SUMMER FOOD HABITS OF GRAY WOLVES IN THE BOREAL FOREST OF THE LAC JACQUES-CARTIER HIGHLANDS, QUÉBEC

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ABSTRACT: As part of a larger study on the ecology of gray wolves (Canis lupus) of the Lac Jacques-Cartier highlands, Québec, the 1996-1997 summer diet of two wolf packs was determined by examining undigested remains in 1,621 scats (Malbaie pack: n = 1,371; Grands-Jardins pack: n = 250). Concern about the fate of a small reintroduced woodland caribou herd stimulated this study. Log-linear analysis performed on the percent volume of prey in scats revealed significant diet variation between packs and years. Corrections for prey digestibility were computed to estimate the biomass and relative numbers of prey eaten. The Malbaie pack consumed more moose (Alces alces) than Grands-Jardins in both years (Malbaie: 95.9-97.3 % total biomass; Grands-Jardins: 65.2-67.9 %). The Grands-Jardins pack consumed more beaver (Castor canadensis) than the Malbaie pack in both years (Malbaie: 1.5-1.9 %; Grands-Jardins: 13.3-33.2 %). In 1997, consumption of caribou (Rangifer tarandus) increased significantly, especially in the Grands-Jardins pack (1996: 1.1 %; 1997: 17.4 %). We suggest that the functional response of wolves of the Lac Jacques-Cartier highlands in summer (i.e., the consumption of different prey in relation to their relative availability) is characteristic of a type III curve which could explain the variations observed in food habits.

ALCES VOL. 37 (1): 1-12 (2001)

Key words: Canis lupus, food habits, functional response, gray wolf, Québec

In North America, the gray wolf (Canis lupus) is a specialist predator preying almost exclusively on ungulates and beavers (Mech 1970, Pimlott 1974, Carbyn 1987). Scat analyses have been widely used to study the predatory behavior of elusive and wide-ranging carnivore species such as wolves (Murie 1944, Thompson 1952, Mech 1966, Pimlott et al. 1969, Van Ballenberghe et al. 1975, Voigt et al. 1976). Regression equations were derived later to correct for differences in prey digestibility (Floyd et al. 1978, Weaver 1993) thus producing better estimates of the diet (Fuller and Keith 1980, Scott and Shackleton 1980, Crête et al. 1981, Fritts and Mech 1981, Messier and Crête 1985, Ballard et al. 1987, Potvin et al. 1988, Fuller 1989, Forbes and Theberge 1996, Spaulding et al. 1998). Selection of food items eaten by wolves are generally

discussed in terms of vulnerability versus availability of prey. Another hypothesis proposes kin selection to explain variations in relation to pack size and food acquisition per wolf (Schmidt and Mech 1997).

The present study is part of a larger study on the ecology of an exploited wolf population in the boreal forest of the Lac Jacques-Cartier highlands, Québec, Canada (Jolicoeur 1998). In a portion of these highlands covered by boreal forest, wolves, moose, and a herd of woodland caribou reintroduced in the late 1960s have evolved at a low density. With the recent increase in logging operations around the study area, this equilibrium may change to the benefit of moose and subsequently the wolf population. If prey are selected in relation to their vulnerability instead of their availability, this could affect negatively a more vulnerable

prey such as the caribou. We have thus estimated the contribution of each prey present in the study area to the total biomass eaten and the relative number of each prey consumed by the two wolf packs evolving in this low density moose-caribou ecosystem and discuss it in relation to different prey availability indices.

METHODS

Study Area

The study area covers approximately 2,500 km² and is located 40 km north of Québec City in the Lac Jacques-Cartier highlands (Fig. 1). The region encompasses more than 8,000 km² of highlands ranging in altitude from 800 to 1,100 m (Li et al. 1997). It is bordered on the east by the St. Lawrence River, on the south by the St. Lawrence River, on the south by the St. Lawrence River.

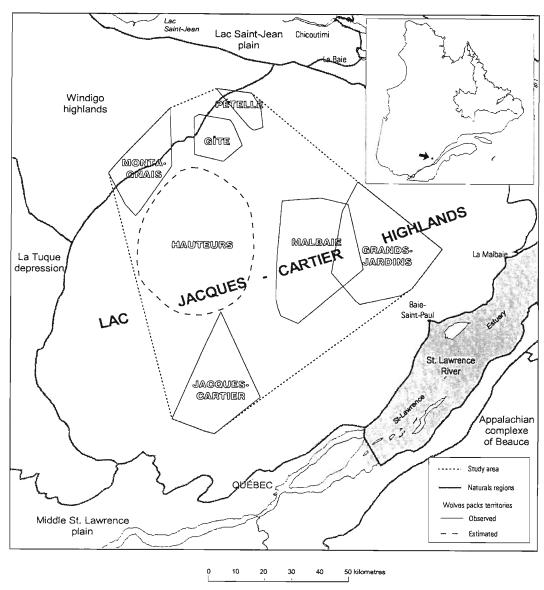


Fig. 1. Location of the study area in the Lac Jacques-Cartier highlands and home range of wolf packs monitored during the course of the study. Food habit studies were conducted on the Malbaie and Grands-Jardins packs.



rence plain, and to the north by the Saguenay River fjord. To the west, the highlands gradually slope downward to an altitude of 400 m. Two conservation parks are present in the highlands: the Jacques-Cartier Park (670 km²) and the Grands-Jardins Park (310 km²). Most of the remaining area is included in the Laurentides Wildlife Reserve (7,461 km²). Vegetation stands are primarily fir (Abies balsamea) mixed with paper birch (Betula papyrifera) and spruce (Picea spp.) at higher elevation. Logging operations have been intensified during the past 20 years. The climate is harsh with mean temperatures varying from -15°C in January to +15°C in July and annual snow fall averaging 400 to 700 cm.

Since 1990, in the central portion of the highlands, wolf density has been kept low by trapping at approximately 0.5 wolves/ 100 km² (Jolicoeur 1998). During the course of the wolf study (1995-1998), a special protection accorded to 2 wolf packs has led to the increase of the wolf density in the study area to 0.74 wolves/100 km² (Jolicoeur 1998). In 1996, 13 wolves composed the Malbaie pack (2 adults, 4 juveniles, and 7 pups) and the Grands-Jardins pack had 7 wolves (2 adults, 1 juvenile, and 5 pups). By 1997, the Malbaie pack had grown to 15 individuals (5 adults, 3 juveniles, and 7 pups) while the Grands-Jardins pack reached 13 (2 adults, 4 juveniles, and 7 pups).

Other large mammals found in the study area are moose (0.8/10 km²; St-Onge et al. 1995), woodland caribou (Rangifer tarandus; 0.33/10 km²; R. Courtois, personal communication) and black bear (Ursus americanus; 2.2/10 km²; Jolicoeur et al. 1993). The density of beaver (Castor canadensis) colonies was estimated at 0.88/10 km² (C. Fortin, Ministère du Loisir, de la Chasse et de la Pêche du Québec, unpublished data). Relative moose and beaver availability among packs have been estimated with local availability indices ex-

tracted from the Société de la faune et des parcs du Québec regional database. The moose local availability index is based on hunting effort of parties of 4 hunters in the controlled hunting zones of the Laurentides Wildlife Reserve encompassed by the Malbaie and Grands-Jardins packs territories (Malbaie: 8.9 hunting days/party of 4 hunters/harvested moose; Grands-Jardins: 4.1 hunting days/party of 4 hunters/harvested moose). The beaver local availability index is based on observations of beaver colonies reported by trappers on registered trap lines (Malbaie: 0.2/10 km²; Grands-Jardins: 0.4/10 km²).

Scat Analysis

Scats were collected in 1996-1997 from May to October by patrolling secondary forest roads. A total of 1,371 samples were gathered within the Malbaie pack territory and 250 in the Grands-Jardins pack territory.

All samples were oven-dried at 70°C for 24 hours and rinsed with water through a 0.5 mm sieve. Macro and microscopic examination of the whole undigested residues of bones, teeth, and hair allowed the identification of prey species (Adorjan and Kolenosky 1969, Moore et al. 1974). We examined the microscopic structure of hair medulla to discriminate between Cervidae and other mammalian hairs, and the microscopic pattern of Cervidae hair scales to distinguish between caribou and moose, as well as between adults and calves (Korschgen 1980). Results were expressed in terms of frequency of occurrence and percent volume in scats. Percent volume occupied by fragments of each food item in a scat was estimated visually to the nearest 5%.

Statistical Analysis

Reynolds and Aebisher's (1991) loglinear model analyses have been adapted to compare the summer diet of the 2 wolf



packs monitored during the 2 years of the study (SAS Institute 1988). Percent volume per prey (Σ relative volume of a prey per scat/total number of scats) served as the basis to calculate the frequency of occurrence in the log-linear models (Messier and Crête 1985). The absence of several prey species in some scats precluded compositional analysis of food habits based on exact percentages (Reynolds and Aebischer 1991). Miscellaneous prey (black bear; snowshoe hare, Lepus americanus; porcupine, Erethizon dorsatum; woodchuck, Marmota monax; red fox, Vulpes vulpes; striped skunk, Mephitis mephitis; lynx, Lynx canadensis, and grass) were dropped from the analysis to reduce interdependence between prey species (i.e., Σ percent volume per prey = 100%). A general model was constructed with all variables (pack, year, and prey item) and their interactions. Interaction terms were deleted one at a time from the model, from higher to lower levels, until only significant interaction remained (Christensen 1990). At each step, the reduced model was compared with the previous one with a likelihood ratio χ^2 test (G²; SAS Institute 1988).

Prey Consumption

The volume of food items was transformed to biomass and relative number of prey eaten (Floyd et al. 1978). We used the refined equation proposed by Weaver (1993) to avoid overestimating large cervids. Results are presented for the whole summer, thus the proportion of total biomass eaten is an average of the results obtained for the biological period of den attendance (1 May-15 July) and pup initiation (15 July-1 October) while relative number of prey consumed is summed for these 2 periods.

RESULTS

Food Habits

The most parsimonious model $(G^2_{(1)} =$

0.15, P = 0.70) included interactions between prey items and pack ($G_{(7)}^2 = 172.51$, P < 0.001), as well as prey items and year ($G_{(7)}^2 = 48.08$, P < 0.001, Table 1).

Adult moose, the main prey consumed by the Malbaie wolf pack in 1996 and 1997 (Table 2), were less important in the Grands-Jardins pack diet (P < 0.01, Table 1) in both years. Beaver formed the bulk of the diet for the Grands-Jardins pack in both years which was significantly more than for the Malbaie pack (P = 0.01, Table 1). Moose calves contributed little to the diet of either pack in 1996, although they were slightly more important for the Grands-Jardins pack (2.5% vs. 1.8% for Malbaie, P = 0.03, Table1). In 1997, they were more important for the Malbaie pack (P = 0.02, Table 1). Caribou consumption was low in both packs in 1996. However, this prey became more important in 1997, especially for the Grands-Jardins pack (17.8% vs 1.3% volume in Malbaie pack, P < 0.01, Table 1). Caribou calves contributed little to the total diet and

Table 1. Estimation of standard parameters of the log-linear model which best explains variations in food habits of wolves of the Lac Jacques-Cartier highlands according to packs and years of study (pack x prey: $G^2_{(7)} = 172.51$, P < 0.001; year x prey: $G^2_{(7)} = 48.08$, P < 0.001).

Prey	Pa	ck	Y	ear
	Z	P	Z	P
Moose	13.15	0.00	0.70	0.40
Moose calf	5.01	0.03	5.76	0.02
Caribou	4.02	0.05	17.49	0.00
Caribou calf	1.07	0.30	0.80	0.37
Beaver	7.53	0.01	0.00	0.98
Wildberry	2.31	0.13	3.85	0.05
Miscellaneous	0.15	0.70	0.19	0.66

¹Overall goodness-of-fit: $G_{(1)}^2 = 0.15, P = 0.70$.



the volume consumed did not differ between packs (P = 0.30, Table 1) and years (P = 0.37, Table 1).

Wildberries (mainly blueberry, *Vaccinium angustifolium*) were an important part of the diet of both packs in 1996 (P = 0.13, Table 1) but dropped significantly in 1997 (P = 0.05, Table 1).

Prey Consumption

Moose (primarily adults) constituted more than 95% of the total animal biomass ingested in both years by the Malbaie pack (Table 2). In the summer of 1996, it represented a relative number of 8.2 adult moose and < 1 calf for the pack. In 1997, with 2 more wolves in the pack, these estimates rose to 9.5 and 2.6, respectively. Although beaver formed the bulk of the volume in the Grands-Jardins pack, it only contributed 33.2% of the total biomass eaten in 1996 and 13.3% in 1997. On the other hand, beaver were the most frequent individual prey harvested by the Grands-Jardins pack. When expressed in terms of total biomass ingested, moose were also an important food source for the Grands-Jardins pack. With 5 more wolves, the relative number of adult moose eaten by this pack rose from 2.7 in 1996 to 5.3 in 1997, and for calves from 0.7 to 1.6. The proportion of large prey eaten by the Grands-Jardins pack (total biomass) was even higher in 1997, primarily due to predation on caribou. Caribou consumption was also slightly higher in 1997 for the Malbaie pack although the relative number of estimated prey did not reach a complete adult or calf.

Other prey rarely exceeded 1% of the total animal biomass consumed, except for black bear in the Malbaie pack (1996). However, when relating the proportion of black bear content in scats to the relative number eaten, it never exceeded 0.1 individuals.

DISCUSSION

Mech (1970) reviewed wolf food habit studies from the 1940s to the 1960s and reported that animals the size of beaver or larger composed 59 - 96% of the food items, expressed as percent of occurrence in scats. In Table 3 we report moose, caribou, deer, and beaver consumption from several gray wolf food habit studies that corrected for prey digestibility following the equation developed by Floyd et al. (1978) and Weaver (1993); those species constituted 88 - 100% of the total biomass consumed. During winter, when 2 ungulate species are present, especially in the deer-moose system (beaver are usually not available then), the smaller, more vulnerable, prey normally are predominant in wolf diets (Pimlott et al. 1969, Van Ballenberghe et al. 1975, Voigt et al. 1976, Crête et al. 1981, Fritts and Mech 1981, Messier and Crête 1985, Potvin et al. 1988, Forbes and Theberge 1996) even when their availability is low (type II functional response; Potvin et al. 1988, Forbes and Theberge 1996). In summer, wolves appear to adjust their prey intake to the availability of ungulates and beaver (type III functional response; Voigt et al. 1976, Potvin et al. 1988, Forbes and Theberge 1996). In a caribou-moose system, Spaulding et al. (1998) suggest that vulnerability of the prey species may also explain differences in summer diet of wolf packs in Alaska.

The 2 packs monitored in this study, although occupying partly overlapping territories, presented significant differences in their summer diet. Yearly variations of the summer diet were also observed in both packs. Data on prey availability in each pack territory are not powerful enough to explain yearly variations but may give some insight into differences observed among packs.

Moose contributed a large proportion of the biomass of food ingested in summer by



Table 2. 1996 and 1997 summer diet of the Lac Jacques-Cartier highlands gray wolves averaged over den attendance (01 June - 15 July) and pup initiation (15 July - 15 September) periods (relative number of prey eaten [N] summed over the 2 periods).

				Malbaie pack (n=505)	n=505)			rands-Jardin	Grands-Jardins pack (n=118)	
Year	Prey	kg/scat1	% volume	% occurrence	%biomass²	N3.4	% volume %	% volume % occurrence	%biomass²	N3,4
9661	Moose ⁵	3.24	70.7	90.1	95.4	8.2	21.8	26.3	63.4	2.7
	Calfmoose ⁵	$0.68(0.92)^6$	1.8	1.8	6.0	0.5	2.5	2.5	1.8	0.7
	Caribou7	1.60	0.3	0.4	0.4	<0.1	8.0	8.0	1.1	0.1
	Calfcaribou7	7 0.54	0.7	8.0	0.2	0.4	0	0	0	0
	Beaver ⁷	0.54	6.3	8.7	1.5	3.5	57.7	72.9	33.2	58.8
	Black bear8	1.16	1.6	1.8	1.5	0.3	0	0	0	0
	Snowshoe hare	are ⁷ 0.45	0.5	8.0	0.2	1.7	0	0	0	0
	Red fox9	0.47	0.2	0.2	<0.1	0.3	0	0	0	0
	$Lynx^{10}$	0.52	0	0	0	0	8.0	8.0	0.2	0.5
	Grass			4.2	15.4		6.0	4.2		
	Wildberry			13.7	32.3		15.5	29.7		
				Malbaie pack $(n=866)$	(998= <i>u</i>			Grands-Jardi	Grands-Jardins pack $(n=132)$	2)
Year	Prey	kg/scat1	% volume	% occurrence	%biomass²	N11,12	% volume %	% volume % occurrence	%biomass²	N ^{11,12}
1997	Moose ⁵	3.24	69.1	80.2	92.6	9.5	29.9	34.8	65.4	5.3
	Calf moose ⁵	$0.68(0.92)^{6}$	10.4	12.0	3.3	2.6	4.6	4.6	2.5	1.6
	Caribou7		1.3	1.5	1.7	0.3	17.8	21.2	17.3	4.0
	Calfcaribou7		0.1	0.1	<0.1	0.1	1.7	2.3	9.0	1.4
	Beaver ⁷	0.54	6.5	7.7	1.9	4.8	37.6	41.7	13.3	32.5
	Black bear8	1.16	0.2	0.2	0	<0.1	0	0	0	0
	Snowshoe hare	_	9.0	8.0	0.1	2.5	1.5	3.8	0.4	7.5
	Striped skunk ¹⁰	k ¹⁰ 0.45	0.3	0.3	0.1	1.4	0	0	0	0
	Porcupine ¹⁰	0.49	0.7	6.0	0.2	8.0	2	2	0	3
	Woodchuck10		0	0	0	0	0.4	8.0	0.2	1.1
	Grass			4.2	14.6		2.3	7.6		
	Wildberry			9.9	14.4		2.9	9.01		

Derived from Weaver's (1993) equation: Y = 0.439 + 0.008X

Derived for each prey species by averaging over den attendance and pup initiation periods the results of the following formula: kg/scat * %volume

/ total kg of all species eaten.

For den attendance (1996), derived by equation: spring wolf population (Malbaie: 6, Grands-Jardins: 3) * consumption rate (3.3 kg/wolf/day; Messier For pup initiation (1996), derived by equation: summer wolfpopulation (Malbaie: 13, Grands-Jardins: 8) * consumption rate (2.6 kg/wolf/day; Messier and Crête 1985) * 45-day period * % biomass / weight of individual prey species.

⁵Assumed weight: adult moose 350 kg, newborn calf moose 30 kg, grown calf moose 60 kg (Messier and Crête 1985). and Crête 1985) * 61-day period * % biomass / weight of individual prey species.

skg/scat for grown calf moose.

'Assumed weight: adult caribou 145 kg, calf caribou 12.1 kg, beaver 12.1 kg, snowshoe hare 1.8 kg (Ballard et al. 1987).

⁸Assumed weight: black bear 90 kg (H. Jolicoeur, unpublished data).

⁹Assumed weight: red fox 3.9 kg (M. Crête, unpublished data).

¹⁰Assumed weight: 1ynx 9.6 kg, striped skunk 1.7 kg, porcupine 6.4 kg, woodchuck 2.5 kg (Banfield 1987).

"For den attendance (1997), derived by equation: spring wolf population (Malbaie: 8, Grands-Jardins: 6) * consumption rate (3.3 kg/wolf/day; Messier and Crête 1985) * 45-day period * % biomass / weight of individual prey species.

¹²For pup initiation (1997), derived by equation: summer wolf population (Malbaie: 15, Grands-Jardins: 13) * consumption rate (2.6 kg/wolf/day; Messier and Crête 1985) * 61-day period * % biomass / weight of individual prey species.

wolves in the study area. The important use of moose, especially adults, by the Malbaie pack exceeded results reported elsewhere (Table 3) while the biomass of moose eaten by the Grands-Jardins pack is included in the range of results reported from studies where 2 ungulate species are sympatric (Scott and Shackleton 1980, Potvin et al. 1988, Spaulding et al. 1988, Forbes and Theberge 1996). On the other hand, caribou consumption was relatively low in the Lac Jacques-Cartier highlands during summer compared to other studies where this prey is reported (Table 3). Where caribou are scarce relative to moose, wolves may functionally not seek this species as prey, as predicted by the type III functional response curve. The curve predicts that the presence of a vulnerable prey at low density may preclude active hunting of this prey, which implies adjustment of search images, hunting area, and hunting techniques (Carbyn 1987).

In this context, it may appear counterintuitive that the local availability index for the Malbaie pack (8.9 huntingdays/harvested moose) is twice as high as in the Grands-Jardins (4.1 hunting-days/ harvested moose) suggesting lower absolute moose availability in the former. However, the moose availability in the Malbaie pack territory may still have exceeded the level below which it is no longer optimal to maintain an active search strategy for this prey. We suggest that the prey species availability hypothesis can explain the importance of moose in the summer diet of both packs. Another explanation refers to the kin selection hypothesis (Schmidt and Mech 1997). According to this hypothesis, the inclusive fitness of a pair could be raised by sharing with their offspring the surplus of kills resulting from pair predation on large mammals. Until they gain physical maturity and sufficient experience, the young wolves could obtain more food, as well as experi-



ence, by remaining with their parents. By doing so, parents could invest in higher post-dispersal survival probabilities for their off-spring, especially at low prey densities. Higher complexity of the pack structure thus induces higher requirements, which could explain why the Malbaie pack consumed more adult moose. This hypothesis could also explain part of the variation observed in 1997 when beaver consumption tended to decrease in the Grands-Jardins pack while caribou became more important in the diet in parallel with the growth of the pack from 7 to 13 wolves.

Young ungulates are often reported to be selected by wolves in summer (Pimlott et al. 1969, Van Ballenberghe et al. 1975, Voigt et al. 1976, Fritts and Mech 1981, Messier and Crête 1985). Both the Malbaie and Grands-Jardins packs had a relatively low proportion of moose and caribou calves in their diet which is not in agreement with results from other studies. As pointed out by Potvin et al. (1988) from elsewhere in Québec, the low incidence of young cervids in the summer diet could be attributed to the low availability of these prey. In the higher elevation of the Lac Jacques-Cartier highlands, the productivity of both moose (39 calves/100 females in winter; St-Onge et al. 1995) and caribou populations (32 calves/ 100 females in winter; Banville 1996) is considered to be low (Courtois et al. 1994, Courtois and Lamontagne 1999).

Forbes and Theberge (1996) suggested that beaver can be an important secondary prey item when ungulates are not abundant. The consumption of beaver by the Malbaie pack was lower than results reported in most studies reviewed, but only one of these studies mentioned higher beaver biomass than what we observed for the Grands-Jardins pack (Potvin et al. 1988; Table 3). This suggests that the availability of this prey for the Malbaie pack was too low to maintain an active search strategy. Indeed,

the beaver local availability index was lower for the Malbaie pack (0.2 colonies/10 km²) than for the Grands-Jardins pack (0.4 colonies/10 km²).

Species other than moose, caribou, or beaver contributed little to the summer diet of the Malbaie and the Grands-Jardins wolf packs. The low consumption of smaller prey suggests that these prey were not actively hunted but may have been the result of opportunistic predation events or eating of carrion. Ballard et al. (1981) reported that high densities of small mammals could be an important food supplement under some circumstances.

Finally, we observed a relatively high occurrence of wildberries (especially blueberry) in diets of the Malbaie pack. In Alaska, Ballard et al. (1987) reported an occurrence of 3.2% of wildberry in scats (adults and pups combined) while it reached 8.0% in the La Vérendrye Wildlife Reserve (adults and pups combined; Messier and Crête 1985). Fuller (1989) reported only traces of wildberry in Minnesota wolf scats. For coyote (Canis latrans), the high occurrence of wildberry may be related to a shortage of animal prey (Crête and Lemieux 1994) or to the higher availability of wildberry (Serafini and Lovari 1993). However, since pup scats were not discriminated from adult, the high occurrence of wildberry may also be related to higher consumption by pups.

At low prey density, the relative availability of prey species seems to explain variations in the summer food habits of the Malbaie and the Grands-Jardins wolf packs. Energetic requirements of the pack, according to the kin selection hypothesis, may influence the use-availability relation. Based on our results, we conclude that caribou, even if it is considered as a more vulnerable prey than the moose, is not selected by wolves occupying their range because they are too scarce. But from a management standpoint, the summer predation on cari-



Table 3. Percent biomass of main prey (age classes pooled) consumed in summer by gray wolves in North America.

	Location		Periods	Moose	Caribou	Deer	Beaver	Study
	BritishColumbia		February-November	28.0	ı	71.4	7:0	Scott and Shackleton (1980)
	Minnesota		April-September April-October	33.8	1 1	56.8 79.0-96.0	1.4	Fritts and Mech (1981) Fuller(1989)
	Ontario: Algonquin Provincial Park	ıcial Park	N.A.	57.6-82.1	1	4.7-27.3	11.1-15.1	Forbes and Theberge (1996)
9	Alaska		August-September May-July	43 <i>2</i> 65.0-89.3	46.9 1.4-23.4	1 1	2.1-7.3	Spaulding et al. (1998) Ballard et al. (1987)
	Alberta		May-September	79.3-93.0	ı	ı	2.1-16.8	Fullerand Keith (1980)
	Southwestern Québec (mixed forest) (boreal forest)	(mixed forest) (boreal forest)	May-November May-November	31.0-58.0	1 1	5.0-22.0	29.0-44.0	Potvin et al. (1988) Crête et al. (1981)
	Québec: Lac Jacques- Gr Cartier Highlands Ma	Grands-Jardins Malbaie	June-September June-September	65.2-67.9 95.9-97.3	1.1-17.9		13.3-33.2	This study This study



bou, although light, is sufficient to reduce the growth rate of the herd in some years. If logging brings substantial habitat modifications and causes an increase of the moose density in the study area, local wolf density should be maintained (or adjusted) according to the caribou management plan (Banville 1998), to a level that will not affect the small reintroduced caribou herd of the Grands-Jardins provincial park. We expect that wolves would concentrate their diet on the more available moose, thereby releasing pressure on the caribou population.

ACKNOWLEDGEMENTS

The authors are indebted to the partners of the Société de la Faune et des Parcs du Québec (FAPAQ). Thanks to Mïkïn Inc., the Société des Établissements de Plein Air du Québec (SÉPAQ), the Société de Développement des Activités dans le Parc de la Jacques-Cartier (SDAPJC), the Fondation de la Faune du Québec (FFQ), the Université Laval, and finally, the Association des trappeurs du Saguenay-Lac-Saint-Jean (ATSLSJ). We also thank all the volunteers, especially S. Czetwertynski and G. Millischer who collected and prepared wolf scats. We thank C. Dussault and E. Reed for valuable comments on earlier drafts of this paper.

REFERENCES

- ADORDJAN, A. S., and G. B. KOLENOSKY. 1969. A manual for the identification of hairs of selected Ontario mammals. Ontario Department of Lands and Forests, Research Report, Number 90. Toronto, Ontario, Canada.
- Ballard, W. B., R. O. Stephenson, and T. H. Spraker. 1981. Nelchina basin wolf studies. Alaska Department of Fish and Game, Juneau, Alaska, USA.
- _____, J. S. WHITMAN, and C. L. GARDNER. 1987. Ecology of an exploited wolf population in south-central Alaska. Wild-

- life Monographs 98.
- Banfield, A. W. F. 1987. The mammals of Canada. National Museum of Natural Sciences, National Museum of Canada. University of Toronto Press, Toronto, Ontario, Canada.
- Banville, D. 1998. Plan de gestion du caribou de Charlevoix. Ministère de l'Environnement et de la Faune du Québec, Direction générale de Québec. Québec, Québec, Canada.
- CARBYN, L. N. 1987. Gray wolf and Red wolf. Pages 359-376 in M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, editors. Wild furbearer management and conservation in North America. Ontario Trappers Association, Toronto, Ontario, Canada.
- CHRISTENSEN, R. 1990. Log-linear models. Springer-Verlag, New York, New York, USA.
- Courtois, R., and G. Lamontagne. 1999. The protection of cows: its impact on moose hunting and moose populations. Alces 35:11-29.
- ———, Y. LEBLANC, J. MALTAIS, and H. CRÉPEAU. 1994. Québec moose aerial surveys: methods to estimate population characteristics and improved sampling strategies. Alces 30:159-171.
- Crête, M., M. Bélanger, and J. Tremblay. 1981. Régime alimentaire du loup dans le sud-ouest du Québec entre les mois de mai et d'octobre. Le Naturaliste Canadien 108:167-173.
- _____, and R. Lemieux. 1994. Dynamique de population des coyotes colonisant la péninsule gaspésienne. Ministère du Loisir, de la Chasse et de la Pêche du Québec. Québec, Québec, Canada.
- FLOYD, T. J., L. D. MECH, and P. A. JORDAN. 1978. Relating wolf scat content to prey consumed. Journal of Wildlife Management 42:528-532.
- Forbes, G.J., and J.B. Theberge. 1996. Response by wolves to prey variation in



- central Ontario. Canadian Journal of Zoology 74: 1511-1520.
- FRITTS, S. H., and L. D. MECH. 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. Wildlife Monographs 80.
- FULLER, T. K. 1989. Populations dynamics of wolves in north-central Minnesota. Wildlife Monographs 105.
- population dynamics and prey relationships in northeastern Alberta. Journal of Wildlife Management 44:583-602.
- Jolicoeur, H. 1998. Le loup du massif du lac Jacques-Cartier. Ministère de l'Environnement et de la Faune du Québec, Direction de la faune et des habitats, Direction de la conservation du patrimoine écologique, Québec, Québec, Canada.
- Radioisotope tagging for the determination of black bear population densities in Québec. Pages 208-220 in E. P. Orff, editor. Proceedings of the 11th Eastern Black Bear Workshop. Waterville Valley, New Hampshire, USA.
- Korschgen, L. J. 1980. Procedures for food-habits analyses. Pages 113-127 in S. D. Schemnitz, editor. Wildlife Management Techniques Manual. Fourth edition. The Wildlife Society, Washington, D.C., USA.
- Li, T., J.-P. Ducruc, and V. Gerardin. 1997. Small-scale ecological mapping of Québec: Description of natural regions case of Lac Jacques-Cartier highlands. Proceedings of the Canadian Council on Ecological Areas. Canadian Society for Landscape Ecology and Management Conference, Regina, Saskatchewan, September 29 October 2, 1996.
- Mech, L. D. 1966. The wolves of Isle Royale. U.S. National Park Service,

- Fauna Series, Number 7. U.S. Government Printing Office, Washington, D.C., USA.
- ——. 1970. The wolf: the ecology and behavior of an endangered species. The Natural History Press, Garden City, New York, USA.
- Messier, F., and M. Crête. 1985. Moosewolf dynamics and the natural regulation of moose populations. Oecologia 65: 503-512.
- Moore, T. D., L. E. Spence, and C. E. Dugnolle. 1974. Identification of the dorsal guard hairs of some mammals of Wyoming. Wyoming Game and Fish Department, Bulletin Number 14.
- Murie, A. 1944. The wolves of Mount McKinley. U.S. National Park Service, Fauna Series, Number 5. U.S. Government Printing Office, Washington, D.C., USA.
- PIMLOTT, D. H. 1974. The ecology of the wolf in North America. Pages 280-285 in M. W. Fox, editor. The wild canids: their systematics, behavioral ecology and evolution. Van Nostrand-Reinhold, New York, New York, USA.
- ——, J. A. SHANNON, and G. B. KOLENOSKY. 1969. The ecology of the timber wolf in Algonquin Provincial Park. Ontario Department of Lands and Forests, Research Report, Number 87. Toronto, Ontario, Canada.
- POTVIN, F., H. JOLICOEUR, and J. HUOT. 1988. Wolf diet and prey selectivity during two periods for deer in Québec: decline versus expansion. Canadian Journal of Zoology 66:1274-1279.
- REYNOLDS, J. C., and N. J. AEBISCHER. 1991. Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the fox *Vulpes vulpes*. Mammal Review 21:97-122.
- SAS INSTITUTE INC. 1988. SAS/STAT User's guide. Release 6.03. SAS Insti-



- tute, Cary, North Carolina, USA.
- SCHMIDT, P. A., and L. D. MECH. 1997. Wolf pack size and food acquisition. American Naturalist 150:513-517.
- Scott, B. M. V., and D. M. SHACKLETON. 1980. Food habits of two Vancouver Island wolf packs: a preliminary study. Canadian Journal of Zoology 58:1203-1207.
- SERAFINI, P., and S. LOVARI. 1993. Food habits and trophic niche overlap of the red fox and the stone marten in a mediterranean rural area. Acta Theriologica 38:233-244.
- Spaulding, R. L., P. R. Krausman, and W. B. Ballard. 1998. Summer diet of gray wolves, *Canis lupus*, in northwestern Alaska. The Canadian Field-Naturalist 112:262-266.
- ST-ONGE, S., L. BRETON, A. BEAUMONT, and R. COURTOIS. 1995. Inventaire aérien de l'orignal dans la réserve faunique des Laurentides à l'hiver 1994. Pages 17-25 in S. St-Onge, R. Courtois, and D. Banville, editors. Inventaires aériens de l'orignal dans les réserves fauniques du Québec. Ministère de l'Environnement et de la Faune du Québec, Direction de la faune et des habitats, Québec, Québec, Canada.
- Thompson, D. Q. 1952. Travel range, and food habits of timber wolves in Wisconsin. Journal of Mammalogy 33:429-452.
- VAN BALLENBERGHE, V., A. W. ERIKSON, and D. BYMAN. 1975. Ecology of the timber wolf in northeastern Minnesota. Wildlife Monographs 43.
- VOIGT, D. R., G. B. KOLENOSKY, and D. H. PIMLOTT. 1976. Changes in summer foods of wolves in central Ontario. Journal of Wildlife Management 40:663-668.
- WEAVER, J. L. 1993. Refining the equation for interpreting prey occurrence in gray wolf scats. Journal of Wildlife Management 57:534-538.

