Habitat partitioning between woodland caribou and moose in Ontario: the potential role of shared predation risk

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Abstract: This paper explores mechanisms of coexistence for woodland caribou (*Rangifer tarandus caribou*) and moose (*Alces alces*) preyed upon by gray wolves (*Canis lupus*) in northern Ontario. Autocorrelation analysis of winter track locations showed habitat partitioning by caribou and moose. Numbers of Delaunay link edges for moose-wolves did not differ significantly from what would be expected by random process, but those for caribou-wolves were significantly fewer. Thus, habitat partitioning provided implicit refuges that put greater distances between caribou and wolves, presumably decreasing predation on the caribou. Yet, direct competition cannot be ruled out; both apparent and direct competition may be involved in real-life situations. A synthesis including both explanations fits ecological theory, as well as current understanding about caribou ecology.

Key words: apparent competition, autocorrelation, competition, gray wolf, *Rangifer, Alces, Canis*

Introduction

Knowledge in woodland caribou ecology, until recently, has lacked the maturity necessary for broad generalizations. But some attempts have been made. In Ontario, Devos & Peterson (1951) pointed out that caribou range continued to shrink, despite closure of legal hunting in 1929 (supported by Cringan, 1957). Simkin (1965) suggested that a caribou decline following moose immigration about 1900 was due to increased biomass supporting higher predator densities; similar to those later reported in British Columbia (Bergerud & Elliot, 1986). Bergerud (1974, 1985) hypothesized that all caribou in Ontario would need islands or shorelines as escape habitat for calving. Other studies supported this generalization (Simkin, 1965; Bergerud, 1985; Cumming & Beange, 1987; Bergerud *et al.*, 1990). Cumming & Beange (1987) concluded that caribou in the boreal forest show fidelity to wintering areas similar to that of white-tailed deer (*Odocoileus virginianus*, Halls, 1978). Cumming & Beange (1993) further showed that timber harvesting in portions of these wintering areas temporarily terminated their use by caribou, the non-use period lasting for at least 10 years; circumstantial evidence suggested that the displacement resulting from entire wintering areas being cut led to extinction of the local caribou band.

Elsewhere in North America, earliest hypotheses tended to be applied to all North American caribou, only incidentally including woodland caribou; even then, views sometimes appeared diametrically opposed (e.g. Scotter, 1972; Bergerud, 1974). Bergerud (1974, 1980) hypothesized that, across North America, predation sets caribou stocking limits at 0.4-0.8/km² or less, well below the levels that would be set by food availability. Support for the importance of predation came from subsequent studies: (Gauthier & Theberge, 1986; Edmonds, 1988; Elliott, 1985; Bergerud & Elliot, 1986; Elliott, 1989; Hayes *et al.*, 1989; Bergerud, 1992). Bergerud (1992) later revised his density figure downward for woodland caribou to 0.04/km². In line with this initial generalization, studies of predator avoidance by cows with calves have provided a catalogue of strategies used by woodland caribou to reduce predation during calving: to the use of islands and shorelines has been added dispersion in mountains (Bergerud *et al.*, 1984) and forest wet-land habitat (Paré & Huot, 1985; Brown *et al.*, 1986). Bergerud (1992) pointed out that, where

special geographic features are not available, caribou can still reduce predation during calving by dispersing to create rareness.

Predation during the rest of the year has received less attention, sometimes for good reason. At Quesnel Lake, and Wells Gray Park, British Columbia, high elevations provided winter refuge (Seip, 1989; Seip, 1990) and, clearly, calf mortality was limiting the caribou population. Still, Bergerud & Elliot (1986) calculated adult mortality across North America at 18-21% (9% after predators were reduced), and other studies have shown the importance of winter mortality. Edmonds (1988) reported 22% adult mortality of woodland caribou in Alberta, all during winter and mostly due to wolves; fall recruitment of calves averaged 15%, a level high enough to have sustained the herd (Seip, 1990; Bergerud, 1992) if it had not been for the high adult mortality. In the Burwash area of the Yukon, Gauthier & Theberge (1986) found disproportionate consumption of caribou relative to available biomass during the rutting and winter periods, but not during calving. Hayes *et al.* (1989), in the Findlayson area of the Yukon, found low recruitment (10%) and high adult mortality (27%) before wolf control; wolves relied heavily on caribou for prey in the areas they occupied, but on moose in other areas. Lately, Seip (1985, 1989, 1992) hypothesized that wolf predation is the major cause of caribou population decline in southeastern British Columbia, that wolf populations are sustained primarily by moose, and that wolf predation on caribou is greater where caribou live in close proximity to the moose. The above studies suggest that this generalization might apply whether the proximity was during calving time or winter.

Yet, apart from populations theory (e.g. Eberhardt, 1991) and optimal foraging theory (Belovsky, 1991) little reference has been made in caribou literature to general ecological theory. In this paper, we present an initial attempt at relating caribou research findings with general theory; toward that end, we present as an example a study of habitat partitioning during winter in Ontario; and we introduce autocorrelation analysis, a statistical method not previously used to analyze caribou data.

Woodland caribou findings and ecological theory
Mathematical models have provided a body of theory in general ecology that seems useful for understanding caribou ecology in a wider context. Holt (1977) drew attention to the fact that although competition for resources is widely recognized, competition to avoid predation is not. He investigated the possibility with multiple models and found that a predator necessarily imposes "reciprocal equi-

librial abundances" upon alternative prey species, even if these species are otherwise independent. Holt (1977) argues that, at equilibrium, the alternate prey species of most food-limited predators should exhibit this "apparent competition". In some cases, the less productive prey can be eliminated. Holt (1977) points out that to some extent, all species in the predator's diet will be to blame for the exclusion of one, and concludes that understanding the factors controlling a species' density requires examination of the entire community in which the species is embedded.

Holt (1984) then investigated requirements for co-existence when two prey species share a common predator. He observes that an influx of predators into a habitat should reduce prey density; however, if a predator can choose where to forage without interference from other predators, (at least) as many species of prey can coexist in the predator's diet as there are distinct patches discriminated by the predator. "Habitat partitioning can permit coexistence even when predation is intense, essentially because it allows the number of predators exploiting a given prey to be determined independently of the availability and productivity of alternative prey," (c.f. Seip, 1992).

Further models (Holt & Kotler, 1987) show that a rare prey species may benefit from co-occurring in patches with a more common prey species (particularly if the rarer prey is less preferred). Consumption of one prey species reduces time available for encountering and capturing the alternative prey; thus, predator selectivity may provide an "implicit refuge" for a low-quality prey. The predator should depart from a patch when its instantaneous rate of foraging decreases to the average rate of yield over the entire habitat in which the predator is foraging. From these results it is possible to plot "constant-yield isoclines". A predator might be expected to leave patches of prey that are unusually low in average foraging return compared with other patches.

On the basis of Seip's (1992) generalizations about woodland caribou and these aspects of ecological theory, we hypothesized that caribou in Ontario some 40-50 years after moose immigration was complete should be spatially separated from moose and wolves in winter. To test the hypothesis we flew transects over a selected study area during four winters (1981-84), plotting locations of tracks for woodland caribou, moose and wolves.

Methods
Study area
The study area encompassed 6 500 km² of boreal forest located 125 km north of Thunder Bay, Ontario. Centered on Wabakimi Lake, it lies on the

eastern edge of glacial Lake Agassiz. Streams and highly divided lakes abound. Stony sand and till thinly cover the Archean granitic uplands, typical of the heavily glaciated Precambrian shield. The terrain displays a smoothly rolling surface into which lakes with gently sloping sides are set (Teller & Clayton, 1983). The surficial geology map shows 24% of the area classified as bedrock. Summer temperatures are cool (mean daily temperature 16°C), winters cold (mean daily January temperature - 20°C). Total precipitation averages 750 mm/year. The maximum snow depth recorded during the 4 winters of the study at Flat Lake, an Ontario Ministry of Natural Resources snow station located in the southeast corner of the study area, was 95 cm. The number of weeks during January to March with snow depth over 50 cm were, by year, 2, 11, 4, 14; the numbers of weeks reporting heavy crusts were 1,0,3,5, usually in March. In addition, winter rains or brief thaws occasionally left thin skims of ice across the snow that would not have been recorded as crusts.

Wildfires have left a mosaic of stands, primarily black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*), but with a few mixed stands including trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*). Mosses, such as *Pleurozium schreberi* cover much of the forest floor, but patches of ground lichens (e.g., *Cladonia mitis, C. rangiferina,* and *C. alpestris*) grow under poorly stocked stands of jack pines on sand flats and under scattered spruce on rock outcrops (Antoniak, 1993). Tree lichens, e. g., *Usnea comosa* and *U. dasypoga,* are common but not especially abundant (Ahti & Hepburn, 1967).

No logging had taken place and no roads entered the study area. The few human activities were extensive in nature: canoe enthusiasts and fly-in anglers (using small boats with outboard motors) traversed major waterways in summer; tourist outfitters flew hunters into remote lakes during autumn; trappers, mostly native, crossed some parts of the area during winter. Tourist outpost camps, trappers' cabins, and some private cottages constituted the only permanent human dwellings. The southern boundary of the study area is approximated by the transcontinental line of the Canadian National Railway. North of the study area the forest stretched unbroken and undisturbed to the Hudson Bay Lowlands.

Data collection
We plotted tracks of woodland caribou, moose, and wolves on 1:126,720-scale maps during transects flown about 300 m above ground level at 3-km intervals during 4 winters (1980-84). Data from a subsequent survey in 1988 were analyzed but not

included here because a thin layer of ice prevented location of wolf tracks. Transects oriented north-south in the southern 2/3 of the study area became east-west in the northern 1/3 to permit boundaries at least 2 transect widths beyond any caribou tracks on all sides, thus including all contiguous and close (i.e. within about 20 km) winter aggregations of caribou centered around Wabakimi Lake. We noticed no difference in observability of tracks due to direction. We recorded tracks wherever located, not only directly on the transect lines, and we turned aside from the transects to examine any tracks seen in the distance, or to follow individual track sets until the species was positively identified, using criteria described by Cumming & Beange (1987). The 3-km spacing of transects left an unexamined strip between transects, but due to the mobility of the animals, and our turning to look at tracks, we believe that we missed few tracks for this reason. Some tracks may have been missed in the northern quarter of the study area when fuel shortages curtailed circling.

Since densities of all species were low, track aggregates were not frequent. Because a letter representing a species covered about 0.05 km² at this scale, we made no effort to delineate track aggregates, but simply recorded presence of tracks wherever a transect crossed them, or allowed them to be located. We recorded wolf tracks by packs, rather than by individual animals. All flights took place during sunny days, at least 3 days after a snowfall, and between 10 AM and 3 PM. One complete survey required about 4 days. Flights were carried out during mid to late February, except for 1983-84 when the survey was delayed until early March.

We looked for tracks in snow rather than for animals because neither woodland caribou nor wolves can be located reliably in forested country. As snow cover was continuous each year from late November to early April, tracks provided records of animal locations from the day of the flight backward in time until at least the last previous snowfall, and sometimes up to a month or more before in the case of "old tracks". Although woodland caribou return to traditional areas each winter (Cumming & Beange, 1987), much like white-tailed deer, they are not so restricted by deep snow and do not congregate under heavy conifers the way deer do. Hence, although tracks in dense conifers are more difficult to locate than tracks in hardwoods or in the open, few animals of the species investigated would remain so sedentary under heavy conifers that their tracks could not be observed around the edges of these stands. Snow conditions probably affected track observability, especially the rare winter rains or thaws that formed icy crusts and made location of wolf tracks difficult. This factor may have contri-

buted to the low number of wolf tracks recorded in the first 2 winters. The high number of wolf tracks recorded in 1984 may have been partly due to the heavy crust (but no ice) that made travel easy. Thus, although we might easily have missed predator prey interactions or their results, such as carcasses that become impossible to locate after a few weeks, we obtained reliable data on animal locations.

Estimates of animal numbers were difficult to obtain. Although track densities may imply relative animal densities, we made no effort to arrive at numbers of animals from this method. Rather we totaled numbers of caribou seen on the ice on a single day in March for a minimum estimate of caribou (Cumming & Beange, 1987), obtained moose densities from routine management aerial surveys, and calculated wolf densities from numbers of packs and size of the only pack in which the animals were seen.

Statistical analysis
The use of tracks rather than direct observations may have influenced the spatial data. Animals may have been more widely separated than the tracks indicated due to time considerations, i. e., a first animal may have been far away by the time a second left tracks near the same location. However, the reverse could not occur. Therefore all track data show minimum distances among individuals and species. Field data were analyzed using an (ARC/INFO) Geographic Information System (GIS) at the Center for the Application of Resources Information Systems, School of Forestry, Lakehead University. With this system, we easily, and with minimal error, transferred field maps to a computerized base map in layers by species and year. To establish computer cells with real reference, we used the distance between transects to determine cell size (approximately 3x3 km, actually 9.29 km²). Cells were then located adjacent to each other centered on transect lines, totaling 697 cells for the entire study area. Due to the low densities of wolf tracks, the within-species dispersion of wolf packs could not be studied using statistical procedures similar to those for moose and caribou.

Chi-square tests
We compared frequency of repeated use of same computer cells from year to year (1-4 winters) for caribou and moose using χ^2, the null-hypothesis being that the frequency distributions were not significantly different among years.

Autocorrelation analysis
Traditional methods of examining space-related data have been criticized by Legendre & Fortin (1989) who advocate instead analysis of spatial autocorrelation, pioneered by Cliff & Ord (1973). A variable is said to be autocorrelated when values at some points in space can be predicted from known values at other known positions. The assumption of independence of observations underlying many traditional statistical methods is not met whenever spatial structure is present, since each new observation contributes an unknown proportion to 1 degree of freedom. We used a spatial autocorrelation analysis program called AUTOCORRELATION for Macintosh (Legendre & Vaudor, 1991) to calculate standard normal deviates (S.N.D.'s) for each distance class from which we plotted correlograms. The null hypothesis for S.N.D.'s is the randomization assumption in which the locations of the points are randomly distributed over the area. The theory behind these computations can be found in Sokal & Oden (1978), Cliff & Ord (1973) and Upton & Fingleton (1985). We plotted correlograms for all 3 species and cross-correlograms for pairs of species.

As recommended by Oden (1984), we used a Bonferroni correction to assess the significance of correlograms. The total level of significance for a correlogram was fixed at 0.05 which was divided by the number of distance classes (20) to test the S. N. D. coefficient value at every distance class.

Schoener's Index of overlap
Spatial overlap between species was examined by calculating Schoener's (1970) index (following McCullough et al., 1989):

$$C_{ih}=1-1/2\sum|P_{(if)}-P_{(hf)}|,$$

where C_{ih} is the overlap of species i on species h, P_{ij} is the proportion of all observations of species j that occurred in grid cell j, $P_{(hj)}$ is the proportion of the other species (h) in the j grid cells. Ranges for C extend from zero (no overlap) to 1 (complete overlap). Multiplying C by 100 provides percentage overlap. This is the same as Whittaker's (1952) index of association for community studies.

Nearest neighbor analysis
To interpret some results from autocorrelation analysis, we tested presence of clumping using the Clark & Evan (1954) distance to nearest neighbor index. Although an older index, R_{CE} (Ward & Parker, 1989) continues to be widely used (e.g., Kenkel, 1988) and improved (e.g., Petrere, 1985). R_{CE} is the ratio between the observed mean distance to nearest neighbor and the expected nearest neighbor distance from an identical population randomly distributed on an infinite plane. Values <1 indicate clumped dispersion; values >1 indicate

uniform dispersion, referred to the standard normal distribution. This index assumes a lack of interdependence that our data do not necessarily show, but errors from this source are relatively small (Donnelly, 1978). More important in many studies is the edge effect, for which Donnelly (1978) proposed a correction. However, a study area of 6 500 km² approaches the theoretical infinite plane closely enough to negate the necessity for such a correction (J. Jarvis, G. Bell, pers. comm.)

Expanded nearest neighbor analysis
Distance to nearest neighbor holds special significance for studies involving predation. Distance from prey to predator could be expected to be negatively correlated with predation risk because predators will require more time to find prey when individual prey animals are located at greater average distances (Cumming, 1975). We measured our distances directly with GIS and compared them with t-tests. We further analyzed the data using Delaunay triangulation (see Upton & Fingleton, 1985), which calculates the number of near neighbors rather than measuring their distances. A program called LINKS (Legendre & Vaudor, 1991) examined (x, y) coordinates of track sightings for each year, both within and among species. The program then used the Delaunay triangulation method to link each point in a plane to its nearest neighboring animals in any direction. Given any triplet of points, the triangle uniting these points was included in the triangulation if₍ and only if₍ the circle passing through the 3 points included no other point in the set of study. Thus the number of link edges indicated how many times an animal's neighbor was a caribou, moose or wolf.

We subdivided the resultant list of link edges by species for comparisons in contingency table analyses, followed, where significant χ^2 values warranted, by Bonferroni confidence intervals (Byers *et al.*, 1984). From Bonferroni's inequality (Neu *et al.*, 1974), a set of simultaneous confidence intervals was constructed such that "one can be at least $100(1 - \alpha)\%$ confident that the intervals contain their respective true proportions, *Pi*:

$$\bar{p}_i - Z_{\alpha/2k}\sqrt{\bar{p}_i(1 - \bar{p}_i)/n} \leq p_i \leq \bar{p}_i + Z_{\alpha/2k}\sqrt{\bar{p}_i(1 - \bar{p}_i)/n}$$

where $Z_{\alpha/2k}$ is the upper standard normal table value corresponding to a probability tail area of $\alpha/2k$; k is the number of categories tested" (Byers *et al.*, 1984. p. 1052). Where the expected proportion P_{io} does not lie within the interval, the expected and actual values differ significantly, in our case with the level of significance fixed at 0.05.

These exploratory tests of link edges may not be valid, because reference to a χ^2 table assumes the
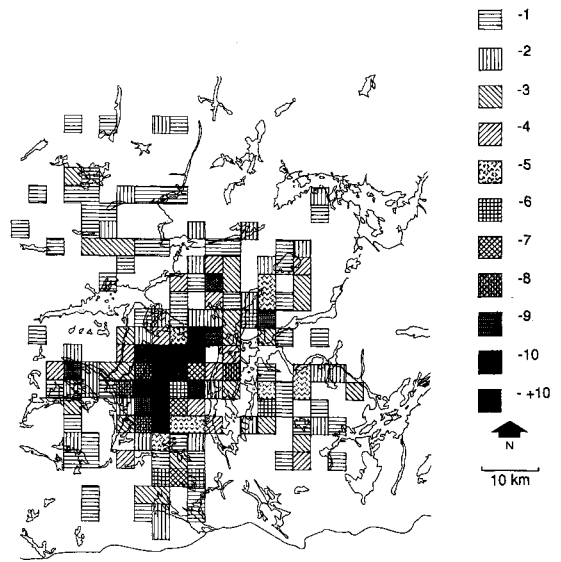

Fig. 1. Caribou track densities revealing a core area with 10+ tracks recorded during 4 winters (by 9.29 km² grid cells).

independence of the observations, a condition that is not met here. To improve confidence in our tests, we replaced observed data for each study year with animal codes randomly assigned to the available x, y coordinates, a method similar to some described by Manly (1991) and Crowley (1992). By maintaining identical numbers of caribou, moose, and wolf sightings, we could follow the same procedures as before to produce links between animals. Observed link counts were then entered into a contingency table, and the χ^2 statistic calculated for the random simulation data. By doing this we simulated a randomization hypothesis technique that does not require independence of observations (Murchison, pers. comm.). The species names become merely labels that could be rearranged in any combination. The random assignment of animal codes to existing points seemed preferable to random selection of new coordinates since the former procedure is in accordance with the autocorrelation hypothesis, and avoids the chance of choosing a location that does not make sense in the real world.

Results
How were caribou, moose and wolves dispersed?
Transects totaling 7 634 km during 4 winters revealed 557 caribou tracks, 631 moose tracks, and 157 wolf-pack tracks. Caribou tracks were located in 22% (1,422 km²) of the study area cells (Fig. 1). These occupied cells showed a strong central ten-

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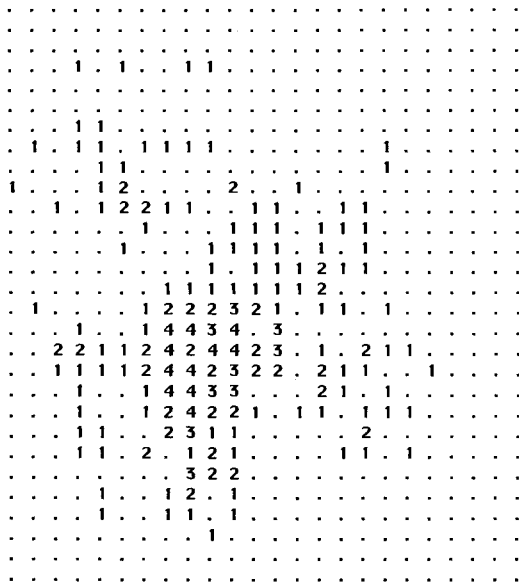
Fig. 2. Numbers of years (out of 4) for which winter tracks of woodland caribou were found in 9.29-km² computer-generated grid cells. In each winter, a core area with tracks was surrounded by other areas used less consistently by caribou.
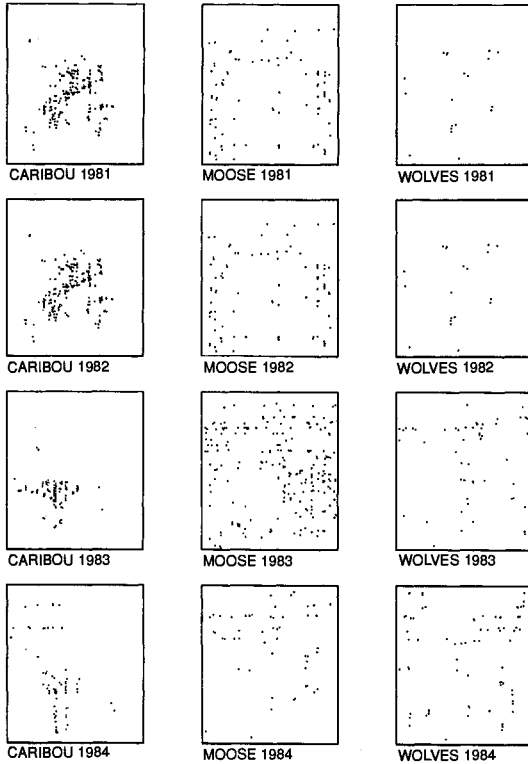

CARIBOU 1981   MOOSE 1981   WOLVES 1981

CARIBOU 1982   MOOSE 1982   WOLVES 1982

CARIBOU 1983   MOOSE 1983   WOLVES 1983

CARIBOU 1984   MOOSE 1984   WOLVES 1984

Fig. 3. Spatial patterns of woodland caribou, moose and wolf packs in northern Ontario based on tracks in snow during 4 winters.

dency: 10 of the 138 tracked cells, located centrally, showed >10 tracks during the 4 years; generally farther from the center, another 14 cells contained 4-10 tracks each; in the remaining cells at greater distances from the core, fewer than 4 tracks/cell were found (Fig. 1). The caribou showed more fidelity to this same central area than to the rest of their range, returning to a 99-km² central area each winter (Fig. 2), an additional 81 km² generally surrounding the core 3 of the 4 years, and another 288 km², for the most part farther from the core, 2 years; peripheral cells totaling 95 km² were used only one year. Moose tracks, on the other hand showed no such central tendency: few moose tracks were located in the area occupied by caribou; elsewhere, moose tracks were distributed without obvious pattern throughout the study area (Fig. 3). Out of 324 computer cells in which moose tracks were recorded, none totaled > 5 tracks/cell for the 4 years. The frequency with which moose repeated use of the same cells from year to year showed a highly significant difference from that of caribou (Table 1, $\chi^2=21.8$, d.f=3, $P=0.0001$): moose used the same cell 1 or 2 years more frequently, while caribou used the same cell during 4 years more frequently. Thus space use by caribou was less homogeneous than that of moose.

Inspection of field maps suggested that wolves inhabited the entire study area, but perhaps at lower densities where caribou were located. Concentrations of tracks were most numerous in the northeast; fewest in the southwest. We identified from tracks about 5 wolf packs in the 6500 km² study area, or about 1 300 km² per pack, but we could not be certain all were present in the more difficult survey years. We saw only one pack of wolves, 8 in number.

Were observations within species autocorrelated?
Correlograms plotted for caribou from standard normal deviates showed consistently significant

Table 1. Annually repeated occupation of same 9.29 km² computer-generated grid cells by caribou and moose from four years' observations of tracks in winter.

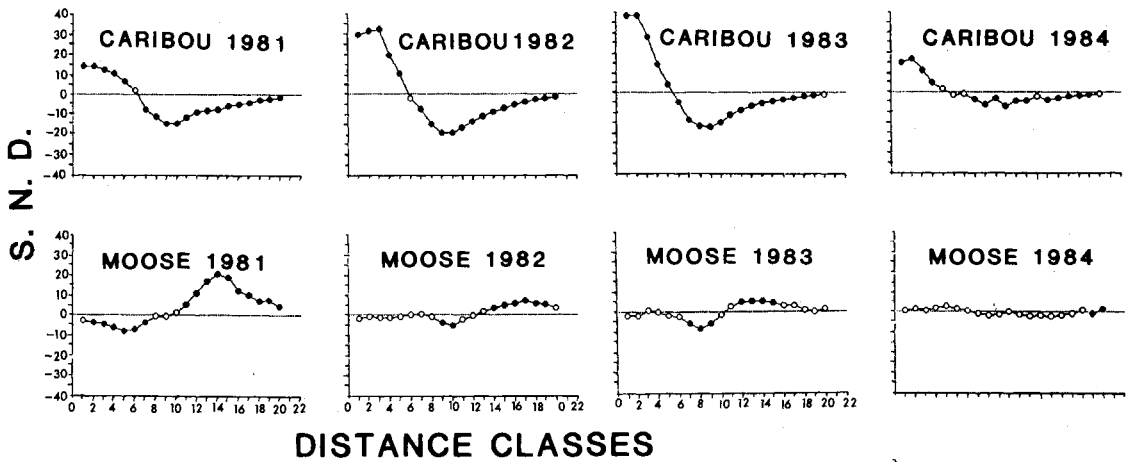| Number of Years' Use	Caribou	Moose
One year only	106	218
Two years	32	102
Three years	9	12
All four years	11	2

$\chi^2=21.8$, d.f.=3, $P=0.0001$

Fig. 4. Spatial correlograms based on standard normal deviates (SND) showed a tendency for caribou to be positively correlated with other members of its own kind at close distances. Negative correlations at longer distances indicated that an individual was not as likely to be found at distance from others of its kind as would be expected by chance. A similar patter was shown in only one year by moose, and in less than half the first 8 classes by wolves. Black squares represent significant values at the a=5% level; white squares are non-significant values. Distance classes were 3.8 km.

positive autocorrelation for short distance classes and significant negative autocorrelation for longer distance classes (Fig. 4). This correlogram pattern is typical ofᵢ a single large patch (Legendre & Fortin, 1989). In these correlograms distances beyond about class 16 should not be considered because too few pairs of points are available for meaningful analysis.

In contrast, moose locations in 1981 were negatively autocorrelated for short distances and highly positively correlated for longer distances. Such a pattern can be explained as a "hole-effect" (Journel & Huijbregts, 1978) resulting from the "doughnut" type of dispersion shown by moose, to some extent each year, but especially in 1981. The more obvious "hole-effect" in 1981 was due to the greater number of observations along the western boundary ofᵢ the study area completing the "doughnut" pattern. To confirm this diagnosis, we removed 46 (from 325) of the western records to destroy the doughnut pattern. The result was a correlogram showing no significant differences, similar to that for 1982, proving that the earlier result was, in fact, a hole-effect artifact, rather than real negative and positive autocorrelation. Moose tracks in all other years showed random distributions over the first 6 distance classes. This finding was unexpected since moose in northern Ontario are usually found in small groups of up to six animals during winter (Cumming, 1972). To further assess these distributions, we calculated Clark & Evans (1954) distance to nearest neighbor indices (R_{CE}) for each species (Table 2). The expec-

Table 2. Dispersion of caribou, moose and wolves in northern Ontario as measured by distances to nearest neighbor (Clark & Evans, 1954) from tracks in snow during 4 winters.

Species	Year	n	R_{CE}[a]	C[b]
Caribou	1981	217	0.33	-18.97
	1982	177	0.40	-15.38
	1983	99	0.28	-13.77
	1984	64	0.43	-8.68
Moose	1981	89	0.75	-4.54
	1982	270	0.82	-5.73
	1983	220	0.81	-3.57
	1984	52	0.74	-3.57
Wolves	1981	19	0.77	-1.90
	1982	9	1.00	0.001
	1983	54	0.78	-3.09
	1984	75	0.63	-6.13

[a] R_{CE} is the ratio between the observed mean distance to nearest neighbor and the expeced nearest neighbor distance, with values <1 indicting clumped dispersion ab values >1 indicating uniform dispersion.

[b] C is related to the normal curve, therefore any value exceeding ±1.96 differs significantly from a random dispersion at the 5 per cent level (Clark & Evans, 1954).
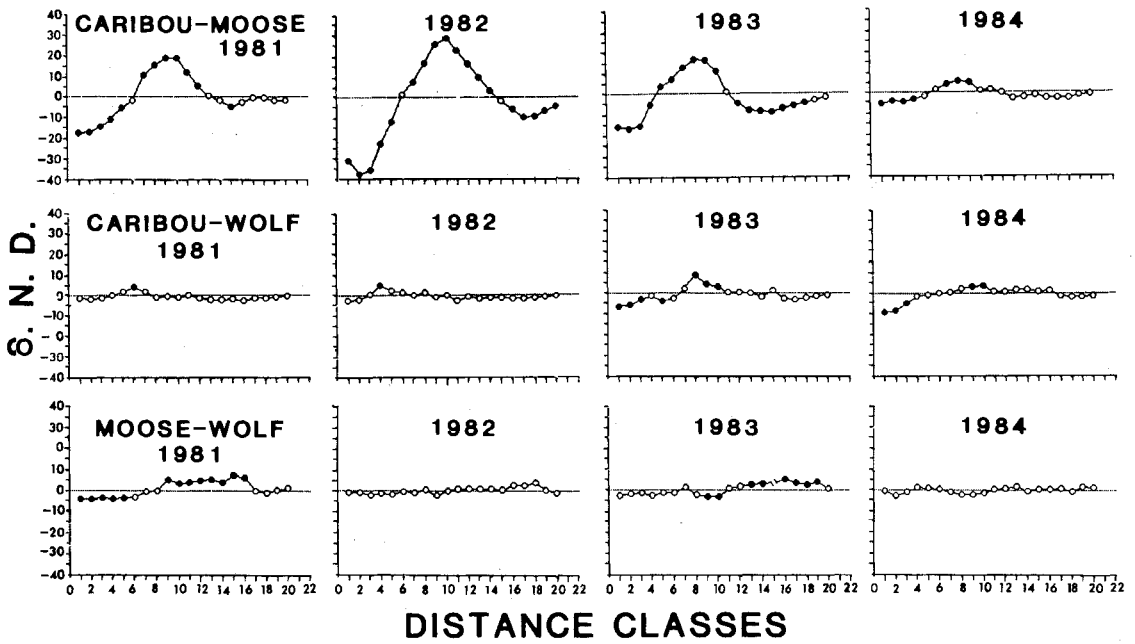
Fig. 5. Spatial cross-correlograms based on standard normal deviates (SND) for pairs of species show negative correlations at shorter distances, indicating that an individual is not as likely to be found near another species as would be expected by chance. Black squares represent significant values at the a=5% level; white squares are non-significant values. Distance classes were 3.8 km.

ted clumped dispersion for caribou was indicated by numbers well below one. A similar low index, but less pronounced, was shown for moose, confirming that moose also clumped together at least to some extent.

Due to relatively small numbers of wolf observations (Fig. 3), we prepared a wolf correlogram only for 1984 when most tracks were recorded. At lags 4, 5, and 7, the graph showed only slight evidence of the negative autocorrelation that would be expected from a territorial animal (Fig. 4). R_{CE} values (Clark & Evans, 1954) revealed no trend here, as they sug-

gested slight clumping tendency for two years, and random dispersion for the other two (Table 2).

What was the autocorrelation structure between species?
Correlograms for caribou-moose always showed strong negative cross-autocorrelations at short distance classes and positive cross-autocorrelations at longer distance classes, indicating negative spatial structure between these species (Fig. 5). Caribou and wolves showed no cross-autocorrelation during 1981, 1982, but the 1983 and 1984 cross-correlograms again showed negative cross-autocorrelation at short

Table 3. Overlapping use of habitat by woodland caribou and moose shown by use of 697 possible 9.29 km² grid cells each year during 4 winters.

Year	Number of cells with tracks			Cells with both caribou and moose tracks	Caribou cells with moose tracks in adjacent cells
	Caribou	Moose	Both	(%)	(%)
1981	80	66	4	5.0	26.3
1982	69	190	4	5.8	24.6
1983	39	159	1	2.6	41.0
1984	43	41	1	2.3	18.6
Total	231	456	10	4.3	26.8

88

Table 4. Schoener's Index of overlap for caribou, moose, and wolves in the Wabakimi Lake study area, based on tracks of each species per computer cell.

Comparison	1981	1982	1983	1984
Caribou/moose	0.071	0.046	0	0.091
Caribou/wolf	0.071	0	0	0.035
Moose/wolf	0.029	0.021	0.064	0.246

Note: Zeros indicate no occurrences of tracks by different species in the same cells.

distances and positive cross-autocorrelation at longer distances. We explain the lack of cross-autocorrelations in the first 2 years by the small number of wolf track observations. Thus, in years when numbers of wolf track observations were adequate, caribou and wolves also showed spatial separation. No pattern of cross-autocorrelation appeared for moose and wolves except in 1981, when the expected negative cross-autocorrelation at short distance classes was observed (although this result might also be explained in part by the same hole effect as for moose alone).

To what extent did areas occupied by the different species overlap?
The presence of negative cross-autocorrelation between species raised questions about the extent of overlap among areas used by these animals. Caribou and moose appeared not to associate with each other. Few computer cell grids (9.29 km²) showed

tracks of both species during any year of the study (Table 3). Of 835 cells for which tracks of one or the other of these 2 species were recorded, only 10 included tracks of both during the same year, and only 27% of cells with caribou tracks showed moose tracks even in adjoining cells (Table 3). Wolf tracks seemed to be more associated with the moose than with the caribou (Fig. 3). Values of Schoener's C index proved to be extremely low for all 3 species, the highest indicating <25% overlap between areas occupied by moose and wolves (Table 4). According to this index, the 3 species occupied distinctly different spaces.

Presumably, such separation could be accomplished by caribou and moose avoiding each other every winter, but only 13% of computer cells recording tracks of either species during the 4 year period showed tracks of both. A similar pattern was recorded once more during the 1988 survey. Thus the differing dispersions indicated habitat partitioning over time, not simply annual avoidance of each other.

Did caribou dispersion increase the distance to predators?
Since predation rates vary with distance between predator and prey (Cumming, 1975), the remoteness of alternative prey species from common predators should provide a measure of relative predation risks for those species. Using simple distance to nearest neighbor measures, mean distance from wolves to caribou over four winters was 15.6 km, significantly greater than that from wolves to moose at only 4.8 km (paired t=9.78, d.f.=156, P<0.001), but more sophisticated measures are available.

Delaunay nearest distance link edges were not independent for the three species (e.g., for 1981, χ^2 = 468, d.f. = 4, P=0.0001) during any year, and the

Table 5. Observed and expected proportions of Delaunay triangulation link edges showing Bonferroni 95% confidence intervals using 1981 data. Where the expected proportion does not lie within the interval, the expected and actual values are significantly different showing that the proportions are not independent. C=caribou, M=moose, P=predator (gray wolf).

	– 5 %	Observed proportion	+5 %	Expected proportion	Significance and direction
p C–C	0.565	0.594	0.623	0.462	⋆ >
p M–M	0.160	0.183	0.206	0.070	⋆ >
p P–P	0.008	0.015	0.022	0.003	⋆ >
p C–M	0.487	0.063	0.077	0.180	⋆ <
p P–M	0.010	0.018	0.026	0.015	
p P–C	0.014	0.023	0.032	0.038	⋆ <

Note: no expected proportions lie near 5% limits (e.g., differences of expected proportions from 5% limits for C–C and P–C, the closest signficant proportions recorded, are 18% of those limits).

Table 6. Significance of Bonferroni 95% confidence intervals and direction of difference for caribou (C), moose (M), and wolf (P) paired associations during four winters.

	1981	1982	1983	1984
p C–C	★ >	★ >	★ >	★ >
p M–M	★ >	★ >	★ >	★ >
p P–P	★ >		★ >	★ >
p C–M	★ <	★ <	★ <	★ <
p P–M				
p P–C	★ <		★ <	★ <

Note: none of the significantly different expected proportions in years 1982-84 lay as close to 5% confidence levels as those recorded for 1981 in Table 5.

1988 data for caribou and moose showed continuation of this pattern. In contrast, data with randomly assigned animal codes showed independence for all comparisons in every year, increasing confidence that our data differed from random. Bonferroni confidence intervals for 1981 (Table 5) showed that caribou-caribou link edges, moose-moose link edges, and wolf-wolf link edges all occurred significantly more frequently than expected, indicating intraspecific clumping. Moose-wolf link edges did not differ significantly from what would be expected by random process, showing that these two species did not react to each other either positively or negatively. In contrast, caribou-moose and caribou-wolf link edges were significantly fewer than expected indicating that the caribou dispersion placed animals of this species at greater than expected distances from both moose and wolves. The importance of this finding was enhanced by the fact that the pattern remained the same each year throughout the study (Table 6), none of the relationships being reversed in any year.

Discussion

Strong negative cross-autocorrelations between caribou and moose, little overlap between occupied areas, and greater than expected (from chance) distance from caribou to the nearest moose all indicated that caribou and moose partitioned the habitat. Negative cross-autocorrelation between caribou and wolves for the only year with sufficient data, and greater than expected distances from caribou to the nearest wolf, suggested that caribou wintering areas constituted implicit refuges. Thus, in Ontario, caribou spaced away from wolves (Bergerud, 1992), thereby fitting the generalizations proposed by Seip (1992)

and the theory of Holt (1977). This finding also supports Bergerud's (1985) contention that all "relic herds" in Ontario have escape habitats which enable them to persist in the face of wolf predation.

Moose showed no autocorrelation, even though Clark & Evans (1954) indices indicated a clumped dispersion, perhaps because the groupings by moose were small enough to be recorded as individual tracks, or on too small a scale for autocorrelation analysis to detect. Wolves failed to show the negative autocorrelation expected of territorial animals. Messier & Crête (1985) suggested that wolf packs would become "detached" at densities <0.23 moose/km², that is, due to severe food limitations, they could not fully colonize the area. If the 8 wolves seen in one pack were representative, the observed packs would total about 40 wolves, or 0.006 wolves/km², a density low enough for these packs to be detached. Wolf packs might also constitute one instance where tracks did not truly indicate the extent of spacing.

Why did wolves specialize on moose?

The observed association of moose and wolf tracks, rather than caribou and wolf tracks, raises a further question: why were wolves found with moose rather than caribou? The relationship may be even stronger than implied because of the added risk of injury to wolves that choose to prey on moose (Mech, 1966). Holleman & Stephenson (1981) working in Alaska concluded that wolves prey on caribou where abundant but will take moose when they are not. One would expect caribou as the smaller prey to be easier to kill; certainly moose are not highly preferred prey when other species of smaller ungulates are available (Murie, 1944; Pimlott et al., 1969).

Three factors may be involved. Firstly, perhaps caribou in Ontario have better escape possibilities than moose, across frozen lakes and in their open-forested wintering areas (Antoniak, 1993). In contrast to the caribou, moose often try to stand (Mech, 1966) and thus may be easier to capture in deep snow. But no real evidence of caribou superiority in escaping wolves is available.

Secondly, the choice may be due to optimal foraging. None of the species could be censused accurately, but totaling the areas of the 9.29 km² cells occupied by caribou (520 km²) and comparing that total with the approximately 100 caribou estimated for the wintering area by Cumming & Beange (1987), suggested a population density of 0.19 caribou/km² in the wintering area (0.015 in the entire study area). An estimate for 1989 using a different method came to 0.11 caribou/km² (Bergerud, 1989) in the portion of the study area that is now a

park (Cumming, 1987a). Moose densities were estimated by the Ontario Ministry of Natural Resources at 0.15 moose/km². Since caribou weigh only about 100 kg, c.f. 400 kg for moose (Banfield, 1974), the biomass/km² provided by the caribou (19 kg/km²) must have been only about 1/3 that provided by the moose (60 kg/km²). Assuming equal vulnerability to wolves, optimal foraging theory suggests that wolves should choose moose because the expectation of yield (in biomass) is greater and, therefore, the moose would constitute the better item (MacArthur, 1972). Wolves should, indeed, pursue only moose since the time required for pursuit would, presumably, be less per unit biomass than for caribou, because the distance wolves had to travel to reach a caribou would be greater (MacArthur, 1972) – a consideration made even more likely by snow depths >50 cm (see Huggard, 1993, for effects of snow on wolf preying behavior).

Thirdly, prey selectivity may depend strictly on prey availability, as concluded by Holleman & Stephenson (1981). Messier & Crête (1985) reported 0.2 moose/km² to be the lowest threshold for supporting wolves. At 0.15 moose/km² even our moose density was well below that threshold. Possibly, caribou biomass, being lower still, was simply too low to support a population of wolves. Presumably, if the caribou population increased sufficiently (i.e. to about 3x their current density) the wolves would be able to switch their attention to the caribou and still survive, as Holt & Kotler (1987) suggested (see also Bergerud, 1983). Therefore, caribou survival may depend on locating places for wintering where moose and wolves are few. In such places they can sustain their populations, but only at low enough densities so that wolves could not specialize on them and survive (perhaps even <0.03/km², Seip, 1992).

Direct competition
But is this predation-related understanding of the results the only one possible? Ecological theorists might choose to ascribe results to direct competition. During winter, moose exploit shrubs and tree regeneration < 3 m in height (Cumming, 1987b). Woodland caribou in Ontario , on the other hand, winter in areas with substantial mats of ground lichens, but few shrubs (Antoniak, 1993). The simplest explanation for the observed habitat partitioning might be that caribou and moose occupy different niches in the boreal forest, partitioning habitat by niche differentiation in a patchy habitat, rather than by a more complicated set of interactions involving wolves. In this case, the simpler explanation should be accepted. However, this view would not explain why caribou numbers in Ontario

remain far below food carrying capacity (Ahti & Hepburn, 1967). Presumably, if niche differentiation were the only explanation, each niche would be filled to capacity. Since they do not appear to be filled, predation may also be involved.

Apparent competition
Support for the idea that changes relate to predation rather than competition only is provided by densities of the three species reported for northern Ontario. The 40 wolves estimated in the study area represent a population density of about 0.006 wolves/km². Ontario Ministry of Natural Resouces surveys in the park portion of the study area during 1961 and 1989 reported two estimates of about 0.004 wolves/km². All three estimates are within the 0.004-0.008 wolves/km² range put forward for this part of Ontario by Kolenosky (1983). In comparison, Kolenosky (1983) suggests densities of 0.002-0.004 wolves/km² for areas farther north where continuous and stable (Darby *et al.*, 1989) caribou populations constitute the major support for wolves, moose being only "common" to "rare", and then mainly along riparian zones (Cumming, 1972). Thus current wolf densities are higher in areas where moose are common, as would be expected from Simkin's (1965) hypothesis.

Direct and apparent competition
But are explanations specifying habitat or predation as limiting factors on caribou populations really competitive, as many biologists in the long controversy over caribou limiting factors (Cumming, 1992) have assumed? Holt (1977) suggested that the realized patterns of abundance probably reflect both direct and apparent competition which may be complementary components (Holt, 1984). Holecamp & Sherman (1989) illustrated the possibility of multiple correct answers to questions of causality in behavioral biology. Could we, as they suggest, consider a synthesis? Enough is not known about woodland caribou to undertake Tinbergen's (1963) 4 levels of explanations, but we can attempt an analysis using Mayr's (1961) proximate and ultimate causes. The direct effect (Armstrong, 1990) of behavior producing the dispersions we observed in our study area was to increase the average distance from caribou to predators, but all these areas were also located in stands with ground lichens (Antoniak, 1993). Thus, the proximate limiting factor of woodland caribou populations in northern Ontario may be predation, but the ultimate hunting factor may be availability of predator-free lichen patches for winter habitat. Both direct competition and apparent competition may contribute to an explanation, as Holt (1977) suggested.

Generalized ecology for woodland caribou in boreal forests of Ontario.

The findings of this study complement several others to make possible the following generalization. In the boreal forests of Ontario, only about 2,000 caribou remain from much higher original numbers (Cumming & Beange, 1993). Moose immigration (beginning about 1900, Peterson, 1955) brought higher wolf densities (Simkin, 1965) that changed conditions for the caribou. Prior to that time, caribou dispersions probably differed from what we find today. Caribou may have occupied more diverse habitats than at present. In addition to the currently used stands of sparsely stocked jack pine and black spruce with substantial ground lichen mats, more heavily stocked stands of these species where ground lichen availability would be marginal, and mixed-wood stands with tree lichens (as currently found on the Slate Islands, Euler *et al.*, 1976), or Canada yew (*Taxus canadensis*, as discussed by Cumming, 1992) could have provided adequate habitat while wolf densities remained low. In some of these habitat types, caribou densities may have built up substantially (similar to recent densities on the Slate Islands, Butler & Bergerud, 1987) leading to early reports of large numbers (DeVos & Peterson, 1951). Caribou probably never used to any extent hardwood stands or moderately- to fully-stocked black spruce stands (e.g., large areas east of Onamon Lake with few moose and few caribou (Cumming & Beange, 1987)).

Decreases in caribou populations before 1900 probably resulted from hunting by European immigrants (DeVos & Peterson, 1951; Cringan, 1957; Bergerud, 1974). From 1900-50, reductions in caribou numbers (DeVos & Peterson, 1951; Cringan, 1957) probably resulted primarily from apparent competition brought about by moose immigration that led to increased wolf densities (Simkin, 1965). Caribou with their lower reproductive rate would have been eliminated from shared marginal coniferous- and mixed-wood stands (as per Holt, 1984), leaving remnant bands only in places where winter predation by wolves could be minimized. Losses after 1950 resulted from disturbance of these wintering areas, often by forest harvesting (Cumming & Beange, 1993).

Continued caribou survival depends on availability of refuges: real refuges on islands or shorelines during open water season, including calving time (Simkin, 1965; Bergerud, 1974; Bergerud, 1985; Cumming & Beange, 1987; Bergerud *et al.*, 1990), and virtual refuges provided by habitat partitioning during winter. Observed caribou recruitment of about 15%; (Cumming & Beange, 1987; Bergerud *et al.*, 1990) has apparently been enough to stabilize caribou in the boreal forest of Ontario in line with Bergerud's (1992) generalization (c.f. heavy adult mortality in Alberta, Edmonds, 1988). Thus, these refuges must be effective. The wintering areas that constitute virtual refuges are forest stands with ground lichens for caribou food, but few shrubs (Antoniak, 1993) to support moose; as a result of optimal foraging choices wolf densities in these areas are generally low (this study, B. Hyer, pers. comm.). Due to this dependence on specific forest stands, caribou wintering areas are relatively fixed. Caribou densities continue well below food carrying capacities (Ahti & Hepburn, 1967) because any major increases would make predation on caribou profitable for the wolves. Despite the apparent excess of foods, caribou probably occupy all winter sites where they can survive.

Caribou bands in Ontario continue to disappear (Cumming & Beange, 1993). Native people currently have little impact on caribou in the boreal forest, perhaps because, like the wolves, they prefer to hunt moose, the more profitable prey (Hamilton, 1984). Loss of caribou geographic range occurs where winter virtual refuges are burned, cut, or invaded by railways and roads, forcing the caribou to move into surrounding areas occupied by moose and wolves at higher densities (Cumming & Beange, 1993). Thus, in the face of apparent competition, survival of woodland caribou in Ontario is dependent on retaining the integrity of refuges for calving, virtual refuges for winter, and travel routes between.

Acknowledgments

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