Distribution of wolf dens on migratory caribou ranges in the Northwest Territories, Canada

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Most wolves (*Canis lupus*) on migratory caribou (*Rangifer tarandus*) ranges in the Northwest Territories den near the tree line, the northern limit of tree growth. Sixty percent of the 209 dens that we located were within 50 km of the tree line, an area representing only 25% of the caribou range. Den density in the forest was significantly lower than expected if dens were randomly dispersed. Within the tundra zone wolves did not show any preference for denning near caribou calving grounds. Most wolves may den at the tree line because caribou are likely available for a greater proportion of the denning period than they would be elsewhere and because caribou are usually abundant near the tree line in September, when the nutritional demands of the pups are greatest. Within the tree-line zone, habitat characteristics appeared to affect the local distribution of dens because wolves preferred to den where the roots of trees and shrubs provided structural support for the tunnels. With most wolves denning at the tree line, density-dependent summer range expansion and contraction by caribou may provide a mechanism by which changing caribou densities could influence the growth rate of the wolf population.

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La plupart des Loups gris (*Canis lupus*) qui fréquentent les territoires des Caribous (*Rangifer tarandus*) migrateurs dans les Territoires du Nord-Ouest ont leur tanière près de la ligne des arbres, la limite boréale de croissance des arbres. Soixante pourcent des 209 tanières repérées étaient à moins de 50 km de la ligne des arbres, une zone qui ne représente que 25% de la répartition des caribous. La densité des tanières dans la forêt était significativement plus faible que si les tanières avaient été réparties de façon aléatoire. Dans la zone de la toundra, les loups ne semblaient pas préférer nicher près des territoires de mise bas des caribous. La plupart des loups font probablement leur tanière près de la ligne des arbres parce que les caribous y sont sans doute disponibles pour une plus grande proportion de la période de reproduction et parce que les caribous sont ordinairement abondants près de la ligne des arbres en septembre, lorsque les besoins nutritifs des louveteaux sont maximaux. Dans la zone des arbres, les caractéristiques de l'habitat semblent influencer la répartition des tanières, puisque les loups préféraient creuser leur tanière aux endroits où les racines des arbres et des arbrisseaux servaient de support à leurs tunnels. Là où la plupart des loups font leur tanière à la ligne des arbres, l'expansion et la contraction du domaine d'été en fonction de la densité chez les caribous donne peut-être lieu à un système dans lequel la densité changeante des caribous peut influencer le taux de croissance de la population de loups.

[Traduit par la rédaction]

Introduction

The annual movements of the large migratory caribou herds (*Rangifer tarandus*) in the Northwest Territories, Yukon Territory, and Alaska follow the same general pattern (Banfield 1954; Kelsall 1968; Hemming 1971; Parker 1972; Gates 1989; Gunn 1989; Heard 1989; Latour 1989). Most caribou spend November through March in the boreal forest. In March and April cows begin their spring migration, reaching tundra calving grounds (Fig. 1) for parturition in early June. Bulls migrate later, but by June most are on the tundra, where they spend July and August. Caribou usually return to the tree line by early September but may not enter the forest until October.

Wolves (*Canis lupis*) inhabiting migratory caribou ranges prey primarily on caribou (Banfield 1954; Kelsall 1968; Clark 1971; Kuyt 1972; Parker 1972, 1973; Stephenson and James 1982; Williams 1990). They do not appear to be territorial throughout the year, as are wolves elsewhere, but move as required to remain with caribou (Banfield 1954; Kelsall 1968; Kuyt 1972; Parker 1972, 1973; Stephenson and James 1982; D. C. Heard, unpublished data). Wolf pups are born in dens in late May and early June and cannot move with the pack until late August (Kuyt 1972; Fritts and Mech 1981). Therefore, wolves that are raising a litter of pups cannot move far relative to other times of the year and relative to the size of a caribou herd's summer range of about 150 000 km^2 (Fig. 1).

There should be strong selection on wolves to locate den sites where caribou are most available during the denning period because caribou remain the primary food of denning wolves (Kuyt 1972; Williams 1990; D. C. Heard, unpublished data), pup survival in summer appears to depend on food availability (Fuller 1989; Williams 1990), and wolves' reproductive success is largely determined by pup survival in summer (Van Ballenberghe and Mech 1975; Keith 1983). Previous researchers generalized that most wolves on migratory caribou ranges den near the tree line (Banfield 1954; Kelsall 1968; Kuyt 1972; Parker 1972, 1973; Parker and Luttich 1986), but none of these authors presented any data to support their conclusion. In this paper we describe the geographic pattern of wolf den distribution on four migratory caribou ranges in the Northwest Territories with respect to the hypothesis that densities of wolf dens, and thus reproductive success of wolves, are greatest near the tree line.

Methods

We collected information on the location and description of wolf dens (*i*) during our fieldwork on wolves and caribou between 1976 and 1990, (*ii*) from published and unpublished reports, (*iii*) by locating radio-collared wolves in 1979 and 1980 (D. C. Heard, unpublished data) and in 1987 and 1988 (Williams 1990), and (*iv*) through interviews with anyone who might have observed dens during work

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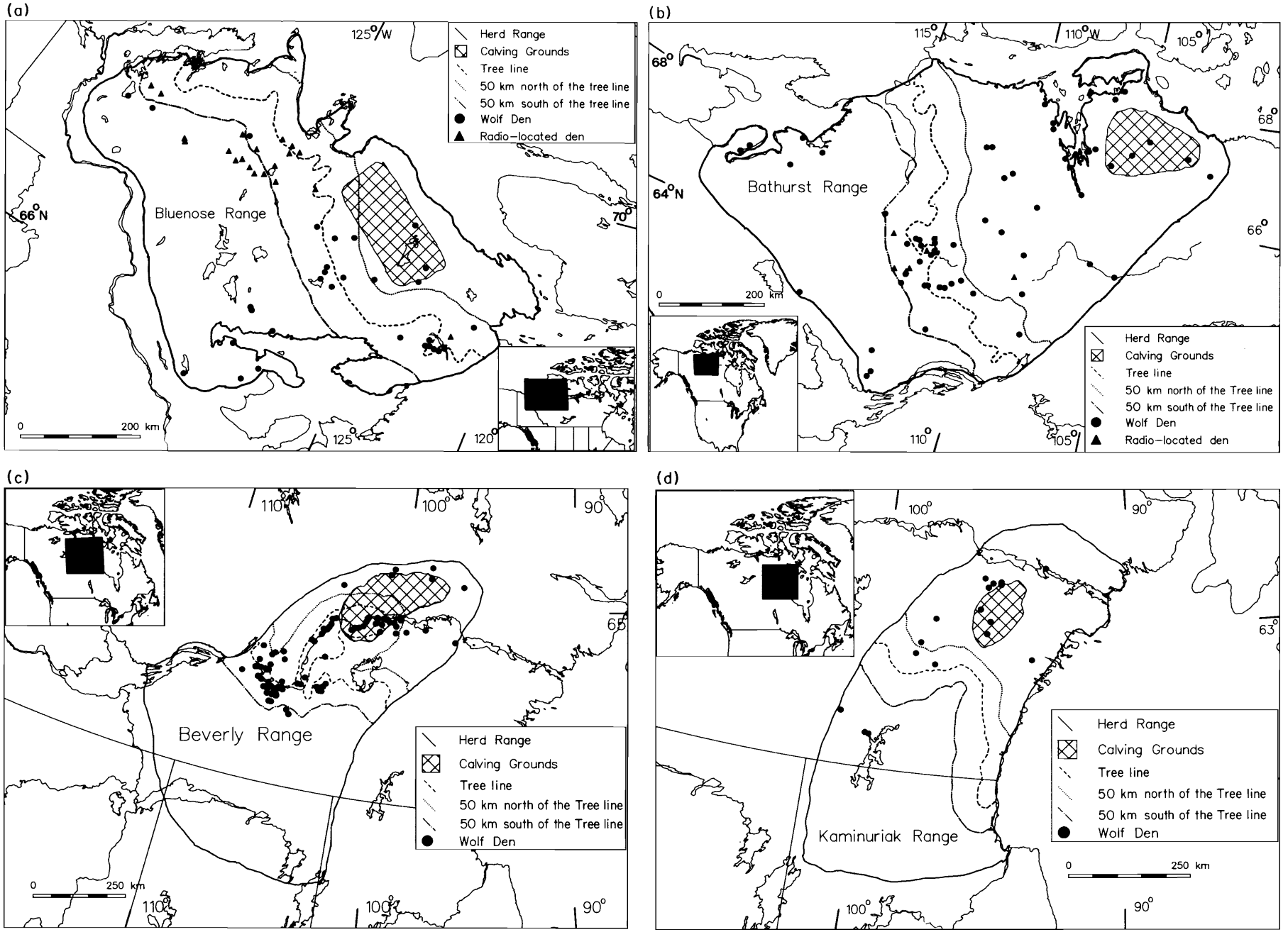

FIG. 1. Distribution of wolf dens on the Bluenose (*a*), Bathurst (*b*), Beverly (*c*), and Kaminuriak (*d*) migratory caribou ranges in the Northwest Territories.

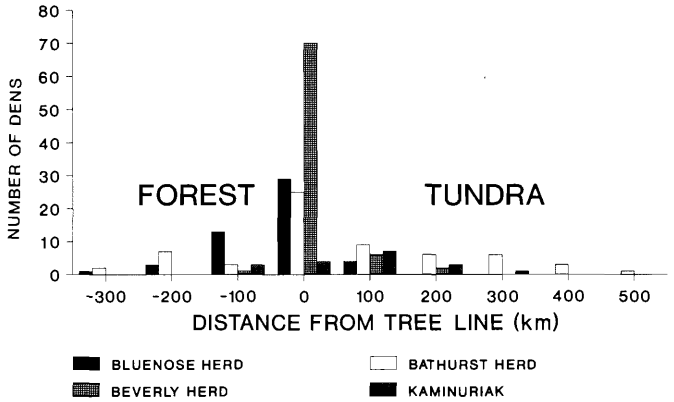

FIG. 2. Numbers of wolf dens on the Bluenose, Bathurst, and Beverly caribou herd ranges in relation to their distance from the tree line, which is indicated in the figure as the midpoint of a 100 km wide range. Zero represents the band 50 km on each side of the tree line.

or recreation (e.g., archaeologists, biologists, hunters, pilots, geologists, and canoeists). Dens were located during aerial wildlife surveys (i.e., primarily not during den searches) by canoeists, and by ground-based observers from 1948 through 1990. Whenever possible, we visited dens to confirm the accuracy of second-hand reports and to collect scats and prey remains. We did not consider all of the reports of dens given to us to be sufficiently reliable to include in this analysis. Our judgement was based on the degree of detail reported (e.g., photographs) and the confidence observers placed in their memory.

We divided the caribou range into four areas based on the distance from the tree line. We defined the tree line as the northern limit of tree growth, specifically the unsmoothed isoline (including burns) of 0% tree cover as plotted by Timoney (1988). The forest zone included forested range greater than 50 km from the tree line, and the tundra zone included tundra range greater than 50 km from the tree line. The tree-line zone was a 100 km wide band centred on the tree line, which we subdivided into the northern tree-line subzone (tundra within 50 km of tree line) and the southern tree-line subzone (forest within 50 km of tree line; Fig. 1). We chose a 50-km band because 50 km was close to the mean diameter of four summer territories of wolves on migratory caribou range in Alaska (mean 49 km; Stephenson and James 1982). We determined if den densities varied among forest, tree-line, and tundra areas using a G-test of goodness of fit, with a continuity correction when the number of dens observed was less than 200. We tested the hypothesis that wolf den densities were greater than expected near the tree line and less than expected elsewhere by comparing the expected number of dens with the 90% Bonferroni confidence intervals on the observed number of dens (Neu et al. 1974; Byers et al. 1984). The expected number of dens in each zone was proportional to the area of that zone within each caribou herd's range. We rejected the null hypothesis of no difference when the expected number of dens in the northern and southern tree-line subzones was lower than the lower confidence limits on the observed values and when the expected number of dens in the forest and tundra zones was greater than the upper confidence limits on the observed values. The probability of making a type I error in those tests was less than 5% because they were one-tailed tests.

We examined the distribution of wolf dens overall and within the annual ranges of the Bluenose, Bathurst, Beverly, and Kaminuriak caribou herds individually (Fig. 1) because radio-collared wolves tended to remain within those ranges (D. C. Heard and P. Clarkson, unpublished data) and because of variation in the size and shape of each herd's range with respect to the location of the tree line (Fig. 1). We calculated den density within successive concentric 100-km bands radiating from calving ground centres and regressed den density, within both the tree-line and tundra zones, against distance from the calving ground. The regression included data from only the Bluenose, Bathurst, and Beverly herds because den densities were similar ($P > 0.05$) within those herd ranges (Table 1).

Results

We considered the documentation on 209 dens to be sufficiently reliable to include those sites in our analysis (Table 2). We visited and confirmed the existence of 70 dens (33%).

The distribution of wolf dens was consistent with the hypothesis that most wolves den near the tree line (Figs. 1 and 2, Table 3). This pattern was evident in the combined data from all caribou herd ranges and in the data from the Bluenose, Bathurst, and Beverly herd ranges individually, but was not found for the Kaminuriak herd's range. Sixty percent of the 209 dens we located were within the tree-line zone, an area representing only 25% of the study area, and 42% of the dens were within the southern tree-line subzone, an area representing only 13% of the area. Woles avoided denning in the forest, but when they did, they still showed an affinity to the tree line. Most dens located in the forest were on the Bluenose caribou herd's range, where 11 of 17 were within 100 km of the tree line (Figs. 1 and 2).

We saw a profusion of old bones and scats around dens located at the tree line more often than around tundra dens, and we observed collapsed dens more often on the tundra. Therefore, it appears that tree-line dens are not only more abundant than tundra dens but they also persist longer and are reused more frequently.

The location of caribou calving grounds did not influence den distribution. Den densities were not related to the distance from calving grounds within either the tree-line or the tundra zone (tundra zone: $y = 1.47 - 0.00218x$, $r^2 = 0.164$, df = 13, $P = 0.15$; tree-line zone: $y = 5.56 - 0.00468x$, $r^2 = 0.042$, df = 14, $P = 0.465$, where y is the number of dens per 10 000 km^2, and x is the distance from the centre of the calving ground to the midpoint of the 100-km band).

Discussion

Potential reporting biases

It is unlikely that the observed concentration of dens near the tree line resulted from differential search effort. We divided the source of den reports according to methods that we could examine for potential search bias (Table 2). The locations of dens found by radio-tracking collared wolves are least likely to be biassed. Wolves were captured when associated with caribou on the forested winter range more than 100 km south of the tree line, and we had no prior knowledge of where they would den in May. There is no reason to suspect that wolves could not have gone anywhere to den, because some wolves not associated with dens moved with the caribou all the way to the calving grounds (D. C. Heard, unpublished data). The pattern of dens found by locating radio-collared wolves on the Bluenose herd's range did not differ from that found using other methods. On the Bathurst herd's range dens were more concentrated at the tree line than dens we found using other methods (Fig. 1, Table 4).

We spent more time conducting low-level aerial surveys over calving grounds than over any other part of the caribou range, but we found few dens there (Fig. 1, Table 2). Thus, those results have little influence on the overall distribution of dens.

The potential for bias among the other searching methods is difficult to evaluate, but we concluded that when considered

TABLE 1. Size of the tundra, northern tree-line, southern tree-line, and tundra zones and the densities of wolf dens recorded within each caribou herd's range

	Bluenose herd	Bathurst herd	Beverly herd	Kaminuriak herd	All herds combined
Area, km^2 (× 1000)					
Tundra	56	167	83	100	406
Northern tree line	40	41	60	26	167
Southern tree line	49	43	47	29	168
Forest	116	133	241	110	600
Total	261	384	431	265	1341
No. of dens					
Observed	50	63	79	17*	209
Expected	41	60	67	41	209
Den density (no. of dens / 10 000 km^2)	1.92	1.64	1.83	0.64	1.56†

*$P < 0.05$, where P represents the probability that there is no difference between the observed and expected number of dens, using a two-tailed test.
†$G = 22.5$, df = 3, and $P < 0.001$, where P represents the probability that there was no difference in den density among all four herd ranges, and $G = 0.747$, df = 2, and $P > 0.05$, where P represents the probability that there was no difference in den density among the Bluenose, Bathurst, and Beverly herd ranges.

TABLE 2. Methods of locating wolf dens on the Bluenose, Bathurst, Beverly, and Kaminuriak caribou herd ranges and the number of those dens visited to confirm their existence

	Location of radio-collared wolves		Aerial survey of calving grounds		Aerial survey		Canoe trips		Ground-based activities[a]		Total	
	N	*C*	*N*	*C*	*N*	*C*	*N*	*C*	*N*	*C*	*N*	*C*
Bluenose	19	18	1	1	15	2	1	0	14	0	50	21
Bathurst	7	7	6	6	18	13	8	4	23	8	62	38
Beverly	0	0	0	0	5	3	27[b]	2	47[c]	1	79	6
Kaminuriak	0	0	1	1	1	0	4	0	12	4	18	5
Total	26	25	8	8	39	18	40	6	96	13	209	70
Percentage	12		4		19		19		46		100	

NOTE: *N*, number of dens reported; *C*, number of dens visited and confirmed.
[a]From information collected by archaeologists, biologists, geologists, and hunters.
[b]Twenty-three from T. Faess (personal communication), East Wind Arctic Tours, Yellowknife, N.W.T.
[c]Thirty-four from E. Kuyt, Canadian Wildlife Service, Edmonton, Alta. (1972 and unpublished data).

together the results are unlikely to be biassed because there was coverage of all parts of the caribou range and observations came from a large number of sources. Two sources, T. Faess and E. Kuyt, reported 57 dens (Table 2), all of which were on the Beverly herd's range. If those observations were biassed, the overall pattern of den distribution could be affected. We concluded that their observations were unlikely to be biassed because they both covered large areas of the Beverly caribou herd's range, and many of the dens mapped in Kuyt (1972) were originally discovered by other observers. When we removed those 57 dens from our analysis there was no change to the pattern of den distribution on the Beverly herd's range. The observed number of dens was still significantly greater than expected in the southern tree-line zone (13 observed and 1 expected) and lower than expected in the forest zone (1 observed and 15 expected).

It is also unlikely that the observed concentration of dens near the tree line resulted from differential sightability. During aerial surveys, dens in the forest and southern tree-line subzone were probably more often overlooked than dens on the tundra because dens are difficult to see from the air when they are dug under trees and shrubs. But the distribution of dens found by locating radio-collared wolves suggests that the number of dens found in the forest was not underrepresented by other methods (Table 4).

We doubt that wolf den distribution on the Kaminuriak caribou herd's range differs from distributions elsewhere (Table 3) because, after a 3-year study of Kaminuriak caribou, Parker (1972, 1973) concluded that most wolves den at the tree line. Unfortunately, Parker did not published any data to support his conclusions. We suspect that we did not find significantly higher den densities near the tree line on the Kaminuriak caribou herd's range as a result of our small sample size (Table 3). This may have been due to relatively low search effort. Because the power of a nonparametric test with a small sample size is low, we cannot conclude that the statistical hypothesis is true, only that it cannot be rejected.

Adaptive significance of denning at the tree line

There are two reasons why most wolves may den at the tree line. First, caribou are likely to be more available near the tree line for a greater proportion of the denning period than in any

TABLE 3. Numbers of wolf dens observed (O) and expected (E) within the four caribou herd ranges within the tundra, northern tree-line, southern tree-line, and tundra zones

	Bluenose		Bathurst		Beverly		Kaminuriak		All herds	
	O	E	O	E	O	E	O	E	O	E
Tundra	4*	11	26	27	10	15	12	6	52	63
Northern tree line	10	8	13	7	13	11	2	2	38*	26
Southern tree line	19*	9	15*	7	54*	9	0	2	88*	26
Forest	17	22	9*	22	2*	44	3*	7	31*	94
Total	50	50	63	63	79	79	17	17	209	209
	$G = 12.9$ df = 3 $P < 0.01^{\dagger}$		$G = 18.7$ df = 3 $P < 0.001^{\dagger}$		$G = 176.7$ df = 3 $P < 0.001^{\dagger}$		$G = 6.8$ df = 3 $P > 0.05^{\dagger}$		$G = 154.0$ df = 3 $P < 0.001^{\dagger}$	

*$P < 0.05$, where P represents the probability that the observed number of tundra and forest dens is not less than expected and that the observed number of tree-line zone dens is not greater than expected.
†P represents the probability that there was no difference in den density among zones.

TABLE 4. Number of wolf dens found by locating radio-collared wolves versus other methods within the Bluenose and Bathurst caribou herd ranges within the tundra, northern tree-line, southern tree-line, and tundra zones

	Bluenose		Bathurst	
	Radio-tracking	Other methods	Radio-tracking	Other methods
Tundra	0	4	1	25
Northern tree line	3	6	1	12
Southern tree line	7	12	5	10
Forest	9	8	0	9
Total	19	30	7	56
	$G = 5.47$ df = 3 $P > 0.05$		$G = 9.33$ df = 3 $P < 0.05$	

NOTE: P represents the probability that the number of dens found within each zone was independent of location method.

other location, and second, caribou are usually abundant near the tree line in September, when the nutritional demands of pups are greatest. Caribou movements in summer influence their availability to wolves denning in different locations. Pregnant caribou begin to leave the forest as early as March, passing through the tree line until early May and arriving on the calving grounds in late May (Kelsall 1968; Parker 1972; Gates 1989; Gunn 1989; Heard 1989; Latour 1989). Bulls lag behind, moving out of the forest and onto the tundra throughout April and May. By late June most of the cows and neonates have left the calving grounds. In July, most caribou are in dense aggregations that move rapidly and unpredictably across the tundra (Kelsall 1968; Hemming 1971; Parker 1972; Fancy et al. 1989). In August, the groups break up and the movement rate slows. Caribou have usually returned to the tree line by early September, but they may not enter the forest until October.

The consequence of those movements is that wolves denning in the forest would be without caribou for the entire denning period. Wolves denning on caribou calving grounds would have access to an abundant and vulnerable prey only until the cows and neonates leave in late June. There may be no place on the tundra between the tree line and the calving grounds where caribou would be present throughout the summer because at any given location, caribou would likely be absent or abundant for only a short time. Therefore, even though there are few caribou at the tree line from mid-June to mid-August, it is probably as good a place as any on the tundra to hunt for caribou during those months.

Movement to the tree line in summer was also shown by another major predator on migratory caribou. Until the 1950s, when people moved to permanent settlements, "Caribou Eater" Chipewyan Indians attempted to maximize their access to caribou by moving from winter settlements in the forest to summer camps near the tree line (Smith 1978). This strategy appears to have been successful because, in contrast to Inuit, Chipewyans have few legends telling of starvation.

Food requirements for pups reach a peak in early September because nutritional demands are proportional to both body size and growth rate. Growth rate is greatest when pups are between 8 and 14 weeks old (Pulliainen 1965; Kuyt 1972; Van Ballenberghe and Mech 1975), when they require 2–3 times more food per kilogram of body weight than older wolves (Mech 1970; see also Lewis et al. 1987 for domestic dogs). The three wolf packs radio-collared by Stephenson and James (1982) also denned where the availability of caribou increased during September. A study of mortality rates of radio-collared calves in the Porcupine caribou herd showed that calf mortality increased in August and September in all 3 years of the study (Whitten et al. 1985, 1987*a*, 1987*b*), as would be expected if wolves on the Porcupine range also den where caribou are found in August and September.

There is no evidence to suggest that the availability of alternative prey influences den-site selection because wolves prey predominantly on caribou during the denning period. We found caribou hair in over 90% of scats we collected from tree-line and tundra zone wolf dens on the Bathurst caribou herd range in 1979, 1982, and 1988 and from tree-line and forest zone dens on the Bluenose caribou herd range in 1987 and 1988 (Williams 1990; D. C. Heard and T. M. Williams, unpublished data). Other studies have also shown that caribou constitute the major component of the summer diet of wolves on migratory caribou ranges (Kuyt 1972; Clark 1971; Stephenson and James 1982; Haugen 1985). Supporting data are lacking, but we suspect that when there are no caribou near their den, wolves move as far as necessary to find them and that their food-consumption rate declines.

Caribou availability is unlikely to be the only factor influencing den-site selection. Even though caribou availability is similar throughout the tree-line zone, more wolves denned south of the tree line, in the southern tree-line subzone, than

in the nearby tundra (Table 3), probably because the roots of trees and shrubs provide structural support for tunnels (Jacobson 1979; Zimen 1981). Thus, habitat characteristics appear to affect only the local distribution of dens. Wolves prefer to den in sandy, well-drained knolls and eskers (Lawhead 1983; Jacobson 1979; Stephenson 1974; Haugen 1985; Weiler and Garner 1987), but soils with these attributes appeared to be available throughout the caribou range.

Implications of wolf den distribution for wolf and caribou ecology

The den distribution pattern we documented supports a mechanism suggested by Heard and Calef (1986) whereby wolves would show a numerical response to changing caribou densities. Caribou show density-dependent range expansion and contraction (Simmons et al. 1979; Bergerud et al. 1984; Heard and Calef 1986; Valkenburg and Davis 1986; Messier et al. 1988; Couturier et al. 1990). Thus, increasing caribou densities lead to more caribou returning earlier to the hunting ranges of tree-line denning wolves. The early return of caribou would lead to increases in wolf numbers if recruitment of pups depends on caribou availability and if production from tree-line denning wolves influences wolf densities throughout the caribou range. Wolf pup survival appears to depend on food availability (Fuller 1989; Williams 1990), and wolf abundance appears to depend on pup survival (Van Ballenberghe and Mech 1975; Keith 1983). The observed concentration of dens near the tree line on the Bluenose, Bathurst, and Beverly herd ranges suggests that production from those dens would have a major influence on wolf numbers throughout the associated caribou ranges. Messier et al. (1988) felt that wolf abundance must be independent of caribou density because pup survival is determined during the 4- to 5-month period when caribou are "inaccessible" to denning wolves despite increasing caribou densities. This is not the situation in the Northwest Territories because caribou are available to wolves for part of the denning period. We believe that the potential exists for wolves to show a numerical response to changing caribou densities. The effect of this numerical response by wolves on caribou numbers will depend on the timing and magnitude of the response.

We are presently testing our ideas by determining how wolf predation rates on caribou change with caribou density both within the denning period and among locations. We are also examining how the rate of wolf predation on caribou affects pup survival, to evaluate the potential for a numerical response by wolves to varying caribou densities.

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