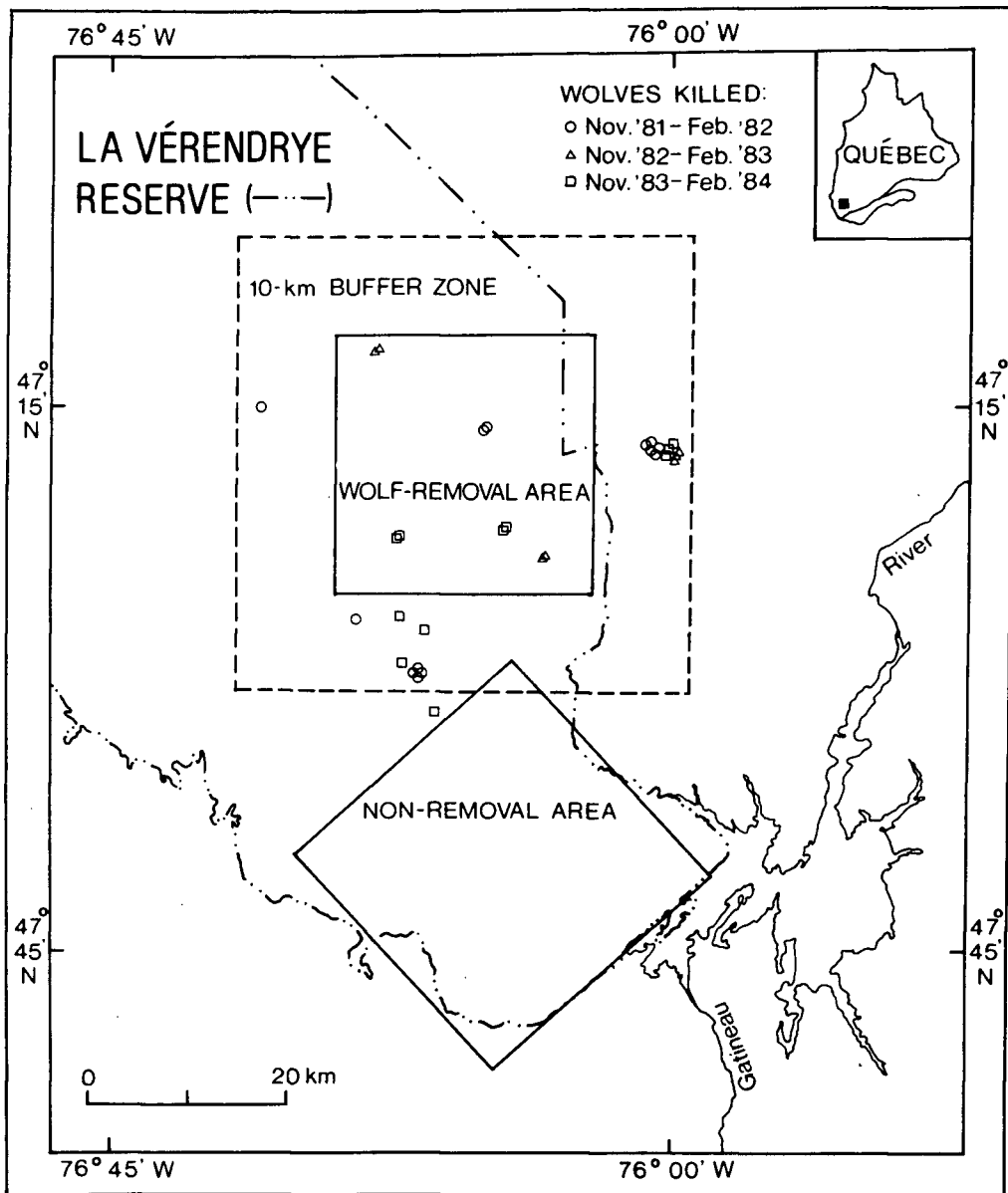


Fig. 14. Description of the study area for the wolf removal experiment, and locations of the wolves killed between November 1981 and March 1984.

October. One person of each party was asked how many wolves he observed during his 1-4 days of hunting, and how many days he heard wolves howling. The location of the area hunted and the number of hunting-days were also noted.

Moose population status was determined by aerial surveys conducted during the first three weeks of January each year (Crête and St-Hilaire 1979). Four plots of 60 km² (6X10 km) were randomly selected in each study area. Within each plot twelve 10-km transects at 500 m intervals were patrolled in fixed-wing aircraft (speed \approx 165 km·h; altitude above ground \approx 120 m). Two observers, one on each side of the aircraft, reported the number of moose seen to a navigator. Number of moose seen per plot was used as an index of moose density. In addition, moose density estimates within plots were derived from the simple regression presented by Crête et al.

(submitted) wherein the number of moose seen per 100 km flown was correlated to the density found by helicopter from total coverage censuses and corrected for visibility bias.

Recruitment, in terms of calf:cow ratios, was estimated during January aerial surveys. From helicopter, sex of adults was ascertained from vulva-patch and antler criteria, and calves were identified by relative size (Roussel 1975). Additional information on calf survival was gained from radio-collared cows in both study areas. Females were monitored intensively during the parturition period to assess the number of calves born. Afterwards cows were located approximately at

1 month intervals to determine calf losses.

Wolf removal began during the third year of the experiment. From November to March, wolves were either captured by local trappers or killed from helicopter. During aerial shooting sessions the aim was to remove entire packs. Also, wolves were killed when they were tracked from the removal area to the 10-km buffer zone.

RESULTS

From November 1981 to February 1984, a minimum of 31 wolves were killed in the 700-km² removal area and the 10-km buffer zone. The annual removals were: 14 in 1981-82, 7 in 1982-83, and 10 in 1983-84. For most wolves killed in the buffer zone (n=20), there was evidence from track observations that they were using part of the removal area. An average of 6.7 h of helicopter time was necessary per wolf killed (n=18). The trapping effort for the remaining 13 wolves captured by local people is unknown. Pups were captured each year (n=17; 12 males, 4 females, 1 unknown). Thus, reproductive adults were never totally eliminated although at least 8 males and 5 females were killed.

Weekly scat counts (Table 18) indicated that the wolf population in the removal area was successfully reduced (Mann-Whitney \underline{U} -test[20,14] = 237.5, \underline{P} <0.01) but remained stable in the non-removal area (\underline{U} -test[20,14] = 153.5, \underline{P} >0.10). Hunter

Table 18. Indices of wolf populations in the non-removal area (N-R) and in the removal area (R) before initiation of the wolf reduction programme (1980, 1981) and during the programme (1982, 1983).

	No. scats per 100 km • week		No. wolves seen per 100 hunting-days (No. of sightings)		No. days with howling per 100 hunting-days (No. days howling)	
	N-R	R	N-R	R	N-R	R
Pre-removal						
1980	5.6	3.1				
1981	4.8	13.1	3.4(3)	8.3(2)	7.0(6)	20.8(5)
Post-removal						
1982	6.0	2.1	2.9(3)	2.1(2)	12.4(13)	10.3(10)
1983	8.0	0.4	5.0(7)	1.0(1)	3.6(5)	8.1(8)

interviews gave inconsistent results; a wolf reduction was indicated by the frequency of wolf sightings, but not from the percentage of days that hunters heard wolves (Table 18). Small sample sizes and the possible lack of independence between observations obscure any statistical analysis of these results. The limitation of hunter interviews when used on a small scale should be recognized.

Before the wolf reduction programme (1981+'82), moose densities were estimated at $0.28 \text{ animal} \cdot \text{km}^{-2}$ in the removal area, and at 0.34 in the non-removal area (Table 19). After the first year of wolf reduction, the moose density significantly increased to an estimated $0.73 \text{ animal} \cdot \text{km}^{-2}$ in the removal area ($t\text{-test}[10] = 2.38$, $P < 0.05$; data of 1981+'82 vs 1983) but remained stable in the non-removal area ($t\text{-test}[10] = 0.38$, $P > 0.10$). Unusual deep snow conditions in 1984 prevented assessment of moose density for the second year of the programme.

Before wolf reduction (1981+'82), calf:cow ratios were approximately 40:100 in both study areas (Table 20). After one year of treatment, calf:cow ratio increased to 68:100 in the removal area but declined to 39:100 the subsequent year. Summing the first two years of the programme, 52 calves:100 cows were counted in the removal area and 36:100 in the non-removal area (significantly lower at $P = 0.07$, Table 20).

A higher calf survival in the removal area was also indicated by the improved survival of calves associated with

Table 19. Average (SE) number of moose observed per 60-km² plot (see methods) and estimates (SE) of the moose density in the non-removal and in the removal area. Results in 1983 were during the wolf reduction programme.

	No. moose observed per 60-km ² plot		Moose density No./km ²	
	Non-removal area	Removal area	Non-removal area	Removal area
Pre-removal				
1981	4.7 (0.8)	2.8 (2.7)	0.36 (0.12)	0.23 (0.21)
1982	4.3 (0.6)	4.3 (2.3)	0.32 (0.11)	0.32 (0.18)
Post-removal				
1983	5.0 (1.5)	10.7 (2.7)	0.37 (0.14)	0.73 (0.22)

Table 20. Calf-cow ratios in the non-removal area and in the removal area before initiation of the wolf reduction programme (1981, 1982), and during the programme (1983, 1984). The ratios were compared with a two-tailed Z-test, $\alpha = 0.10$.

	No. calves: 100 cows \pm 90% CL (n)		<u>Z</u> -test
	Non-removal area	Removal area	
Pre-removal			
1981	65 \pm 30 (43)	30 \pm 18 (35)	n.s.
1982	24 \pm 11 (56)	52 \pm 25 (38)	n.s.
Post-removal			
1983	45 \pm 17 (61)	68 \pm 29 (47)	n.s.
1984	30 \pm 11 (74)	39 \pm 18 (50)	n.s.
1981 + 82	39 \pm 11 (116)	40 \pm 15 (73)	n.s.
1983 + 84	36 \pm 8 (154)	52 \pm 16 (97)	<u>P</u> = 0.07

radio-collared females. In the removal area, calves had a survival rate of $\approx 65\%$ compared to $\approx 50\%$ in the non-removal area (Fig. 15).

DISCUSSION

Although the results are preliminary and their precision can be improved, they are consistent with the hypothesis that predation maintains moose populations at densities well below the food carrying capacity.

The wolf population in the removal area was likely reduced by at least 40% in 1981-82, and subsequently held at this level. In the removal area and its buffer zone (i.e., 2150 km²), wolf removal represented 0.7, 0.3, and 0.5 animal per 100 km² in 1981-82, 1982-83, and 1983-84. As an estimate of the wolf density before wolf removal, wolf density in the non-removal area averaged 1.4 animals \cdot 100 km⁻² from 1980-81 to 1983-84 (from intensive radio-tracking; Messier in press a). Keith (1983) and Peterson et al. (1984b) argued that a removal rate exceeding 30% causes a wolf population to decline. Scat counts and the number of wolves seen per 100 hunting-days suggested a reduction in the wolf population.

Moose density increased during the first year of the wolf reduction programme. However, I have some reservations about the density increment (0.28 to 0.73 moose \cdot km⁻²), but nonetheless a trend is indicated. Aerial survey precision

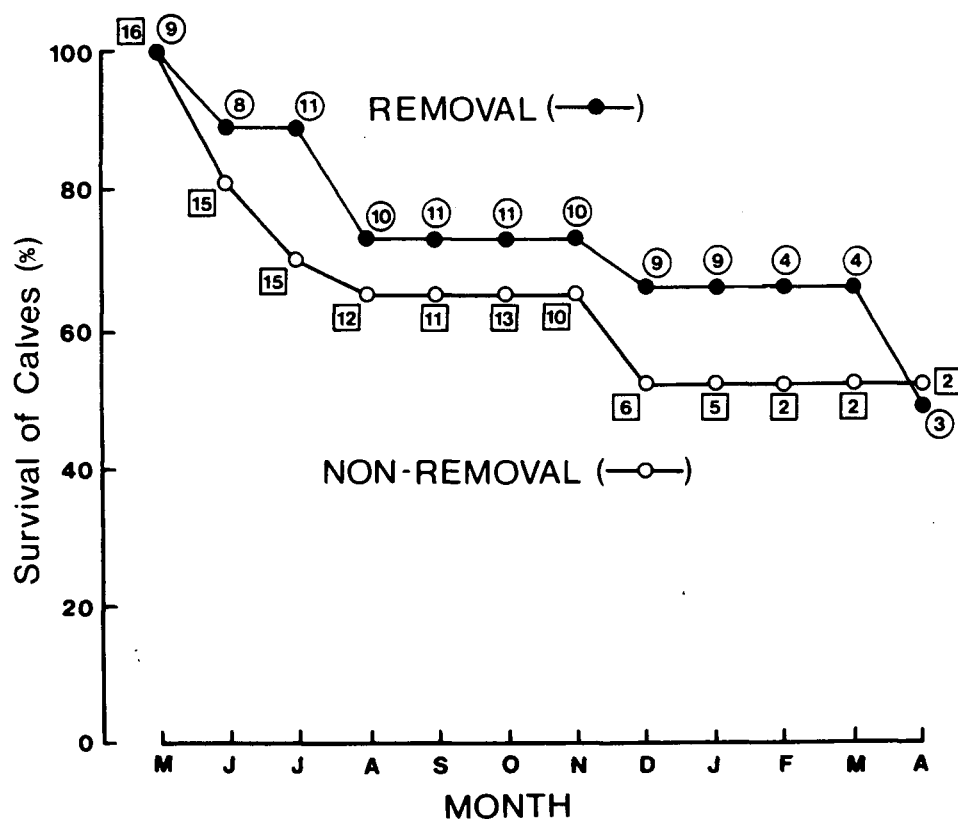


Fig. 15. Percent survival of calves associated with radio-collared female moose in the wolf removal and the non-removal area. Total numbers of calves followed through the subsequent month are in circles and squares.

must be improved to quantify more properly population increment. Moose inventory technique will be revised in 1985 to meet this goal (Crête et al. submitted).

Higher recruitment, as expressed by the 6-month calf:cow ratio, represents the most important indicator of a moose population relieved from intensive predation (Gasaway et al. 1983). In this study, recruitment increased from 40 calves:100 cows to 68:100 in the first year of wolf removal and declined to 39:100 for the second year. Probably the second year reduction was created by a larger non-reproductive yearling cohort entering the cow population (i.e., cows ≥ 1.5 yr old in our counts). As a result of the higher recruitment in 1983, yearling males (spiked antler) represented 53% (n=17) of all males in the removal area but only 23% (n=31) in the non-removal area (two-tailed Z -test = 2.13, $P < 0.05$). If I assume similar percentages for yearling females, the number of calves:100 cows ≥ 2.5 yr old was 82 in the removal area and 39 in the non-removal area. Thus there was an indication that the recruitment was much improved in both years of wolf reduction. This conclusion will be supplemented in the future by more precise recruitment estimates where sample sizes should be approximately doubled.

The evaluation of survival rate of calves associated with radio-collared females gave a less pronounced response. The small number of cows tracked to date necessitates a cautious interpretation of these preliminary results.

Black bears are common in both study sites at a minimum density of $0.25 \text{ animal} \cdot \text{km}^{-2}$ (Lachapelle et al. 1984). They are potential calf predators (Franzmann et al. 1980), and probably impose a limit to the increase in calf survival even if the wolf population was reduced more severely. A bear removal experiment was initiated in 1983 within a third study site in the reserve. This project should provide some insights on the importance of bears as calf predators.

Management implications

Predator control represents one of the many possible options to stimulate population growth of ungulates (Connolly 1978; Gasaway et al. 1983). The immediate purpose of the present wolf removal is to experimentally determine if moose populations are regulated at low densities by predation. If this hypothesis is true, moose managers face a dilemma. They may accept that the 'natural harvestable surplus' is limited. For example, the density offering a maximum sustained yield without interference in Québec was estimated at only $0.2\text{--}0.3 \text{ moose} \cdot \text{km}^{-2}$ (Crête et al. 1981). With this alternative, hunting success would remain low (e.g., the 1983 province wide hunting success was 8%), and available food resources could not be used to support higher moose populations. Alternatively, they may advocate that the pristine nature of the predator-moose-vegetation system are perturbed by man. In this perspective, and considering the large demand for moose

hunting in some areas, an integrated ungulate management policy may include options to simultaneously manage predator populations by means of trapping and hunting.

Chapter V

GENERAL DISCUSSION AND CONCLUSIONS

Predator-moose-vegetation dynamics can be summarized by a graphical representation (Fig. 16). In a predator-free area, a moose population is expected to display logistic growth, resulting in a single, upper density equilibrium (D_4), as suggested for other ungulate species (Caughley 1976; Sinclair 1977; McCullough 1979). In this situation, competition for nutritious forage with increasing population density restrains fecundity and accentuates chronic mortality until population growth is no longer possible.

In the presence of predators, systems may have qualitatively 3 variants, but a continuum of possible outcomes exists. In the first variant, predation reduces the increment of a moose population, but never sufficiently to create an equilibrium density without competition for forage having a depressive effect (i.e., food-induced equilibrium, D_3). The second variant is a system characterized by a lower (predator-induced) and an upper (food-induced) equilibrium density. This type of system implies that predators can stop population growth at a density where forage competition has no detrimental effect (D_1), but at higher moose densities, a lessening of predation rate permits population growth until

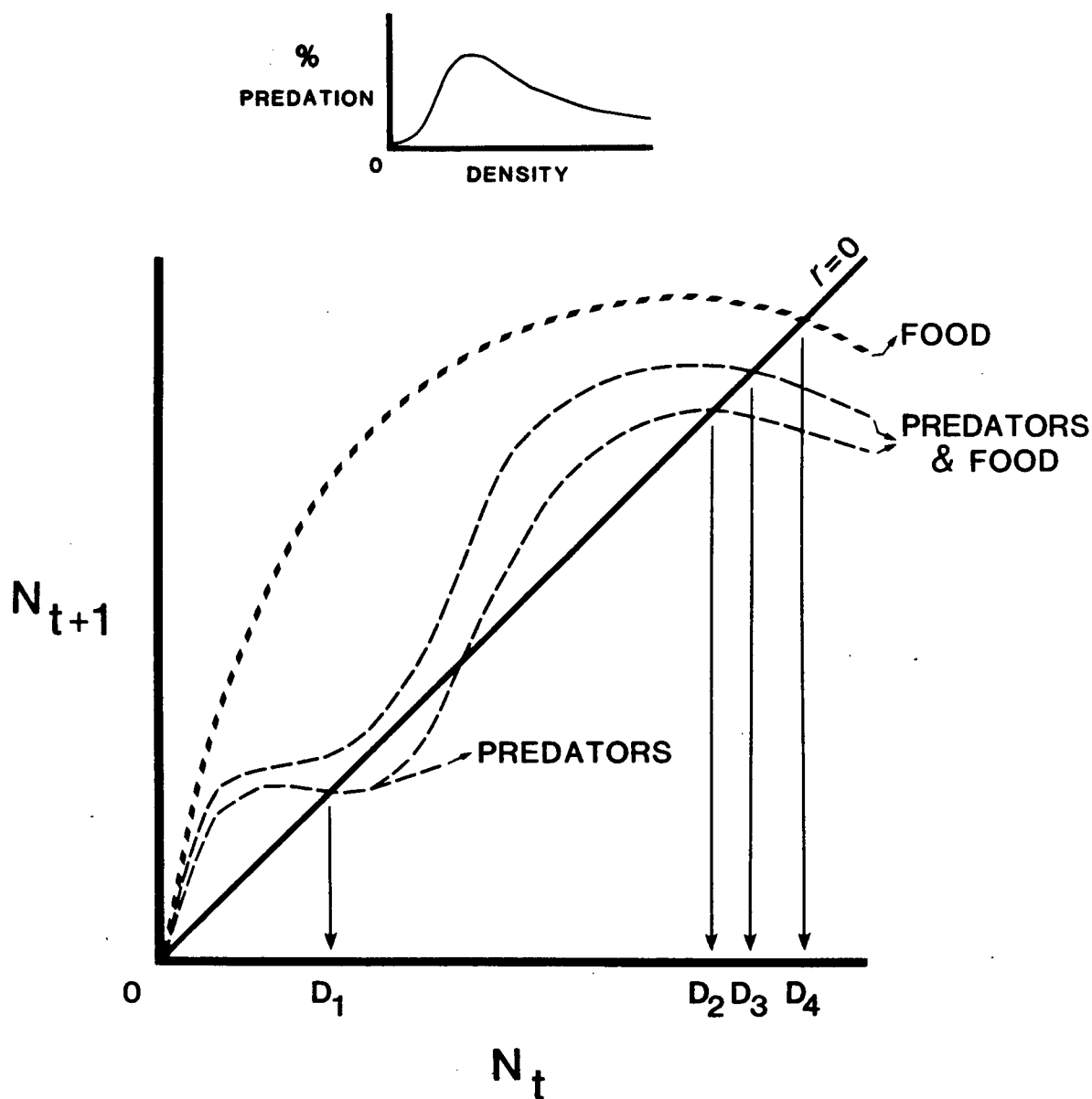


Fig. 16. The proposed conceptual model of predator-moose-food supply dynamics. In predator-free areas, moose populations are hypothesized to stabilize at high density (D_4 equilibrium). Where predation occurs, 3 variants of system behavior are possible: 1) a single, upper equilibrium (D_3), 2) a lower, predator-induced equilibrium (D_1) and an upper, food-induced equilibrium (D_2), and 3) a single, lower equilibrium (D_1). In this model, predation is envisioned as having a density-dependent phase followed by an inverse density-dependent phase (inset).

competition for forage has a regulatory effect (D_2). The third variant consists of a system stabilizing at a low density (D_1) due to heavy predation. In this case, the persistent effect of a high predation rate precludes population growth at higher densities (negative increment, Fig. 16).

The crucial element in determining the system's behavior is the relationship between predation rate and moose density. Walters et al. (1981), and Gasaway et al. (1983) argued that the impact of wolf predation increases during a moose population decline. This so-called depensatory impact may force a moose population to extinction, but such an event was never reported in the literature. Consequently, some feedback mechanisms must be involved. In this study, I have demonstrated the density-dependent influence of wolf predation at the lower range of moose densities. Overall, the predation rate by wolves appears to be characterized by a density-dependent phase followed by an inverse density-dependent phase (inset of Fig. 16). Holling (1959) in his pioneering work with mammalian predators found a similar relationship (see also Hassell 1978 for examples in arthropod predator-prey systems). At very low moose densities (<0.2 moose \cdot km $^{-2}$), predation by wolves appears negligible because wolves are nutritionally stressed and therefore rare or absent, and also because they tend to consume alternative food resources. When moose density increases above the density threshold of ≈ 0.2

moose·km⁻², wolves can colonize the system, but in their initial struggle to subsist they must exploit their territories intensively (Messier in press a). During this colonization phase (approximately between 0.2 and 0.5 moose·km⁻²) predation rate appears to increase dramatically, providing a strong feedback mechanism. At densities higher than 0.5-1.0 moose·km⁻², the impact of wolf predation likely decreases for 2 reasons: 1) social behavior (territoriality, deferred reproduction) would restrain wolf population growth (Packard and Mech 1980; Packard et al. 1983), and 2) substandard moose individuals are more available and would compose a greater fraction of wolf's kills (Peterson et al. 1984b).

The realization that predation rate peaks somewhere between low and moderate moose densities has important implications on moose population dynamics. For example, the annual increment curve may not have a bell shape as suggested by Caughley (1976). Rather, the general form of the annual increment curve in the presence of predation may be bimodal, with a range of densities at which the harvestable surplus is limited or nil (Fig. 16). This phenomenon poses a problem for wildlife managers because such a "predator pit" increases the risk of an unexpected decline when human-exploitation is liberalized at high moose densities. Moreover, the consequences of an initial decline can be aggravated by the typical lag response of wolf numbers to decreasing ungulate

densities (Mech and Karns 1977; Gasaway et al. 1983; Peterson and Page 1983).

Because little information is available, the form of the predator pit is hypothetical, but some predictions may be proposed at this time. In areas where moose cohabit with other ungulate species (e.g., Carbyn 1983), the predator pit should be less pronounced because part of the impact of predation is likely to be absorbed by the other ungulate species. This effect decreases the possibility that moose stabilize at low density due to wolf predation. Alternatively, if a second species of predators is present (e.g., black bear), I expect the predator pit to be relatively deep because the recruitment will be reduced by this second predator. In such situations (as in southwestern Québec), moose populations are more likely to stabilize at low densities, and may never increase naturally to higher densities.

Gasaway et al. (1983) argued that a "prudent" predator (Slobodkin 1974) is required to explain a stable moose-wolf system. Evidence exists that some naturally regulated moose populations are in fact remarkably stable. In Denali National Park, Alaska, Haber (1977) reported no major irruptions for at least 30-40 years or any obvious crashes following severe winters (density = $0.3-0.4$ moose \cdot km $^{-2}$). In area H, Messier and Crête (1984) could not detect any changes in moose density between 1967 to 1983. Among the 3 study areas, predation rate

increased sharply from 6.1% (Area L) to 19.3% (area H), and moreover, predation rate did not appear to be at its maximum, judging by the low killing rate and food intake. Wolves were able to prevent an increase in the moose population precisely because they were very efficient, rather than prudent predators. The sharp change in predation rate within a narrow range of moose densities constitutes an effective feedback mechanism. In this sense, predator-moose-vegetation systems are not always dynamic as postulated by Peek (1981), but may be fairly stable where predation represents the regulatory mechanism.

Evidence also exists that naturally regulated moose populations may undergo major fluctuations, the best example being the Isle Royale population (Peterson and Page 1983). From the conceptual model, I predict rather chaotic changes in moose numbers around the upper equilibria D_2 and D_3 . At the high range of densities (1 to ≈ 4 moose \cdot km $^{-2}$), forage competition induces a density-dependent effect on recruitment (Blood 1973; Saether and Haagenrud 1983) and presumably on chronic mortality. However, the impact of predation likely decreases at the same time (above). Because these 2 population processes are antagonistic, it is reasonable to believe that the net result would be a weak regulatory feedback mechanism at high moose densities; that is, population growth rate does not change rapidly with population density. Occasional severe winters may cause important

fluctuations of moose numbers at high densities (Peterson 1977). It may well be that the phenomenon observed on Isle Royale over the past 15 years (Peterson and Page 1983) was in essence one of these stochastic (in contrast to cyclic) disturbances exaggerated by the multiplier effect of predation; the lack of an effective feedback mechanism at high density being the fundamental reason. Although this view represents my interpretation, the basic phenomenon remains untested and other explanations are plausible (Bergerud et al. 1983; Peterson et al. 1984a).

Caughley (1977) and McCullough (1979) proposed that predation diverts an ungulate population to a new and lower equilibrium than in a predator-free situation. But, how much lower will this new equilibrium be? Both authors argued that predators cannot prevent an ungulate population from increasing to a level where forage competition has a depressive effect. Therefore, they are referring to the decrease from D_4 to D_3 (Fig. 16). Two predictions can be formulated regarding D_3 or D_4 : 1) moose individuals must be nutritionally stressed, and 2) enrichment of forage will create an upsurge of moose density (Peek 1980). There is no indication that these two predictions are true in southwestern Québec (Messier and Crête 1984). Alternatively, one prediction can be formulated regarding D_1 : predation must be density-dependent up to this density. Because this prediction appears true, I conclude that moose populations are either

predator-regulated, or stabilized at low density below a predator pit (i.e., multiple equilibria system). Crête and Messier (1984) are currently attempting to discriminate between these 2 alternatives by means of a wolf removal experiment.

At this time, it is uncertain that a moose population could stabilize at high densities after a temporary wolf reduction programme; moose may return to their former low density due to heavy predation after recovery of the wolf population. Furthermore, the stability of a high density equilibrium remains to be demonstrated, habitat over-utilization and natural crashes still represent possible outcomes.

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Appendix

SOLITARY LIVING AND EXTRA-TERRITORIAL MOVEMENTS OF WOLVES IN RELATION TO SOCIAL STATUS AND PREY ABUNDANCE

INTRODUCTION

In social birds and mammals, the dispersal of group members may play a central role in group dynamics and population regulation (Brown 1983; Macdonald 1983). The behavioural and ecological antecedents of dispersal, or of natal philopatry, have attracted biologists' interest in the last decade. The understanding of such antecedents should help to comprehend sociality (Barash 1974; Armitage 1977; Bekoff 1977; Emlen 1982; Brown 1983; Waser and Jones 1983).

In Carnivora, group living operates within a framework of cost-benefit constraints determined largely by: 1) the dispersion and abundance of food resources, 2) the competition for space (habitat saturation), 3) the competition with other predators over carcasses, and 4) the assistance needed to rear young optimally (reviews in Lamprecht 1981; Macdonald and Moehlman 1982; Messier and Barrette 1982; Macdonald 1983; Bekoff et al. in press). I propose that, in wolves (Canis lupus), factors 1 and 2 govern the tendency of an individual to live temporarily apart from its pack (solitary living), and

to engage in solo extra-territorial movements. As an extension of this proposal, I suggest that food resources in conjunction with territory vacancy ultimately set the rules for the dispersal strategy of pack members (see also Zimen 1976; Packard and Mech 1980; Macdonald 1983).

Here I report on solitary living and extra-territorial movements of 54 wolves studied during a 4-year research programme. Data are interpreted in relation to prey abundance, age of the animals, their sex, and the spatial distribution of packs. Observations of pack excursions are included for comparison. Mech (1977), Fritts and Mech (1981), Stephenson and James (1982), Van Ballenberghe (1983), and Peterson et al. (1984) published related field observations which are discussed.

STUDY AREA AND METHODS

Wolf spatial distribution was investigated in a 6400-km² area of southwestern Québec, Canada (47°N, 77°W) from June 1980 to February 1984. This area was deliberately selected because it covered a 3000-km² high prey area (HP) in La Vérendrye reserve, and a 3400-km² low prey area (LP) south of the reserve (i.e., same study area than Chapter II).

Fifty-four wolves from 14 contiguous packs were radio-tracked by airplanes. Some 4700 wolf locations were accumulated during the 2000 h of flying time. Wolves were

visually observed in 75% of the locations during winter, but rarely in other periods. Each wolf observation included the group size, whether or not all the animals were seen (i.e., in open habitat), and the identity of marked individuals.

Captured wolves were classified as either pup (<12 months, starting 1 May), yearling (12-24 months), or adult (>24 months). Pups were aged accurately from tooth eruption patterns. Yearlings were either of known age (trapped as pups or aged after death, $n=5$), or of assumed age ($n=3$) from their canine lengths, tooth wear, and reproductive status. The possibility that yearlings were mistaken as adults is believed to be minimal; if so, they would have been young, non-reproductive adults.

Solitary living could be studied reliably only from 1 December to 30 April each year (winter period) when wolves could be observed directly from airplanes. In this paper, I used only observations for which I was certain whether or not a wolf seen from the air was accompanied by other pack members. Frequency analyses on the full set of reliable observations ($n=1192$) were based on contingency tables and G -tests (Sokal and Rohlf 1981: 747-764). Frequencies at which wolves were observed apart from the packs (i.e., distant more than 500 m) were related to the age of animals, their sex, and the abundance of prey (HP or LP). I used similar analyses to relate the portion of these observations outside the pack's territory. Data from known lone wolves, including animals

during their actual or assumed definitive dispersal, were eliminated from these analyses and were treated separately because they represent a different phenomenon.

I defined extra-territorial excursions as being any travel 5 km beyond the boundary of the year-long territory of the pack. Such areas were delineated by the convex-polygon containing 95% of the closest locations of instrumented pack member(s) obtained during the current 1-year period (1 May to 30 April). In the 3 cases where the annual territory could not be properly defined because of insufficient data, I took the boundary of the previous or subsequent year. The minimum straight line distance of an excursion was measured from the most distant wolf location to the closest point of the home territory. The approximate duration of each excursion was calculated from the mid-date between the last location inside the territory and the first location of the excursion, to the mid-date between the last location of the excursion and the first location on return to the territory. Elapsed time was not computed if the excursion was not bounded by a pre- and a post-excursion location within 5 days, or if an actual or assumed dispersal occurred.

Radio fixes during an excursion were assumed to be independent because most locations were within 1 or 2 travelling days (30-40 km) from the pack's territory. Therefore, wolves had, in most days, the opportunity either to continue foraging or to be in their home territory by the next

day. On average, I recorded an observation of solitary animals that met my constraints each 4 days. Radio fixes of animals separated from their pack, but within the territory, also were assumed to be independent.

Radio fixes of solitary wolves were analysed in relation to the configuration of pack territories. In the cases of pack members, I used only locations during extra-territorial movements. Because such observations were available from 1980 to 1984, pack territories were delineated from the 1980-84 data set in this analysis; most year-long territories were fairly stable and the 2 new territories formed during the study covered few locations of solitary wolves. Radio fixes were categorized within territory cores, buffer zones, or interstices. Planimetry of these areas was conducted as follows: territory cores = territory areas minus the 2-km wide buffer zones bordering internally each territory; interstices = areas between territories plus a 2-km strip bordering externally the whole territory mosaic. The total area equalled interstices, plus buffer areas, plus territory cores. Locations outside the total area were excluded.

Nonparametric statistical tests (Siegel 1956; Sokal and Rohlf 1981) were used if the assumptions of parametric tests were violated. All tests except F-test were two-tailed, and probabilities greater than 0.05 were judged to be not significant.

RESULTS

Solitary living

Wolves which were constantly observed alone were uncommon in the study area. Out of 54 wolves tracked, 2 animals (both females) could not be associated with established packs, and 3 others dispersed shortly after their capture which casts doubt on their pack origin. One lone animal covered 2310 km² across 7 pack territories during a period of 13 months postcapture. The second covered 710 km² across 3 pack territories during the 9 months postcapture. The latter animal was located mostly within one pack territory (85% of locations, n=93), which suggests a previous area familiarity and group association (perhaps the natal pack). Movements of these 2 lone wolves can be described as "itinerant" but not with a random orientation because they regularly returned to familiar areas. In contrast to pack members, the area each lone animal covered increased with the number of locations. This observation implies that occasionally new areas were being visited.

The most frequently observed solitary wolves were pack members temporarily dissociated from their social groups during periods extending from a few days to a few months. From the contingency table analysis on the full set of winter data, I rejected the null hypothesis of independency between prey abundance and age ($G[2]=18.48$, $P<0.01$). A low prey base caused yearlings to break ties more frequently with their pack (45%

of locations in HP vs 80% in LP, $n=122$ and 61), as compared to pups (26% vs 36%, $n=242$ and 53) or adults (17% vs 26%, $n=390$ and 324). Because of this interaction, I proceeded from a 3-way analysis to a 2-way analysis (i.e., prey base and sex) within separate age classes.

Pups were observed alone in 28% of the observations (Fig. 1). The non-significant G -tests (Table 1) indicate that solitary living among pups was independent of both prey abundance ($P>0.15$), and sex of the animals ($P>0.20$). In terms of pack dissociation, pups showed a qualitative similarity to (Fig. 1), but a quantitative difference from adult wolves ($G[1]=5.82$, $P=0.02$).

Yearlings represented the most loosely associated pack members. I observed yearlings alone in 57% of winter observations (Fig. 1), a much greater frequency than adults (21%; $G[1]=84.72$, $P<0.01$), or pups (28%; $G[1]$, $P<0.01$). Both abundance of prey and sex strongly influenced the tendency of yearlings to leave their pack temporarily (Table 1). Male and female yearlings exhibited a lower pack affiliation in the low prey area. In addition, yearling females lived more solitarily than yearling males (Fig. 1). The non-significant interaction between prey abundance and sex indicates an additivity of their effects (Table 1).

Adults maintained the closest contact with their social groups (Fig. 1). Nonetheless, abundance of prey and sex significantly influenced solitary living of adults (Table 1).

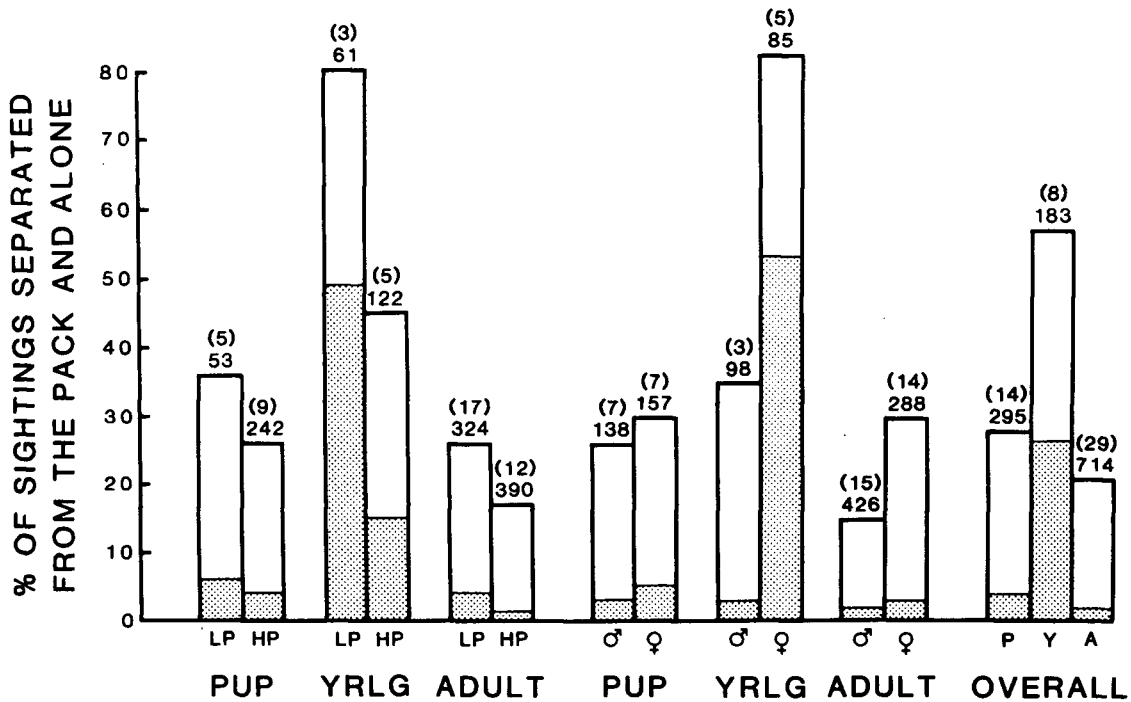


Fig. 1. Percentage of sightings when wolves were observed alone and separated from their packs in relation to prey abundance (LP or HP), age of the animals, and their sex. Number of sightings is given above the columns, and the figure in parentheses denotes the number of animals involved. The portion of sightings during extra-territorial movements is stippled.

Table 1. Summary of the contingency table analyses, within age classes, where the effects of prey base (HP or LP) and sex were related to the frequency that a wolf left temporally its pack (A), and the portion of these observations outside the pack's territory (B). The G-test values (d.f. = 1 for all) are presented, as well as their probability levels (). Observations were collected from 1 December to 30 April.

Hypothesis tested	Pup	Yearling	Adult
(A)			
Prey base	1.82 (>0.15)	21.86 (<0.01)	9.72 (<0.01)
Sex	0.52 (>0.20)	44.54 (<0.01)	22.42 (<0.01)
Interaction	1.76 (>0.15)	1.67 (>0.15)	1.50 (>0.20)
(B)			
Prey base	0.04 (>0.20)	8.30 (<0.01)	2.80 (=0.09)
Sex	0.02 (>0.20)	58.22 (<0.01)	0.22 (>0.20)
Interaction	1.80 (>0.15)	2.52 (>0.10)	0.02 (>0.20)

As with yearlings, adult females travelled alone more frequently than males. A low prey base significantly increased the frequency at which adults of both sexes temporarily left their pack. Once again, the lack of interaction between prey base and sex suggests that their effects were additive (Table 1).

As winter progressed, the frequency of pack dissociation increased in pups ($G[3]=9.47$, $P=0.03$), yearlings ($G[3]=16.7$, $P<0.01$), and adults ($G[3]=104.06$, $P<0.01$; Fig. 2).

From early May to the end of November (summer period), it was usually impossible to assess with certainty whether or not a wolf was with other pack members. From monitoring movements closely, yearlings appeared to be more independent of pack activities. In summer, adult movements converged to predictable sites such as natal dens and pup resting areas. Although some yearlings demonstrated this pattern, they definitely tended to wander more extensively than adults throughout the territory during prolonged periods, presumably dissociated from the pack, and with no apparent attempt to visit the focal activity sites of the pack.

Individual extra-territorial movements

I recorded 56 instances of wolves that individually engaged in extra-territorial movements (Fig. 3). In 9 cases, the animals did not renew ties with their packs. They represented: 4 successful dispersals where 2 animals acquired

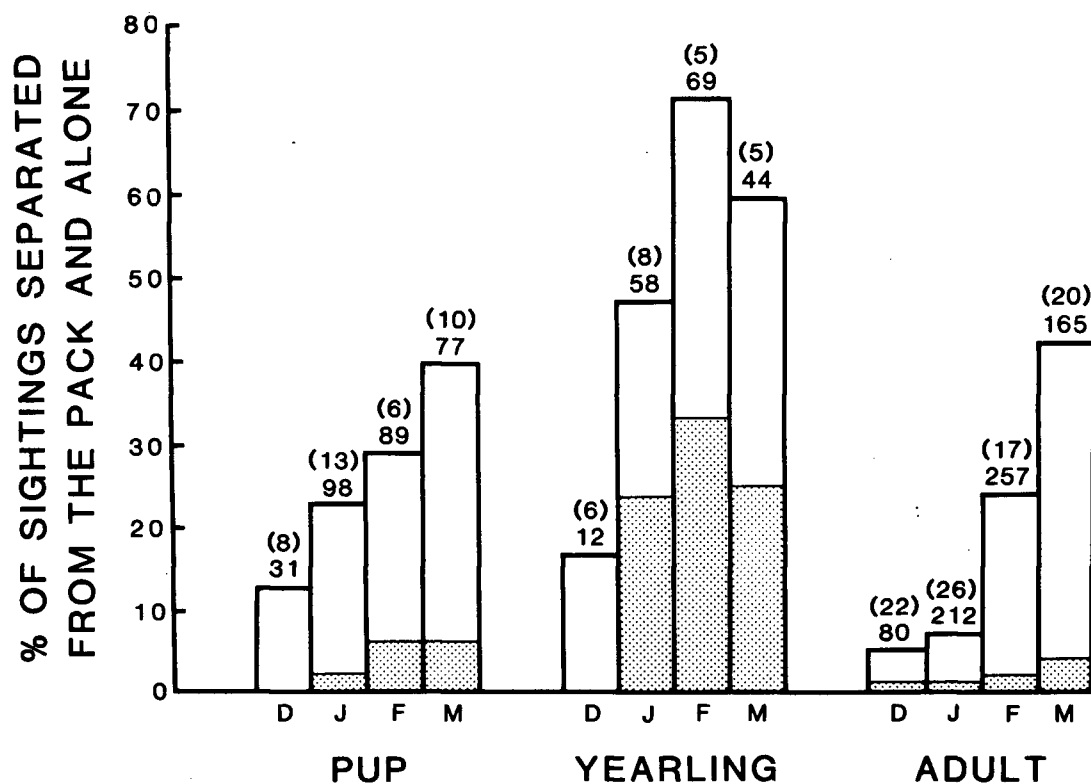


Fig. 2. December to March changes in the percentage of sightings when pup, yearling, and adult wolves were observed alone and separated from their packs. Number of sightings is given above the columns, and the figure in parentheses denotes the number of animals involved. The portion of sightings during extra-territorial movements is stippled.

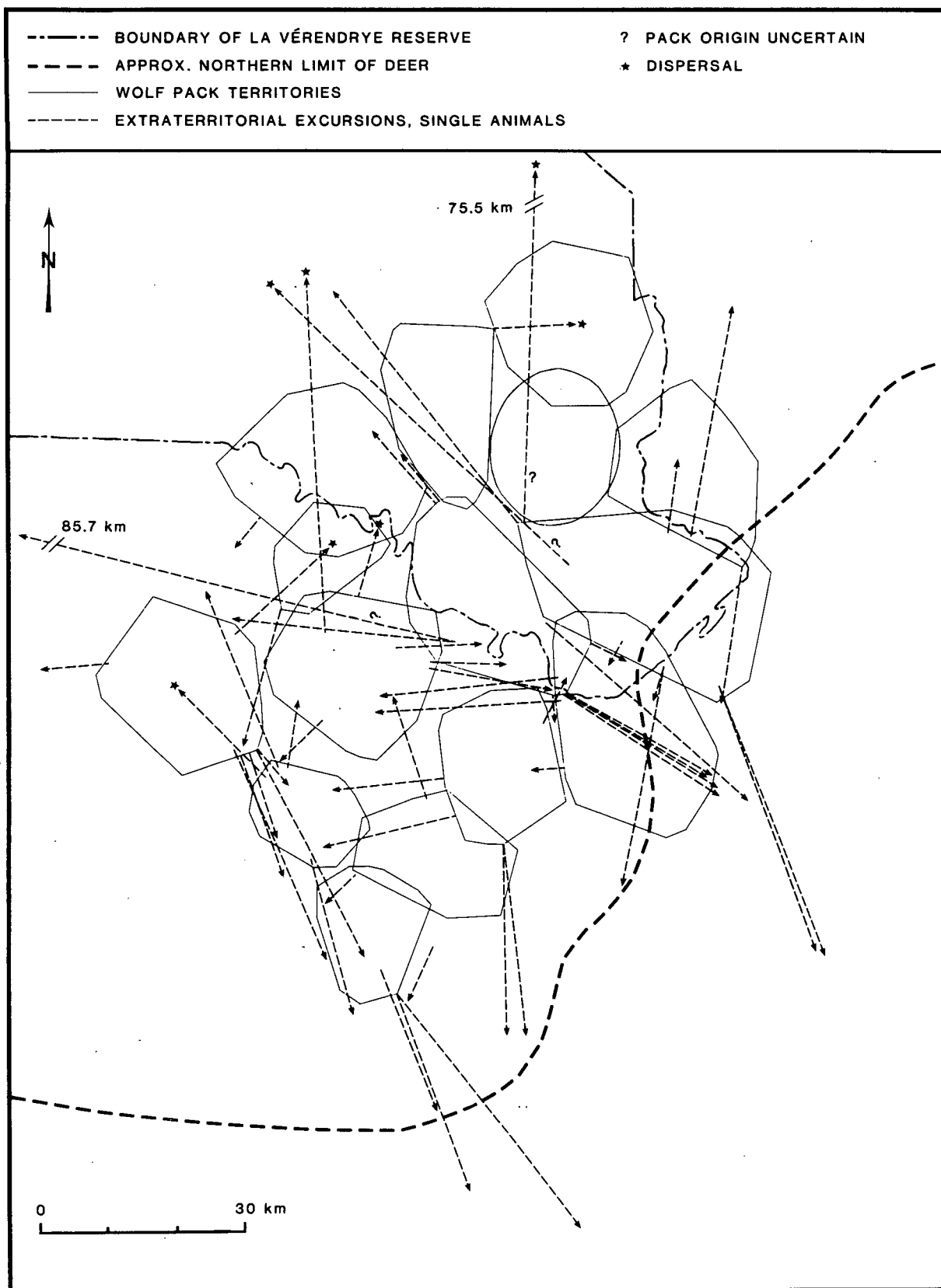


Fig. 3. The 56 extra-territorial excursions made by single wolves during the study. The excursions are presented as the minimum straight line distances.

a new associate and formed a pack nucleus, and 2 were accepted by an adjacent pack; 3 probable dispersals during which we lost all radio-contact after extensive journeying; and 2 mortalities. Dispersals involved 4 males and 3 females and occurred exclusively from mid-April to August (Fig. 4). Each wolf that dispersed definitively, initiated a minimum of 2.1 pre-dispersal trips, on average. Wolves accepted by adjacent packs were both young adult males (1 in March and 1 in May). In 1 case (March), the presumed dominant male of a trio-pack was killed (possibly by the incomer) when the change occurred.

Excursion frequency of pups (9), yearlings (21), and adults (26), differed significantly from the expected frequencies calculated from the radio-tracking times (101, 86, and 317 months respectively; $G[2]=13.2$, $P<0.01$). Pups and adults initiated fewer solo excursions than expected (1.1 and 1.0 per year respectively), whereas yearlings were much more prone to foray outside the pack's territory (3.0 excursions per year).

Thirty-eight of the 56 excursions occurred during the winter period, but the seasonal patterns differed between age classes (Fig. 4). Pups did not venture outside the pack's territory alone before mid-February. Yearling excursions were restricted primarily to the winter period, whereas adult forays showed no obvious seasonal pattern. At least 8 of the 15 adult excursions during the summer period involved young non-reproductive adults (24 to 30 months, from known-age

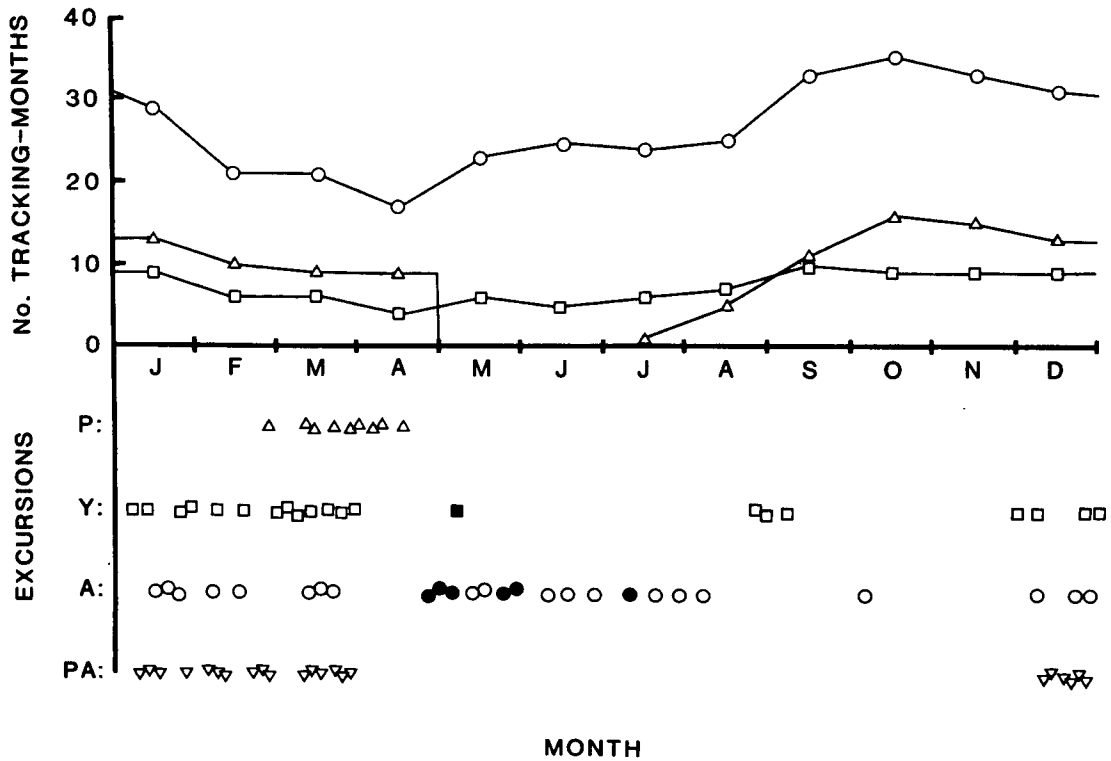


Fig. 4. Chronological distributions of the initiation of extra-territorial excursions made by single pups (P), single yearlings (Y), single adults (A), and packs (PA). The close symbols denote the excursions which resulted in an actual or assumed definitive dispersal. A measure of radio-tracking time (number of animal-months with operating transmitters) is presented to facilitate interpretation.

animals). In summer, I did not observe known or presumed reproductive adults initiate extra-territorial movements. Also, I never had evidence that a pack engaged in extra-territorial movements in summer (i.e., when more than 1 wolf were marked). Therefore, I assumed that all movements outside the territory implicated single wolf.

The duration of excursions averaged $9.1 \pm (\text{SE})2.6$ days for pups, 13.3 ± 3.2 for yearlings, and 10.3 ± 2.1 for adults. No difference among age classes could be detected (one-way ANOVA, $F[2,40]=0.54$, $P>0.20$). Likewise, the minimum straight line distance of excursions did not differ among age classes (one-way ANOVA, $F[2,53]=0.30$, $P>0.20$), and averaged $22.2 \pm (\text{SE})5.3$ km for pups, 21.7 ± 2.6 for yearlings, and 25.5 ± 4.2 for adults. These data indicate that the higher tendency of yearlings to be outside the pack's territory (Fig. 1) was caused mainly by the higher rate at which they initiated excursions as opposed to the duration or length of these excursions.

To examine the possible effects of prey abundance and sex upon extra-territorial movements, I conducted contingency table analyses on the age-specific winter observations (Table 1). Neither prey abundance nor sex influenced extra-territorial movements of pups ($P>0.20$). Both factors affected the tendency of yearlings to leave the pack's territory ($P<0.01$); these effects were not interactive ($P>0.10$). In adults, only prey abundance was potentially effective

($P=0.09$). Among age classes, the difference was highly significant ($G[2]=45.8$, $P<0.01$); pups and adults had comparable foraging tendencies, but yearlings were more inclined to travel outside the pack's territory (Fig. 1).

Locations of lone wolves and pack members during extra-territorial movements ($n=359$) were analysed in relation to pack territories (depicted in Fig. 3; the hypothesis being that solitary wolves would tend to avoid territory cores and to use preferentially the edges of the territories. I observed solo foraging pack members less frequently than expected (i.e., assuming homogeneous distribution) within territory cores of neighbouring packs, and more frequently within the 2-km wide buffer zones bordering these territories (Table 2). However, they used the interstices between territories less frequently (Table 2), even though these areas presumably represented the safest places in which to avoid pack interactions. Known lone wolves showed a different pattern; they used territory cores intensively, and interstices less than expected (Table 2). Altogether, the analysis does not reveal a progressive increase of use from territory cores to buffer zones, and to interstices.

Pack extra-territorial movements

I observed 23 instances of packs engaged in extra-territorial movements (Fig. 5). These excursions were observed exclusively from 1 December to 30 March, and many of them (13)

Table 2. Location frequencies of pack members during solo extra-territorial excursions and of lone wolves, are reported for the territory cores, the 2-km wide buffer zones, and the interstices (see methods). Also presented are the χ^2 -tests of homogeneity, and their probability level (d.f.=2 for all).

	Territory cores		Buffer zones		Interstices		χ^2	P
	% area	%fixes	%area	%fixes	%area	%fixes		
Pack members	56	33(57)	24	48(84)	20	19(33)	59.4	<0.01
Lone Wolves	56	80(148)	24	16(29)	20	4(8)	47.0	<0.01
Total	56	57(205)	24	32(113)	20	11(41)	21.6	<0.01

() = sample size

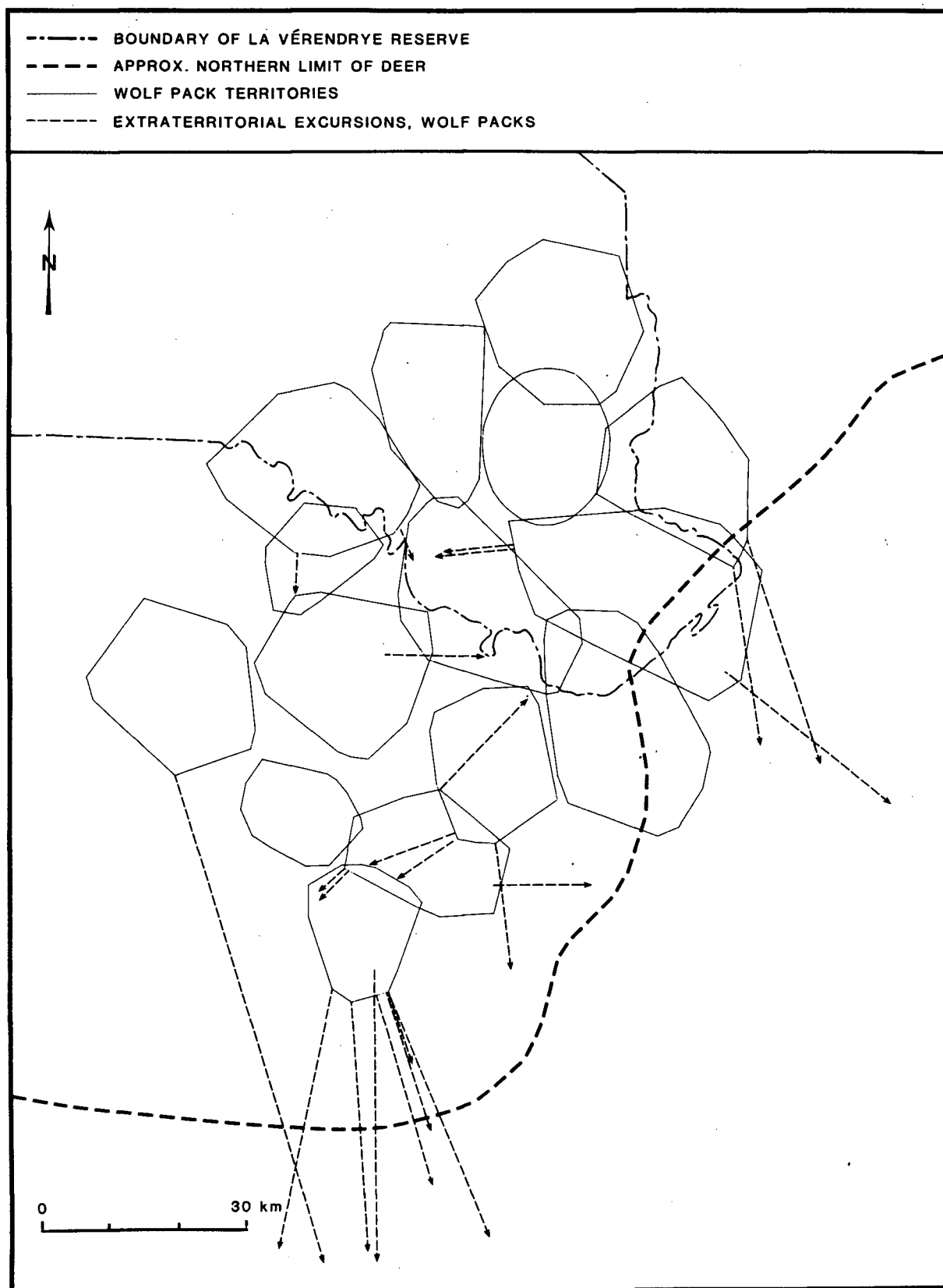


Fig. 5. The 23 extra-territorial excursions made by wolf packs during the study. Excursions are presented as the minimum straight line distances.

were destined to deer wintering areas. A minimum of 8 deer were killed by wolves during these excursions but likely more were victims. Given the difficulty of detecting deer carcasses from aerial tracking, the exact number could not be ascertained. As depicted by Fig. 5, packs close to deer distribution were more inclined to make excursions from their territories and to exploit deer.

Excursion frequency was higher for packs associated with a low prey abundance ($n=18$, 60 tracking-months of packs during winter), as compared to packs in the high prey base area ($n=5$, 46 tracking-months; $\chi^2[1]=4.39$, $P=0.04$). The minimum straight line distance of excursions was also greater in LP (average=26.1 km, range=5.0 to 75.7) than in HP (average=12.0 km, range=5.5 to 30.7; Mann-Whitney U -test[18,5]=72, $P=0.03$). The duration of excursions showed the same trend between areas (LP average=16.5 days, range=2 to 84; HP average=7.0 days, range=2 to 25), but the difference was not strongly expressed (Mann-Whitney U -test[13,5]=47, $P=0.10$).

DISCUSSION

Solitary living, extra-territorial movements, and dispersal

To many people "dispersal" connotes a "movement of an individual from its natal site and out of the home range of its parent(s) to another site at which it breeds, or at least attempts to pair with a conspecific of the opposite sex for

purpose of breeding" (Bekoff 1977:715). The first conclusion to be drawn from the present wolf study is that dispersal is not an unique "one decision - one trip" event. Dispersal appeared to be a dynamic and gradual process, with a wolf breaking ties with its pack over a protracted period of a few months to a few years beginning as early as 10 months of age. Recently in central Alaska, Van Ballenberghe (1983) reported that dispersing wolves showed a common pattern of one or more preliminary extra-territorial trips. In this study, I observed that yearling wolves initiated on average 3 extra-territorial forays per year, although most dispersed permanently at an adult age (6 out of 7 dispersals). Even among adults, of which only a fraction were non-breeders and therefore prone to disperse, an average frequency of 1 solo excursion per year was recorded. From these observations, I addressed the question of what had constituted the incentive for such extra-territorial forays.

Age of the animals was identified as a predominant factor influencing solitary living and exterritorial movements. Yearlings are animals reaching puberty, and were clearly the animals most likely to travel solitarily and to spend prolonged periods out of their natal territories. Many yearlings and young non-reproductive adults acted as loosely-associated pack members, apparently with a minimal role in the pack. It has been suggested that the assistance of yearlings and other auxiliaries in providing food for wolf pups does not

influence their survival (Harrington and Mech 1982; Harrington et al. 1983; Fig. 13 in Peterson et al. 1984). Thus, many yearlings and young non-reproductive adults could be typified biologically as "floater animals", but with the peculiarity that they keep a minimal association with their packs; possibly, they use other packmates selfishly as an aid in surviving and ultimately in achieving breeder status. It is in the parents' interest to facilitate the survival and breeding probability of these highly-valued offspring.

Concomitant with the effect of age, low prey abundance increased pack dissociation and extra-territorial movements. Without access to sufficient prey during an extended period, a subordinate wolf may either be actively evicted from the pack, or it may voluntarily forage alone (Zimen 1976, 1982). Both yearlings and adults had a greater tendency to live solitarily and to make excursions in the low prey area (Table 1). During winter, wolf packs used an average of 6.2 moose per 100 days in HP but only 3.2 in LP (Messier and Crête in press). In the low prey area, packs were experiencing periods of food scarcity which undoubtedly encouraged pack dissociation. Under these circumstances, forays cannot be ascribed to a specific dispersal strategy, but rather as an immediate necessity to survive through a temporary resource failure. However, the information acquired during these excursions may be advantageous subsequently (e.g., territory vacancy, prey distribution including the locations of deer wintering areas).

The greater tendency of yearling females and adult females to dissociate from the pack, and to foray outside the territory (yearlings only), appears largely attributable to the relatively low availability of moose carcasses to the packs. Under nutritional stress, females are more often subordinate and harassed by other pack members than are males (Zimen 1976, 1982). These aggressive interactions may result in weak pack bonds or even in a temporary pack eviction. Not enough is known about wolf dispersal strategy to suggest that females are more inclined than males to depart voluntarily from the pack. However, a sex-specific difference in dispersal strategy is not excluded (Zimen 1982).

Extra-territorial movements can often be interpreted as pre-dispersal forays during which territory vacancy can be assessed. The tendency of wolves to return to their territory and to rejoin their pack reflects their failure to find quickly a receptive, alien wolf and/or a suitable vacant area (Van Ballenberghe 1983). Conceivably, a wolf could use its natal social unit (and area) as a base from which to find a receptive pack or to form a nucleus of a new pack during its exploratory excursions (see Messier and Barrette 1982). If habitat saturation is high, dispersing wolves may have to travel great distances before they can settle. This process may necessitate many pre-dispersal trips. The results of this study appear to be in conflict with this view. More extra-territorial excursions were observed in LP than in HP area

even though vacant areas were more available in LP (Messier in press). However, the low prey abundance in LP most likely prompted subordinate animals to initiate excursions more frequently. This poor prey base would also tend to make any vacant areas unfavourable for reproduction. These two factors have likely confounded the results. Of interest is the fact that Fritts and Mech (1981) rarely observed pre-dispersal forays when they studied a newly-protected wolf population in Minnesota. The Minnesota population was, however, not saturated and wolves there were experiencing an ample prey base.

The higher social stress within packs prior to and during the breeding season (approxmatively from 1 February to 15 March) likely explains the increasing tendency of some individuals to leave their pack during this period. Studies in captivity showed that reproductive wolves exert a greater dominance over other pack members during this period (Rabb et al. 1967; Zimen 1982). Recently, Peterson et al. (1984) reported that extra-territorial movements were undertaken more commonly by subordinate wolves during the breeding season. An alternative explanation based on a higher food stress at the end of the winter is less probable. I have an indication of a stable, but low food availability throughout the winter. Pack excursions, which usually signify a shortage of food (Mech 1977; this study), were evenly distributed from December to March (Fig. 4).

Solitary animals and pack spatial distribution

Often, it has been postulated that locations of lone wolves were primarily in areas less utilized by packs (see Fritts and Mech 1981: 44). However, published evidence supported by quantitative data is not yet available to my knowledge. The observations reported here, based on 25 different animals, did not reveal that interstices between territories were more frequently used by solitary animals. The habitat within interstices was not noticeably different from that of surrounding areas. Dissociated pack members appeared to utilize the periphery of neighbouring territories more frequently. However, this trend was induced largely by a single animal which undertook 4 prolonged excursions to a particular buffer zone (38 observations) where butcher offal was available (a minimum of 9 beef gut piles; see the 4 parallel arrows in the east side of Fig. 4). If this animal is excepted, the analysis reveals no trend. The 2 known lone wolves used territory cores more frequently. I conclude that wolves did not avoid territory cores. I do not suggest, however, that solitary wolves did not avoid contact with alien packs, but it appears that this temporal segregation did not produce a spatial segregation.

Pack extra-territorial movements

Four packs undertook extensive winter movements apparently to exploit deer. In one case (the southernmost

pack), the wolves had been repeating each year what appears to be a traditional pattern of movements at the onset of winter. The low moose density in the study area, and the relative ease of capturing deer in their wintering areas, probably encouraged such pack excursions. Other pack excursions were shorter with no apparent premeditated destination. Mech (1977) argued that malnutrition incites packs to trespass across neighbouring territories. My data conform to Mech's (1977) interpretation. Packs associated with a low prey abundance initiated more excursions than packs in HP. Moreover, the excursions of LP packs were substantially longer. These observations also suggest that wolves in low prey areas have a weaker territorial habit in winter than wolves with ample prey. Such pattern of space use resembles the territorial instability of wolves relying on a spatially changeable prey base (Kuyt 1972; Stephenson and James 1982).

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