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FEEDING HABITS OF SYMPATRIC CANIDS IN AN AREA OF MODERATE UNGULATE DENSITY

by

DENNIS W. MELESHKO

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled FEEDING HABITS OF SYMPATRIC CANIDS IN AN AREA OF MODERATE UNGULATE DENSITY submitted by DENNIS W. MELESHKO in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE.

W. A. Fuller
Supervisor
....
....
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Date April 21, 1986

ABSTRACT

The food habits of wolves (*Canis lupus*) and coyotes (*Canis latrans*) in Riding Mountain National Park, Manitoba, were investigated by collecting scats and analyzing their contents. Seasonal results obtained for July 1982 to June 1984, indicated year round heavy use of elk (*Cervus canadensis*) by wolves. Beaver (*Castor canadensis*), cervid young and white-tailed deer (*Odocoileus virginianus*) were seasonally important items. Coyote feeding habits were more varied, with small food items such as cricetid rodents and snowshoe hare (*Lepus americanus*) being of greater importance for them than for wolves. Elk hair was common in winter and spring coyote scats and likely resulted from scavenging wolf and winter kills. Moose (*Alces alces*) and elk populations in the park reached a peak in the late 1970s and have since declined. Elk calf/cow ratios in the early winter have been particularly low. Wolf predation, black bear (*Ursus americanus*) predation and winter weather conditions, both singly and together, appear inadequate to explain the low elk calf production and the continual decline of the population. The overlap in use of elk by wolves and coyotes, especially in winter, provides opportunities for competitive interactions. A continual decline in elk numbers would likely increase the chances of antagonistic encounters between the two canid species.

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I. INTRODUCTION

The food habits of many wildlife species vary over the course of the year. Such variation is influenced by the interactions of a number of factors including the relative availability of different foods, weather and the presence or absence of predators and competitors. Knowledge of seasonal patterns helps to elucidate the relationships among the various species in a community, information that may be of much value to the wildlife manager.

Seasonal variation in the diets of both wolves (*Canis lupus*) and coyotes (*Canis latrans*) has been examined in many parts of North America. Availability and vulnerability of prey species are two factors that influence canid feeding behaviour. Availability, the qualitative assessment of a species' abundance and accessibility for consumption, can be considered in either absolute terms or relative to other prey species. Vulnerability refers to the ease of capture or acquisition by the predator of one prey item relative to others.

Although coyotes are widely distributed across North America and wolves are locally abundant, little is known about their ecological relationship in areas where they coexist. Antagonistic behaviour between the two species, including the killing of coyotes by wolves, has been reported from northern Minnesota (Stenlund 1955, Berg and Chesness 1978) and suggested as having occurred on Isle Royale (Krefting 1969). Radio-collared coyotes have been found to avoid the core areas of wolf territories (Berg and Chesness 1978, Fuller and Keith 1981).

Possible instances of competition between other closely related canids have been reported in the literature. In Alberta, Dekker (1983) noticed coyotes chasing red foxes (*Vulpes vulpes*) and foxes barking at coyotes. Voigt and Earle (1983) suggested that interference competition took the form of interspecific territoriality between red foxes and coyotes in Ontario. Green and Flinders (1981) studied the food habits of the same sympatric canids in Idaho, and concluded that in the absence of coyotes, red foxes may move into their vacated niche. In Africa, jackals (*Canis aureus*) were frequently seen stealing meat from the kills of wild dogs (*Lycaon pictus*) (Estes and Goddard 1967).

Other sympatric carnivores also show some evidence of competition. Myers (1977) considered cheetah (*Acinonyx jubatus*) numbers and distribution to be negatively effected by the presence of spotted hyenas (*Crocuta crocuta*) owing to competition for prey. High overlap in the winter diets of martens (*Martes americana*) and fishers (*Martes pennanti*) suggested the possibility of competitive interactions at least for a short period of time (Clem 1977).

Information on the food habits of wolves and coyotes where both occur together is limited. Berg and Chesness (1978) reported on the food habits of coyotes living on the periphery of wolf territories in northern Minnesota.

Feeding habits of sympatric canids may be influenced by competition. The concept of an ecological niche suggests that in a given area, no two species interact with the environment in precisely the same way (Gause 1934). Although partial overlap of niches could occur, complete overlap would either cause one of the species to disappear or one or both to shift their requirements (Gause 1934). Hence, in natural communities, similar species should differ significantly in some aspect of their ecological requirements (e.g. food, habitat) in order to minimize competition (Krebs 1978).

Base line information on the ecology of wolves in Riding Mountain National Park (R.M.N.P.) was collected from 1975-1979 by L. Carbyn of the Canadian Wildlife Service as one component of the Large Mammal System Studies (Carbyn 1980). The data suggested a need to continue research on predator-prey relationships in the park. The collection of data over a long period of time is a pre-requisite for complete understanding of the dynamics of predator/prey cycles.

Carbyn (1980) reported on the basic relationships between wolves and their prey in R.M.N.P. His report included an analysis of wolf food habits based upon scat contents and winter kill remains. Data on coyote feeding behaviour were also collected (Carbyn unpubl. data). Evidence from that first study indicated that wolves kill coyotes and, although not conclusive, suggested that coyotes survived best along the edges of wolf territories (Carbyn 1982).

The presence of substantial populations of both wolves and coyotes in R.M.N.P. provides an opportunity to investigate one aspect of possible competition between the two species. The main objective of this study was to assess the seasonal food patterns of the two canids by examining the contents of their scats. The collection and analysis of scats, although time consuming, provides year round information on food habits. The main disadvantage of scat analysis is the inability to differentiate between scavenging and predation. Hence it was desirable to supplement this method with field observations and additional sources of data (e.g. kill remains, literature reviews). The tracking of radio-collared animals, although likely the most efficient method of determining feeding habits in winter, is not well suited for detecting the use of small food items that may be rapidly consumed. Furthermore, radio telemetry studies require time to trap and collar the target animals, a condition not possible to satisfy in this study since trapping was not permitted on park land itself.

The primary questions asked were:

1) Are there differences in past and present food habits of wolves and coyotes in the park?

2) What are the seasonal changes (if any) in food consumption for wolves and coyotes?

3) Can any changes in food habits, be related to changes in prey availability or vulnerability, weather conditions, relative numbers of the two canid species, or other external factors? For example, did environmental conditions favour predation on beaver (*Castor canadensis*) by either wolves or coyotes in a particular season?

4) Are there differences in the distributional and grouping patterns of elk (*Cervus canadensis*) and moose (*Alces alces*) compared with earlier results for the park? Can any changes be related to current wolf and coyote feeding habits?

5) Are competitive relationships between wolves and coyotes discernible from seasonal food patterns?

6) Has the influence of wolf predation on the elk population increased over time?

7) Is there any evidence of bears or weather having a [illegible]scernible effect on ungulates in the park?

II. STUDY AREA

Research was conducted in Riding Mountain National Park, a 2974 km² region of boreal mixedwood forest located in southwestern Manitoba, approximately 255 km northwest of Winnipeg (Fig. 1). The park can be considered to be an ecological island since it is surrounded on all sides by farmland. Access into the park is provided by several roads and trails.

Vegetation in the park is diverse, producing a variety of cover types. Predominant are aspen and mixed aspen-white spruce forests, with interspersions of fescue prairie and other grasslands, wetlands, and coniferous forest (Rowe 1972).

Most of the park lies on the Saskatchewan Plain, a gently rolling upland with little vertical relief. Toward the eastern edge of the park is the Manitoba escarpment, a sedimentary formation that drops 450-600 m to the Manitoba Plain below. Numerous waterbodies occur throughout the park. Drainage is poor in the west and central portions of the park; lakes, small ponds, and slow flowing streams are common. In contrast, many fast flowing streams are associated with the escarpment in the east.

The climate of the area is typical of the continental climate of the prairies. Winters are long and cold with moderate snow depths. Summers are short, warm, and dry (Keck 1975).

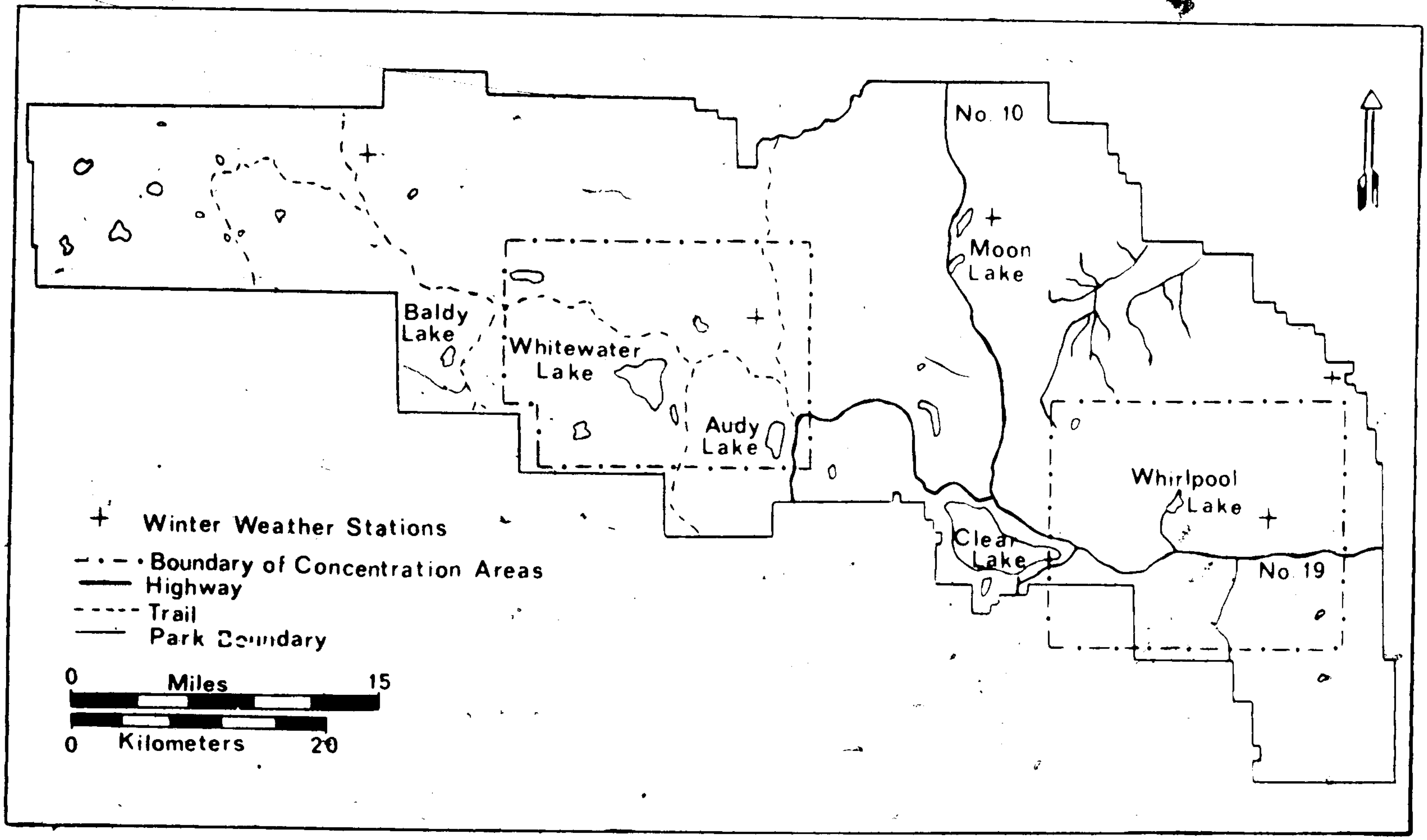


FIG. 1 Map of Riding Mountain National Park, Manitoba

Over 230 species of birds (Soper 1953a) and over 50 species of mammmals (Soper 1953b) have been recorded within R.M.N.P. Resident park populations of large mammals include elk, moose, white-tailed deer (*Odocoileus virginianus*) and beaver, all potential food sources for predators in the park.

III. METHODS

Field work took place periodically from July 1982 to June 1984. Time was spent in Riding Mountain National Park during a portion of each season, each year. Work was spread out over the 2-year period so as to dampen any yearly variation that could be reflected in the data. Scats were collected during each season of each year.

Food habits of wolves and coyotes were determined by analyzing the contents of their scats. These were collected along roads and trails and classified as to their origin on the basis of size (Weaver and Fritts 1979). Scats with a diameter of 30 mm or more were considered to be wolf, while those less than 25 mm were classified as coyote. Those scat in the intermediate range of 25 to 30 mm were discarded unless tracks were present for verification. Scats of wolf pups were distinguished by their occurrence at known wolf dens or rendezvous sites. Black bear (*Ursus americanus*) scats were collected during the summer.

Frequency of coverage of the various trails and roads varied according to a number of factors including weather and other field commitments. The more accessible areas were covered frequently; usually once every two weeks. Remote, and often less productive, areas were covered once or twice during each season. Overall, coverage was concentrated on the trails and roads centered on Whitewater Lake, Lake Audy and Highway #19 (Fig. 1). In all cases, only relatively fresh scats were picked up in order to give validity to their seasonal classification. In summer, weathering of scats was quite pronounced, which allowed for adequate discrimination. In winter, old scats would eventually be covered by snow or melted into it. (Consistency and colour of scats may be of help in determining time of deposition relative to occurrence of last meal; Appendix 1.)

For analysis, seasons were defined as follows: Winter (December to March), Spring (April and May), Summer (June to September) and Fall (October and November). These periods coincide with the seasons used by Carbyn (1980), based upon biological events for wolves.

Certain precautions were taken when handling canid scat because of the risk of *Echinococcus* spp. infection. In the field, samples were picked up by inverting plastic bags over them. After double-bagging them, scat samples were placed in a freezer. Processing of the material took place in an independently ventilated lab. Gloves and a facial mask were used at all times.

Analysis of scat contents followed methods outlined by Kennedy and Carbyn (1981). Frozen material was thawed under hot water and hair and bone samples were separated from detrital material by the use of sieves. Washed samples were placed in an oven to dry for 30 minutes at 120° C. The dried material was then spread out in an observation pan and representative hairs were picked out. Any distinctive bone material was noted at that time. The hairs selected were laid out upon an acetate strip and then sandwiched between two microscope slides by the use of large paper clips. The preparation was placed in the oven at 110° C for 10 minutes. Upon retrieval, the hairs were displaced 1-2 mm off their impressions and a cover slip was applied.

Although some identification of contents was possible from bone material or gross morphology of hair, most analysis required the use of a compound microscope to examine hair structure in detail. The key provided by Kennedy and Carbyn (1981) allowed for separation to species (in most cases) on the basis of cuticular scale pattern, medulla characteristics and external features. The key also allowed for distinguishing between the hair of adult and young cervids in summer scats. Although there are some microscopic differences between the hair of deer fawns, elk calves and moose calves, too little confidence in separating them, resulted in no further identification than a grouped category of cervid young. Beaver and muskrat hair are also very similar in appearance and hence some minor error in separating them might have occurred.

Hair or bone material identified in a scat as coming from one prey species, was considered as a single food item. Some scats contained hair from more than one prey species and hence total number of food items found was larger than the total number of scats. The results of the scat analyses for both canids were, for each different food item, expressed as frequency of occurrence and percent frequency of occurrence based upon total number of food items.

Important food items were considered to be those consumed in relatively large quantities as indicated by their large frequencies of occurrence. Weighted frequencies of occurrence were also derived from the contents of both wolf and coyote scats. In that method, when more than one prey item occurred in a scat, each prey item was weighted the same (i.e. no attempt was made to estimate the relative amounts of different items in a scat). For example, if two items occurred in a scat, each was given a value of 0.5. Three items were assigned a value of 0.3 each. Unweighted frequency data were used in comparison with other studies and in statistical treatments. Weighted data might more accurately reflect food habits and were used in the calculations of biomass equivalences.

For six food items, frequencies of occurrence in winter and summer scats were converted to values representing the biomass and the number of individuals consumed. From the experimental feeding of captive wolves, Floyd et al. (1978) derived a regression equation:

$$y = 0.38 + 0.02x$$

where y is the kg of prey per collectible scat and x is the assumed weight (kg) of an individual of a given prey type.

Food items from adult prey found in scats were separated into three categories on the basis of weight (following Bowen 1981). The first category consisted of food items greater in weight than that of the predator (i.e. >50 kg for wolves, >15 kg for coyotes). For both canids, this category contained those items for which group hunting would be advantageous. The second category included items weighing less than the predator but more than 2 kg. In this case foraging alone would usually be sufficient, although interaction with conspecifics may be beneficial. The third category included all items under 2 kg. Foraging could be done by a single animal.

Population surveys of beaver, elk and moose are regularly carried out by the warden service of R.M.N.P. The ungulate survey, conducted in mid to late February, consists of flying systematic north-south transects at 1.6 km intervals and recording all moose and elk observed within a 200 m strip on both sides of the transect. Since coverage is approximately 25%, estimates of total park numbers are calculated by multiplying the total count by four. A statistical sampling method can be used to provide population estimates with 95% confidence limits (Cochrane 1977). Transects were divided into 575 blocks (3.2 km by 0.4 km) and the mean number of elk/moose per block was calculated; with total estimates for the park based upon 2326 total blocks (for detailed example of method see Ristau and Meleshko 1983). In the beaver survey, a complete census of food caches in 30 blocks (each 23 km²) was carried out from the air giving about 23% coverage of the park. Allowing for an average of five beavers per food cache or colony (Denny 1952, cited by Hill 1982), estimates of total numbers were derived (for details see Trottier 1980). The survey was conducted in mid-October, after freeze-up but before significant snow fall. Both surveys were flown in a Cessna 206 with a pilot, navigator, two observers and a recorder.

Separate counts of elk and moose, classified by age and sex, were carried out in November 1983, and in March and November 1984 in areas of ungulate concentrations, noted in previous studies and surveys. Areas were also chosen to give representative sampling of the park habitats and relative moose and elk densities. It was judged that sightings of approximately 25% of both moose and elk (based upon the most recent warden survey) would provide a reasonable sample size (Czaplewski et al. 1983). A structured sampling design would have entailed much greater cost.

A Cessna 172, with pilot, navigator/front-right observer, and rear-left observer was used. All animals (elk, moose, and deer) that could be classified were recorded from both the concentration areas and flight lines across the park to those areas. Transects at about 800 m intervals were done in the concentration areas, direction of flight being determined by navigational considerations (e.g. landmarks, safety). All sightings were used in the calculations of overall sex and age ratios.

Altitude above ground varied from about 60 m to 250 m. Initially higher altitudes were maintained in order to facilitate the spotting of groups. Low level flying, which often included circling, was necessary to completely and confidently classify groups.

A single observer was usually able to classify the animals seen in small groups (generally fewer than ten animals). For larger groups, animals were circled clockwise and one observer counted calves while the other counted bulls and total animals. Several passes and counts were made (if necessary) until both observers were satisfied with the accuracy of the count.

Animals were classified as adult cows (≥ 1 year old), adult bulls (≥ 2 years old), yearling bulls (≥ 1 year old and < 2 years old) and calves (< 1 year old). (Spike or yearling bulls were distinguished by their degree of antler growth, although this method is not without some error, especially for moose.) These categories were also used in the recording of year-round observations of ungulates seen in the park.

Analysis of the frequency data for canid food habits was done using the G-test statistic, which was preferred over χ^2 because of its additivity (Sokal and Rohlf 1981:692). The smaller frequency food items were grouped together, giving a total of eight categories to examine statistically (muskrat was separated from other cricetid rodents.) For some of the analysis, since multiple comparisons were done, it was necessary to consult a table based upon Sidak's multiplicative inequality. At the first level of analysis 12 comparisons were made and the G value of significance at the 5% level was 20.685 (24.759 at 1% level). At the second level there were 96 (12x8) individual comparisons and an estimated G value of significance at the 5% level was calculated to be 12.25 (15.32 at the .1% level).

Morisita's (1959) coefficient of similarity was also used in examining seasonal differences in feeding patterns between wolves and coyotes. The coefficient is calculated from the equation:

$$C = \frac{2\left(\sum_{i=1}^{s} x_i y_i\right)}{\left(\sum_{i=1}^{s} x_i^2 + \sum_{i=1}^{s} y_i^2\right)}$$

where s is the total number of food species and x_i and y_i are the proportions of species i in the diets of species x and species y.

Variance to mean ratios, x^2, mean centers of distribution, standard distances and the Poisson distribution were used to analyze the dispersion of moose and elk. An ANOVA was performed on the survey data to examine the significance of the variation in the total counts from year to year. Unplanned comparisons among means were made using the Welsch Step-up Procedure (Sokal and Rohlf 1981). Confidence limits for classified surveys followed the method of Czaplewski et al. (1983). Data on group sizes of cow/calf and cow/calfless aggregations were analyzed by Student's t-test.

Weather data were collected from park records and summarized. Winter data were taken from five weather stations scattered through the park (Fig. 1). Mean monthly temperature (MT), snow depth (SD1), snow density (SD2) and an ocular estimate of snow hardness (SH) were used to calculate a monthly winter severity index (MS) (Dolan and Tempany 1980) by the following formula:

$$MS = SD1 + SD2 + SH + MT \text{ (if } - {}^{\circ}C\text{) or } - MT \text{ (if } + {}^{\circ}C\text{)}$$

Total winter severity was calculated by adding the monthly values together (for November to April) along with a value representing the difference between date of the year's green-up and the mean green-up date of May 11.

Nonparametric and parametric correlation coefficients were calculated where appropriate. Unless otherwise stated, the level of significance was 5%.

IV. RESULTS

A. General food habits

Wolf

In all 1027 scats, containing 1194 food items, were collected. On a seasonal basis, 429 scats with 528 food items were obtained in the summer, 136 scats with 170 items in autumn, 263 scats with 273 items in winter and 199 scats with 223 items in spring.

Throughout the course of the study, elk was clearly the most important food item for wolves with a frequency of occurrence of almost 42% (Fig. 2). The second most important item, beaver, occurred less than half as often at 16.8%. All other food items were under 10%, with moose, white-tailed deer, snowshoe hare (*Lepus americanus*) and cervid young all near 7%.

Overall, mammalian items totalled 97.9% with ungulates (moose, elk, deer and cervid young) comprising 62.4%. Non-mammalian food items were of minor importance (Fig. 2). Large prey items (>50 kg) were 55.5% of the diet, medium items (2.0-50 kg) 19.8% and small items (<2.0 kg) 16.0%.

The hair of cervid young is indistinguishable from adults after late summer/early fall, so percent frequency is likely underestimated. The overall total of 6.9% should be considered a lower limit, since young of the year were likely also taken in late fall, winter and spring. Hence the

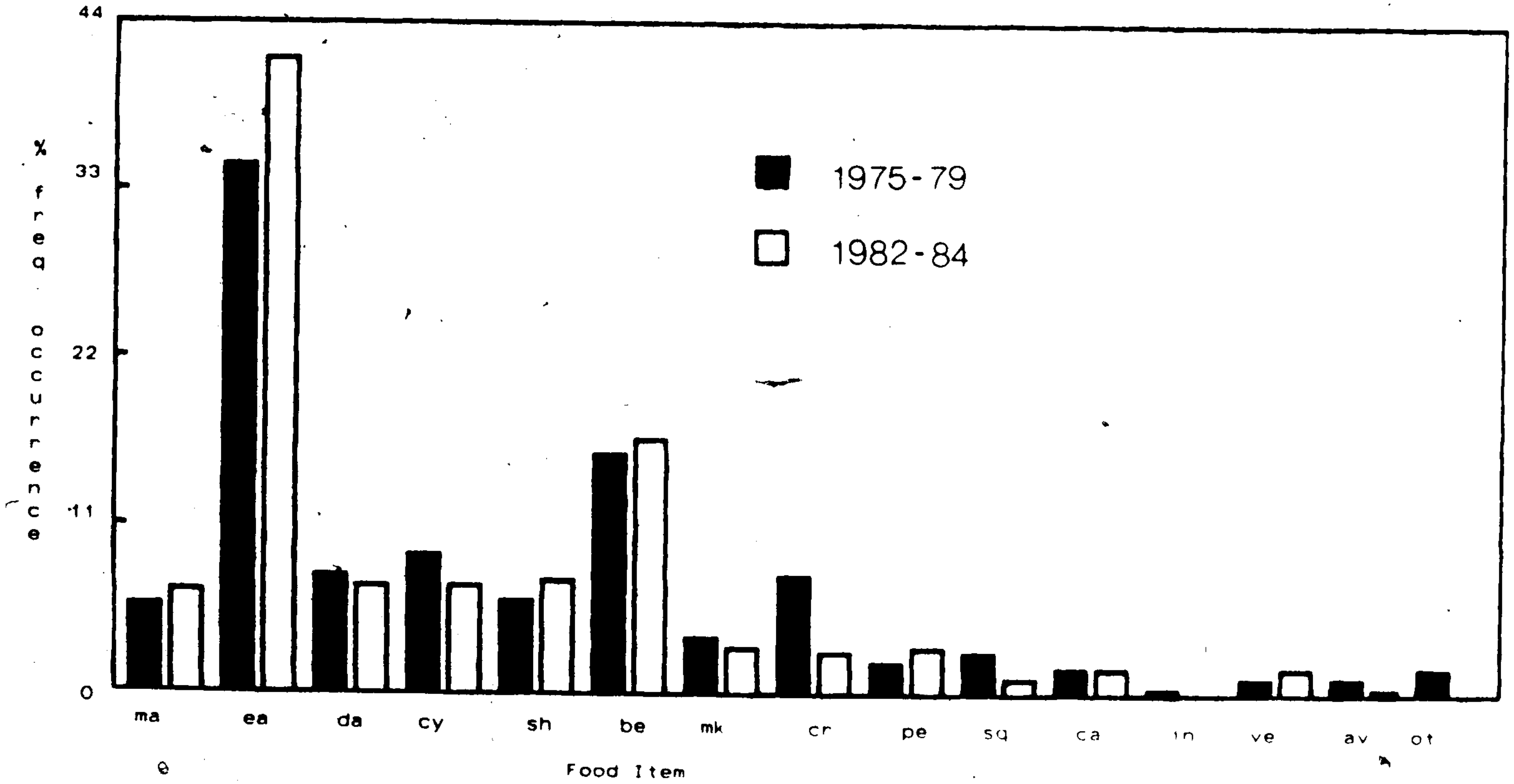


FIG. 2. Percent frequency of occurrence of food items in wolf scats from two studies in R.M.N.P. (ma=moose, ea=elk, da=deer, cy=cervid young, sh=snowshoe hare, be=beaver, mk=muskrat, cr=cricetid, pe=porcupine, sq=squirrel, ca=canid, in=insect, ve=vegetation, av=bird, ot=others).

elk, moose and deer totals include calves and fawns from the winter and spring periods.

Canids were listed as a food item although this is not necessarily the case. Light microscope methods do not allow for adequate discrimination between wolf and coyote hairs (Kennedy 1982). Hence, incidental wolf hair, possibly from grooming can occur in the scats. This supposition was supported by frequent occurrences of other food items in the scats containing canid hair. Wolves also occasionally kill other wolves (Marhenke 1971) and hence may swallow wolf hair even if the carcass is not eaten. In addition, wolves are known to kill coyotes, so canid hair in scats could also be from coyotes.

The overall yearly feeding pattern was not affected much by the unequal sample sizes collected for each season. Although approximately 1.6 times more summer than winter scats were collected, weighted mean values of percent frequency were not much different from the unweighted values. The largest difference was for elk, which, owing to its high winter frequency of 59.9%, would increase overall by 2.1% to 43.7%. The largest drop was found in the beaver component, which went from 16.8% to 15.3% in overall use. Most other food categories varied by less than 1.0%.

Overall wolf feeding habits as determined from scat analysis, are similar to those reported in an earlier study in R.M.N.P. (Carbyn 1980) (Fig. 2). Although the overall G value was significant ($G=34.3$, $p < 0.01$), partitioning of this value indicated that only the food category of Cricetidae varied significantly ($G=24.4$, $p < 0.01$) between the two studies. Use of mice dropped from 7.5% to 2.7%. The only other major difference, although not statistically significant, was for elk, which increased from 34.6% to 41.6%. The "others" category from the first study included domestic cattle (*Bos* spp.), with a frequency of occurrence of 1.0%. There was no evidence from scat analysis in this study of wolves preying or scavenging on domestic livestock.

The overall occurrence of mammalian food items in the first study was 96.0% and for ungulates it was 56.7%. These values approximate those found in this study, although they are somewhat lower, suggesting slightly less reliance on those items in the past.

Coyote

Altogether 1811 food items were found in the 1430 scats collected. Seasonally there were 786 food items in 585 summer scats, 310 items in 252 fall scats, 411 items in 348 winter scats and 304 items in 244 spring scats.

As for wolves, the two most important food items for coyotes, as indicated by their frequency of occurrence in scats, were elk (27.9%) and beaver (19.0%) (Fig. 3). Other items used frequently were snowshoe hare (13.2%) and cricetid rodents (9.3%). Canid hair, insects and bird remains occurred infrequently.

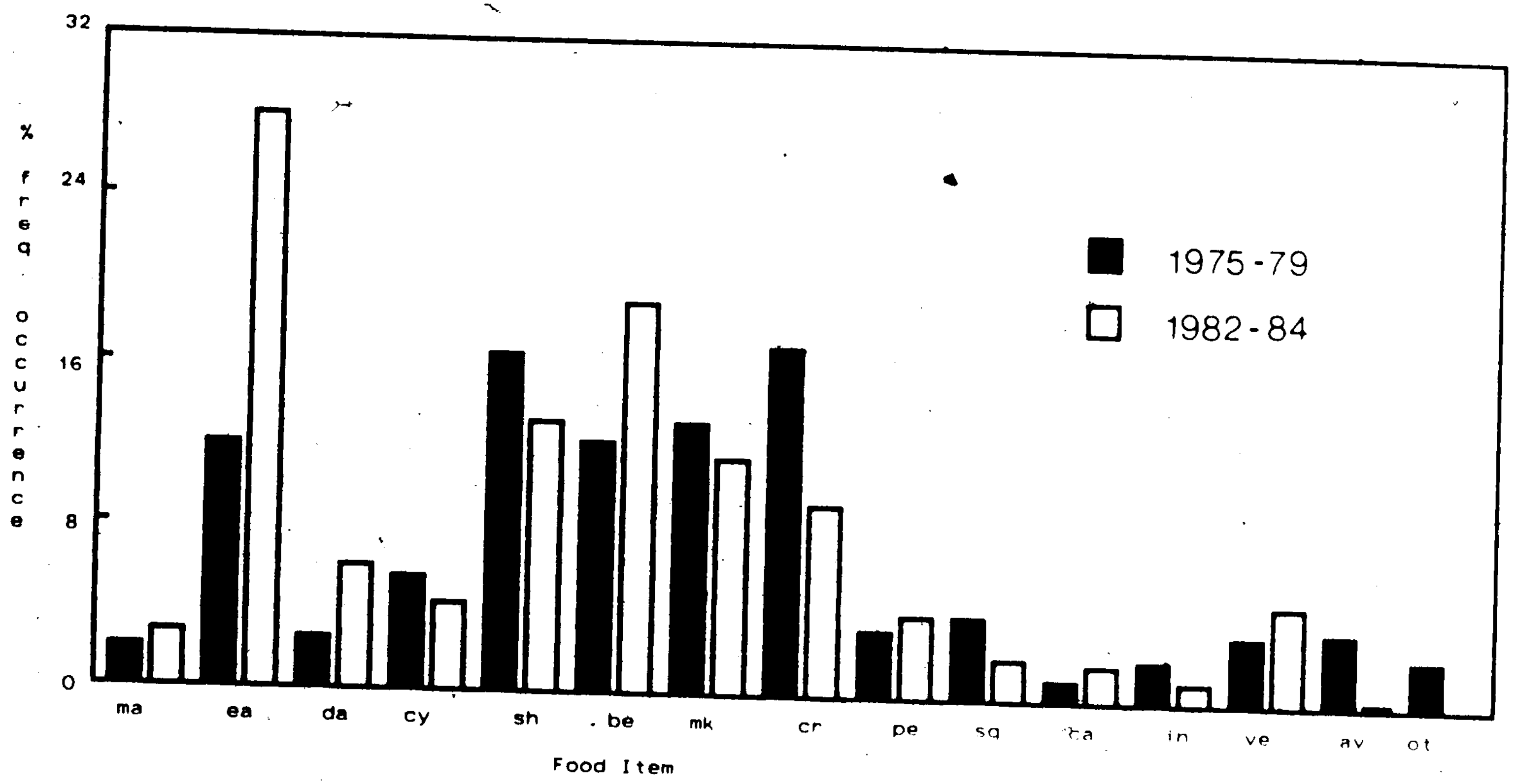


FIG. 3. Percent frequency of occurrence of food items in coyote scats from two studies in R.M.N.P. (Abbreviations as in Fig. 2.)

The total ungulate occurrence was 41.0%, while all mammalian items comprised 94.2%. By weight, prey larger than 15 kg occurred at 36.6%, medium size prey, those between 15 kg and 2.0 kg, occurred at 22.9%, and prey less than 2.0 kg at 34.2%.

Cervid young again were probably underestimated. The occasional occurrence of canid hair in the scats could result from incidental swallowing of fur while eating or grooming.

The frequency of occurrence of food items in this study differed quite markedly from that in the previous study in the park (Fig. 3) (Carbyn unpubl. data). The G statistic for the overall comparison was highly significant ($G=276.7$, $p < 0.01$), with six of the eight individual categories showing a significant change. Only moose and snowshoe hare did not differ significantly . Both elk and deer more than doubled, with elk going from 12.0% to 27.9%. Beaver increased from 12.3% to 19.0%. Three food categories decreased significantly; muskrat decreased from 13.2% to 3.8%, Cricetidae from 16.9% to 9.3% and miscellaneous items from 24.4% to 18.0%. Muskrat and elk had the largest individual G values of 86.1 and 95.0, respectively. The "other" category for the first study included fish, raccoon (*Procyon lotor*) and domestic cattle, none of which was identified in scats during the present study.

B. Seasonality

Wolf

Seasonal data were compared across the two years of the study to examine any trends (Fig. 4). Elk was the only food item to exhibit a consistent pattern, with percent frequency of occurrence for all four seasons being greater in the second year of the study compared with the first. Small sample sizes precluded any statistical analysis on a yearly-seasonal basis; however the total yearly use data pool was deemed sufficiently large for analysis. Analysis of data on this basis showed little variation. Snowshoe hare consumption decreased significantly ($G=17.0$, $p < 0.01$) from the first year of the study (summer 1982 to spring 1983) to the second year (summer 1983 to spring 1984): 12.2% to 5.0%. No other food categories changed significantly.

Overall G values were significant for all pairwise comparisons of seasons (both years pooled). The largest difference was between summer and winter ($G = 195.11$, $p \ll 0.01$) and the smallest between winter and spring ($G = 36.7$, $p < 0.01$).

Elk and moose occurred most often in wolf scats from winter and spring (Table 1). Deer consumption was large in winter and fall. For all three ungulates, winter occurrence was significantly greater than that for summer.

Beaver consumption did not show any significant variation among fall, spring and summer. Winter use,

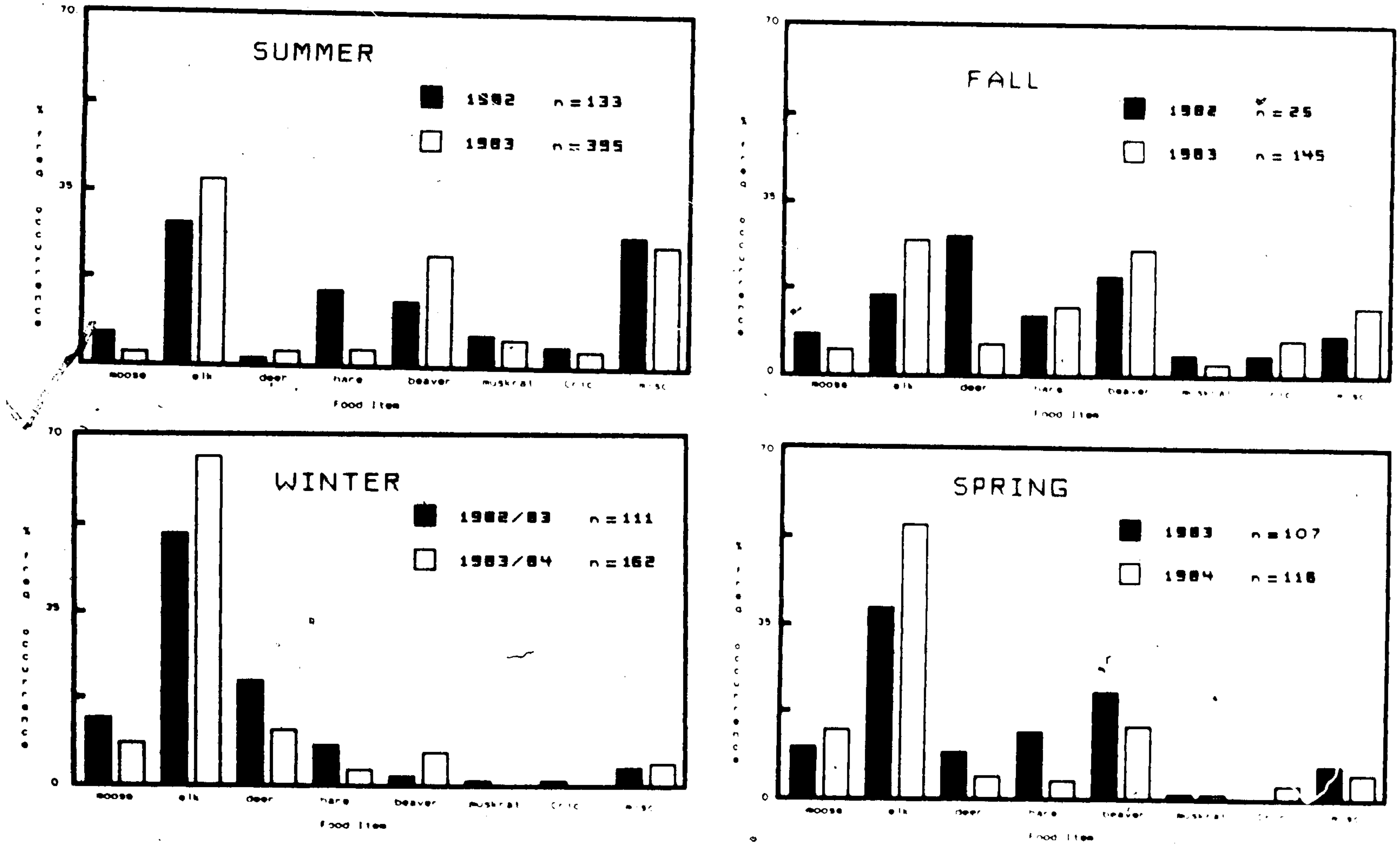


FIG. 4 Seasonal occurrences of food items in wolf scats (Cric =Cricetidae misc =miscellaneous)

Table 1 Comparison of wolf and coyote seasonal use of food items
Use expressed as a percentage

	Summer	Fall	Winter	Spring	Seasonal comparisons[1]					
					s-w	s-f	s-sp	f-w	w-sp	f-sp
Wolf										
Elk	35.2•[2]	25.3	59.7	47.1	•			•		•
Beaver	19.9	24.7	14.8	17.9	•			•	•	
Snowshoe Hare	6.1	13.5	5.1•	8.1						
Deer	2.5	9.4•	15.0	6.7	•	•				
Moose	3.0	5.3•	10.6	12.1	•		•			
Muskrat	5.3	2.4	0.4	0.9	•					
Cricetidae	3.2•	6.5	0.4	1.3				•		
Miscellaneous	24.8	13.0	4.0	5.8	•		•			
Coyote										
Elk	19.0•	19.7	44.8	36.8	•		•	•		•
Beaver	18.3	31.0	12.7	17.1		•		•		•
Snowshoe Hare	10.3	13.2	14.6•	18.8						
Deer	4.6	1.9•	11.7	5.6	•			•		
Moose	1.5	0.0•	5.1	5.6				•		•
Muskrat	5.7	3.2	1.5	2.3	•					
Cricetidae	12.1•	12.6	3.6	6.6	•			•		
Miscellaneous	28.5	18.2	6.0	7.3	•		•	•		•

1 Legend s-w summer-winter; s-f summer-fall, s-sp summer-spring
f-w fall-winter; w-sp winter-spring, f-sp fall-spring

2 Indicates statistical difference in use of food item between wolves and coyotes

• $p < 0.05$

however, was significantly less than in any other season with an occurrence of less than 5%. Muskrat use exceeded 5% only in summer, and this differed significantly from winter. The amount of snowshoe hare did not exhibit any significant seasonal variation, although fall was the only season in which it exceeded 10%.

Cricetidae accounted for 6.5% of the diet in fall and this differed significantly from a low winter use. Summer use (3.2%) was also relatively high but it did not differ significantly from either winter or spring (1.3%).

Consumption of the various miscellaneous items was greatest in summer, when it was significantly different from spring and winter. Fall use was intermediate in occurrence and not significantly different from other seasons. The comparisons are biased by the inclusion of cervid young in only the summer (15.0%) and fall (2.4%) categories. However, elimination of cervid young from the analysis did not change the statistical results. The few occurrences of insects and bird remains in the scats all were in the fall and summer. Porcupine did not occur in the spring, and vegetation was consumed only by wolves in summer and fall. Squirrel use was greatest in summer.

Compared with the results of the the first study (Appendix 2), summer and fall overall were significantly different (G= 36.87 and 27.15, respectively, $p < 0.01$) while winter was not (G= 13.20, $p > 0.05$). The only significant individual difference in summer occurred for Cricetidae, which dropped from 10.0% to 3.2%. In the fall, snowshoe hare was up significantly in this study, rising from 0.8% to 13.5% (Table 1).

Correlation coefficients among elk, moose, deer and beaver were examined on a yearly and seasonal basis. After adjustment of the significance level owing to multiple comparisons, none of the six associations was significant. In general, however, all three ungulate species were negatively associated with beaver. Elk and moose had the highest degree of association with each other ($r_s=0.64$, $p > 0.05$).

Coyote

The seasonal data were divided into their yearly components to assess any trends in the data over the course of the study (Fig. 5). Percent frequency of occurrence of beaver and elk was greater and snowshoe hare less in every season of the second year compared with the first. Analysis of yearly data showed significant variation between years ($G=192.96$, $p < 0.01$). Beaver displayed a significant increase in use from 7.8% in 1982/83 to 23.1% in 1983/84 ($G=51.83$, $p < 0.01$). Both moose and snowshoe hare dropped significantly; moose from 5.8% to 1.7% ($G=18.90$, $p < 0.01$) and hare from 26.4% to 8.4% ($G=76.36$, $p <0.01$). Miscellaneous items increased significantly from 9.4% in 1982/83 to 21.3% in 1983/84 ($G=31.07$, $p < 0.01$). The four

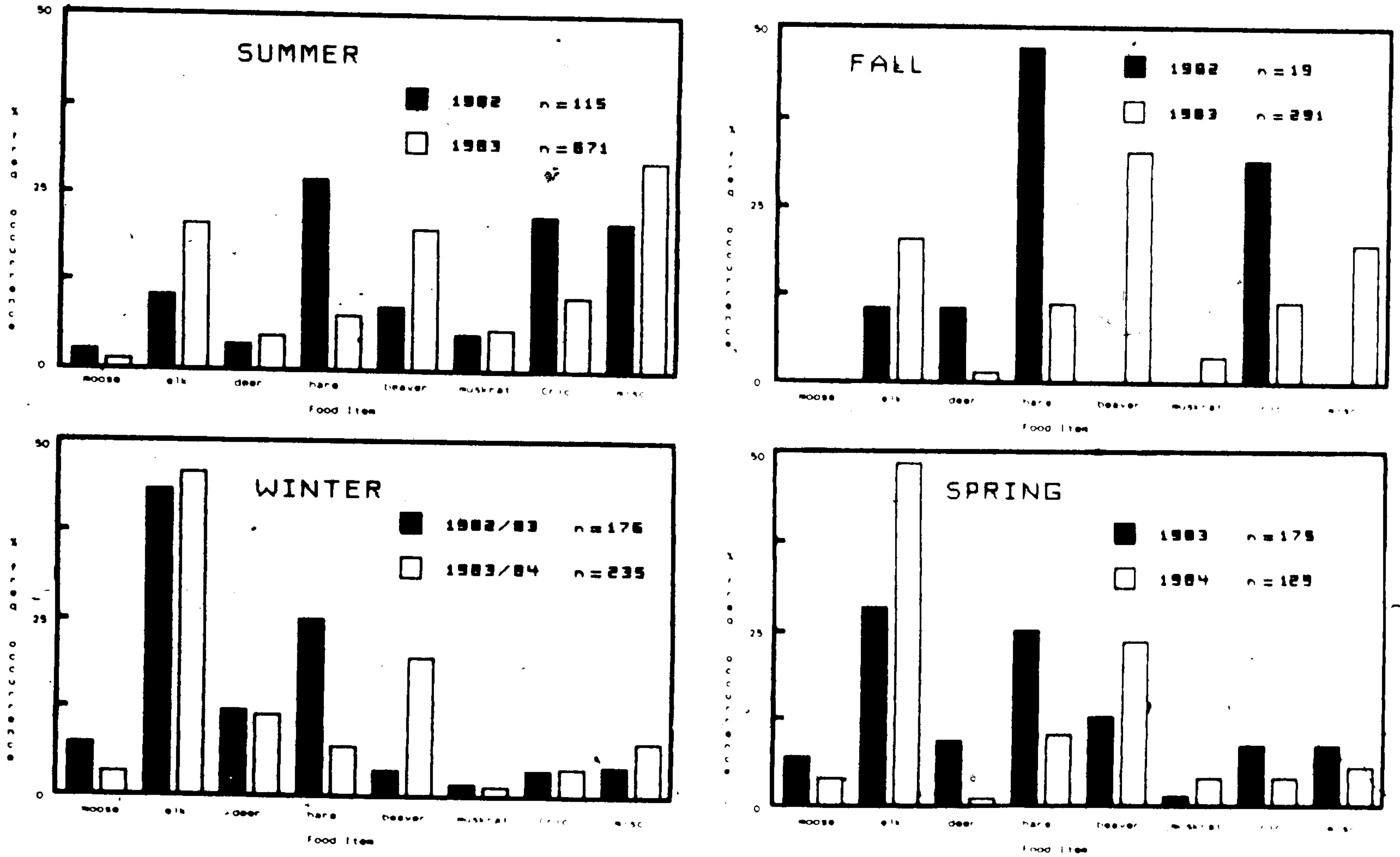


FIG. 5 Seasonal occurrences of food items in coyote scats (Cric =Cricetidae, misc =miscellaneous)

other food categories did not show significant changes.

Five out of six seasonal comparisons (both years pooled) were significant. There were no major differences in consumption of the various food items between winter and spring. Summer and winter differed the most ($G=217.95$, $p < 0.01$).

Consumption of all three ungulate species was greatest in winter and spring (Table 1). Fall use was significantly less than winter use. Moose hair did not occur in any fall coyote scats and deer hair was infrequent.

Hair of beaver was identified in all four seasons, with the fall frequency of 31.0% being significantly greater than that for all other seasons. Use in summer and spring was similar, with a slight drop in winter. Muskrat consumption was highest in summer and this differed significantly from winter. For snowshoe hare, although the trend from greatest to least use was spring, winter, fall and summer (an overall difference of 8.8%), no seasonal comparisons differed significantly.

The eating of mice and voles by coyotes was significantly greater in fall and summer than in winter. Remnants of miscellaneous items occurred significantly more often in summer and fall than in spring and winter. In large part this was due to cervid young (9.8% in summer, 0.9% in fall), but squirrel, porcupine and vegetation also occurred less in winter and spring than in the other two seasons. The only two occurrences of bird feathers were in summer scats, and 16 out of 17 insect remains occurred in that season as well.

The frequency data for all four seasons differed significantly from that recorded from 1975-79 (Appendix 3). In the summers of 1982 and 1983, use of elk, deer and beaver was up while use of snowshoe hare and cricetids was down. In fall, frequency of beaver hair in scats increased. In winter, miscellaneous items decreased and snowshoe hare increased in frequency of occurrence. The occurrence of muskrat hair was less in every season of this study than in Carbyn's (1980).

Correlation coefficients were calculated for elk, moose, deer and beaver percent use on a seasonal-yearly basis. None of the r_s values were significant. Moose and deer were negatively associated with beaver; all other values were positive. Deer and beaver use showed the greatest association ($r_s=-0.70$).

C. Biomass consumption

Calculation of biomass equivalences from frequency data and assumed weights, provides a different perspective for looking at data derived from scat contents. Floyd et al. (1978) argued that frequency data, because of a varying surface to volume ratio, would tend to underestimate the contribution in terms of weight of larger prey and overestimate that of smaller prey. The reverse would be the case in terms of prey numbers.

Wolf

Table 2 shows the results of biomass calculations for summer wolf scats. In terms of individuals eaten, wolves consumed approximately equal numbers of elk, beaver, muskrat and snowshoe hare. Moose and deer were taken in a ratio of about 11 elk for each moose and deer.

In terms of the six categories considered, frequency data (column 4) showed elk, a large prey item, occurring in 51.9% of the scats, and snowshoe hare, a small prey item, occurring in 6.3% of the scats. However in terms of mass (column 6), elk comprised 83.7% and snowshoe hare only 0.7%. Conversely, in terms of numbers (column 7), elk dropped to 20.9% and snowshoe hare increased to 27.0%. Cervid young could have been included in the table if the proportions of elk calves, moose calves and deer fawns were assumed to be the same as that reported by Carbyn (1980). In such a case, elk calf, moose calf and deer fawn hair, which occurred in 51.5, 2.0 and 11.7 scats, respectively, would have comprised 5.6% of the summer diet by weight and 11.4% by number of individuals (assuming average weights of 30, 58 and 20 kg for elk calf, moose calf and deer fawn, respectively).

In winter, elk is not only the most important item in terms of mass (76.9%), but also in terms of numbers (41.6%) (Table 3). For every 10 elk eaten, approximately 2 moose,

TABLE 2. Biomass equivalent calculations derived from number of prey items in summer wolf scats

Prey Item	Assumed wt. (kg)[1]	Estim. kg eaten/scat[2]	No. scat with item	kg eaten	kg eaten live wt.[3]	No. individuals eaten	Ratio of individuals eaten
Elk	247	5.32	165.33	879.56	1172.75	4.75	1.00
Moose	302	6.42	14.50	93.09	124.12	0.41	0.09
Deer	64	1.66	11.50	19.09	25.45	0.40	0.08
Beaver	12.5	0.63	87.00	54.81	60.90	4.87	1.03
Snowshoe Hare	1.5	0.41	20.16	8.27	9.19	6.13	1.29
Muskrat	1.5	0.41	20.16	8.27	9.19	6.13	1.29

[1] Sources of weights from Carbyn and Kingsley (1979)
[2] Derived from Floyd et al. (1978)
[3] Following Fuller and Keith (1980). Dead weight (i.e. kg eaten) was considered to be 75% of live weight of cervids, 90% for smaller prey

TABLE 3. Biomass equivalent calculations derived from number of prey items in winter wolf scats

Prey Item	Assumed wt. (kg)[1]	Estim. kg eaten/scat[2]	No. scat with item	kg eaten	kg eaten live wt.[3]	No. individuals eaten	Ratio of individuals eaten
Elk	247	5.32	160.50	853.86	1138.48	4.61	1.00
Moose	302	6.42	28.00	179.76	239.68	0.79	0.17
Deer	64	1.66	40.00	66.40	88.53	1.38	0.30
Beaver	12.5	0.63	11.50	7.25	8.06	0.64	0.14
Snowshoe Hare	1.5	0.41	11.50	4.72	5.24	3.50	0.76
Muskrat	1.5	0.41	0.50	0.21	0.23	0.16	0.03

[1] Sources of weights from Carbyn and Kingsley (1979)
[2] Derived from Floyd et al. ([illegible]78)
[3] Following Fuller and Keith (1980). Dead weight (i.e. kg eaten) was considered to be 75% of live weight of cervids, 90% for smaller prey

1.5 beaver and 3 deer are consumed. These results are in general agreement with those for number of kills located in the park at the same time as scat samples were collected (P. Paquet pers. comm.), when the ratio was approximately 10 elk for 2.5 moose and 1.5 deer. The lower value for deer is understandable considering its smaller size and the rapid rate at which it is consumed, and hence the greater probability of missing such a kill when searching. In terms of weight, the differences between summer and winter were increases in moose and deer and decreases in beaver, muskrat and snowshoe hare.

Coyote

In the summer (Table 4), percentages of individuals consumed (column 7) as derived from the equation of Floyd et al. (1978) were: elk 9.5, moose 0.7, deer 3.0, beaver 17.5, snowshoe hare 44.3 and muskrat 25.0. By weight, elk was clearly the most important item at 76.1%, and moose and deer occur at 7.2% and 6.2%, respectively. Beaver was the third most important item at 7.1%, with snowshoe hare (2.2%) and muskrat (1.2%) of only minor importance.

In winter (Table 5) snowshoe hare remained the most important item in terms of numbers eaten, with approximately three hares consumed for each elk eaten. Moose remained the least important item at 2.2% frequency by numbers. In terms of weight, elk remained the most important item at 78.7%,

TABLE 4. Biomass equivalent calculations derived from number of food items in summer coyote scats

Food Item	Assumed wt. (kg)[1]	Estim. kg eaten/scat[2]	No. scat with item	kg eaten	kg eaten live wt.[3]	No. individuals eaten	Ratio of individuals eaten
Elk	247	5.32	126.81	674.63	899.51	3.64	1.00
Moose	302	6.42	10.00	64.20	85.60	0.28	0.08
Deer	64	1.66	33.00	54.78	73.04	1.14	0.31
Beaver	12.5	0.63	120.50	75.92	84.36	6.75	1.85
Snowshoe Hare	1.5	0.41	56.16	23.03	25.59	17.06	4.69
Muskrat	1.5	0.41	31.66	12.98	14.42	9.61	2.64

[1] Sources of weights from Carbyn and Kingsley (1979)

[2] Derived from Floyd et al. (1978)

[3] Following Fuller and Keith (1980). Dead weight (i.e. kg eaten) was considered to be 75% of live weight of cervids, 90% for smaller prey

TABLE 5 Biomass equivalent calculations derived from number of food items in winter coyote scats

Food Item	Assumed wt (kg)¹	Estim kg eaten/scat²	No scat with item	kg eaten	kg eaten live wt³	No individuals eaten	Ratio of individuals eaten
Elk	247	5 32	163 33	868 92	1158 56	4 69	1 00
Moose	302	6 42	19 00	121 98	162 61	0 54	0 12
Deer	64	1 66	45 00	74 70	99 60	1 56	0 33
Beaver	12 5	0 63	41 50	26 15	29 06	2 32	0 49
Snowshoe Hare	1 5	0 41	46 16	18 93	21 03	14 02	2 99
Muskrat	1 5	0 41	4 50	1 85	2 06	1 37	0 29

1 Sources of weights from Carbyn and Kingsley (1979)
2 Derived from Floyd et al (1978)
3 Following Fuller and Keith (1980) Dead weight (i e kg eaten) was considered to be 75% of live weight of cervids 90% for smaller prey

with moose and deer at 11.0% and 6.8%, respectively. Beaver, snowshoe hare and muskrat together only comprised 3.5%.

Like wolf, the changes for coyote from summer to winter were an increase in proportion by relative weight of moose and deer, and a decrease in muskrat, snowshoe hare and beaver. In terms of numbers, moose, deer, elk and snowshoe hare increased markedly and beaver and muskrat decreased significantly.

D. Interspecific variation

The comparisons of frequency of occurrence of food items eaten by wolves and coyotes were statistically significant for all four seasons and in total ($G=153.74$, $p < 0.01$). For summer, fall, winter and spring, the G values were 81.55, 41.07, 55.18 and 32.38, respectively. These values roughly indicated a greater difference in summer diets and a lesser difference in spring.

Wolves took significantly more elk than coyotes did in summer ($G=31.99$, $p < 0.01$) and in total ($G=39.53$, $p < 0.01$) (Table 1). They also took significantly more moose in fall ($G=18.65$, $p < 0.01$) and in total ($G=25.96$, $p < 0.01$). The only season in which there was a significant difference in use of deer was fall, when wolves used more than coyotes (9.4% vs 1.9%, $G=12.68$, $p < 0.01$).

Beaver consumption was very similar for the two canids (16.8% wolf, 19.0% coyote). None of the seasonal comparisons was statistically significant. In all seasons and in total, coyotes may have consumed more muskrats than did wolves. However, none of the variation was significant. Coyotes consumed more snowshoe hare than did wolves in winter ($G=15.05$, $p < 0.05$) and in total ($G=24.42$, $p < 0.01$).

The frequency of occurrence of cricetids was greater for coyotes in summer ($G=33.26$, $p < 0.01$) and in total ($G=54.02$, $p < 0.01$). None of the comparisons for the miscellaneous category was significant.

Morisita's (1959) overlap coefficient was also used to compare diets seasonally. Summer had the smallest overlap with a value of 0.87. Fall, winter and spring had values of 0.94, 0.93 and 0.94, respectively. The overall value of overlap was 0.92.

Patterns of use of elk, moose and deer by wolves and coyotes were very similar over the course of the study. There was a significant relationship in use of elk ($r_s=0.91$, $p < 0.01$) (Fig. 6). Significant patterns in use of moose ($r_s=0.76$, $p < 0.05$) and deer ($r_s= 0.74$, $p < 0.05$) also occurred. Beaver use by wolves and coyotes showed only moderate association ($r_s=0.52$, $p > 0.05$).

E. Bear food habits

Bear scats were collected from late May to early August during the summers of 1982 and 1983. Of 122 scats collected, only 40 (32.8%) had hair in them. In total, 44 different

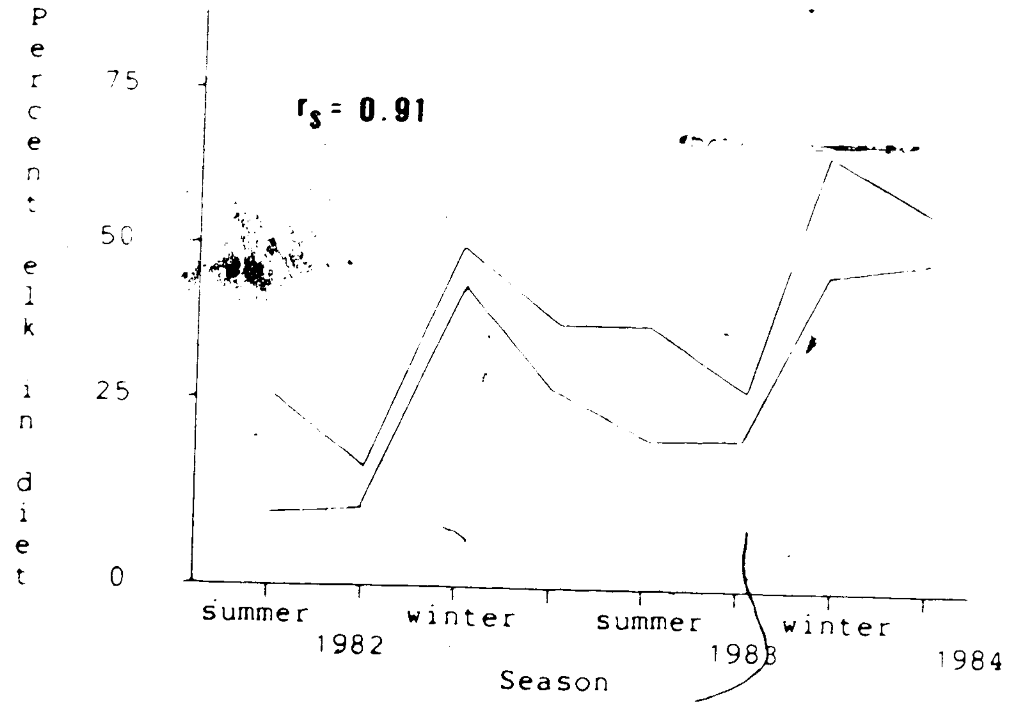


FIG. 6. Percent frequency of occurrence of elk in wolf and coyote scats over course of study.

prey items were identified (Table 6). Of the animal remains found in the scats, elk was the major food item both years and overall accounted for 12.7% of the diet. Cervid young were next in importance with a frequency of occurrence of almost 8%. Beaver and deer accounted for 6.3% and 4.0%, respectively, of the diet. Scats that did not contain hair, consisted mainly of vegetation, berries in particular.

F. Wolf food habits at homesites

Wolf scats were collected from two rendezvous and two den sites during the summer of 1983 (Table 7). Seventy-two food items were identified in 57 scats, 10 of which were pup scats (13 items).

A G analysis indicated no significant difference in scat contents between those from homesite areas and those from nearby trails ($G=8.52$, $p > 0.10$). The two major food items from both areas were adult elk and beaver.

A comparison between wolf scats from homesites and all other summer scats was significant ($G=19.51$, $p < 0.01$). Individual comparisons indicated two major sources of variation: beaver ($G=4.66$, $p < 0.05$) and miscellaneous items ($G=9.66$, $p < 0.01$). The frequency of beaver from homesite areas (33.3%) was significantly greater than that for the park as a whole (16.8%). Conversely, the frequency of miscellaneous items was significantly less from homesites (8.3%) than from the rest of the park (24.8%).

TABLE 6. Frequency of occurrence of food items in summer bear scats.

Food Item	Year 1983	Year 1984	Total	%
Elk	8	8	16	12.7
Deer	5	0	5	4.0
Cervid Young	8	2	10	7.9
Beaver	6	2	8	6.3
Snowshoe Hare	0	1	1	0.8
Muskrat	1	0	1	0.8
Cricetidae[1]	0	2	2	1.6
Squirrel	1	0	1	0.8
Vegetation	39	43	82	65.1

[1] Excluding muskrat.

TABLE 7. Summary of food items found at wolf homesites and nearby trails

	Homesites		Trails	
	# of items	%	# of items	%
Elk	27	37.5	11	34.4
Moose	4	5.6	0	0.0
Deer	4	5.6	1	3.1
Cervid Young	4	5.6	7	21.9
Beaver	24	33.3	10	31.3
Snowshoe Hare	2	2.8	1	3.1
Muskrat	4	5.6	1	3.1
Cricetidae[1]	1	1.4	0	0.0
Porcupine	0	0.0	1	3.1
Squirrel	2	2.8	0	0.0

[1] Excluding muskrat

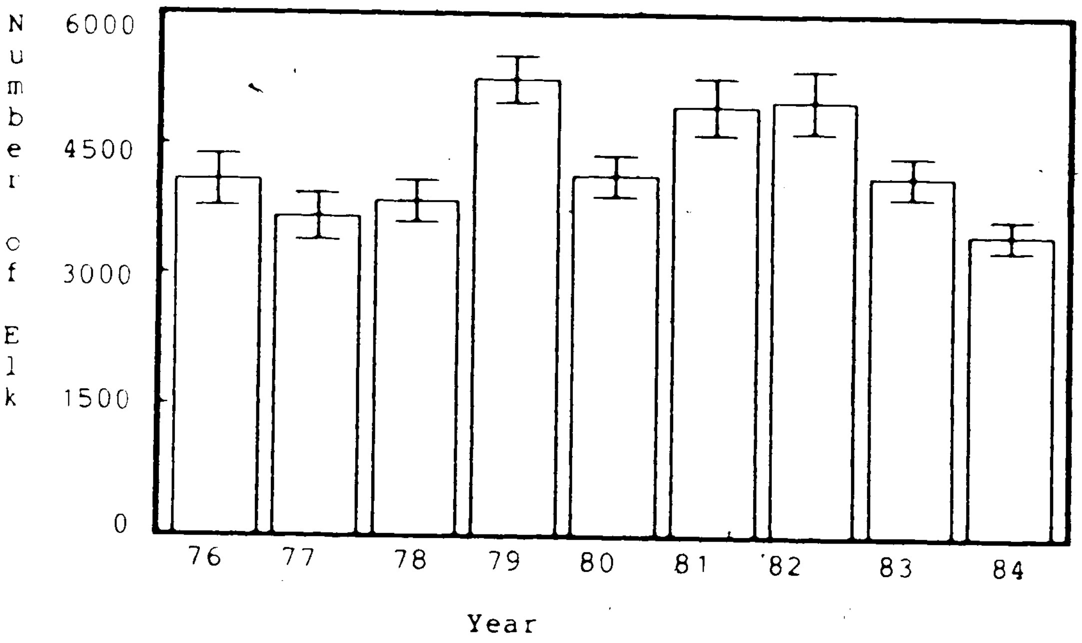
G. Ungulate distribution and densities

Mid-winter counts of elk and moose have been conducted regularly in R.M.N.P. since 1976. A simple estimate method (i.e. multiplying animals seen by a factor of four) has traditionally been used by park personnel to calculate population numbers. Using that method, the estimated populations of elk and moose during the course of the study were 4936 and 3140, 4092 and 3292, and 3440 and 2764, respectively, as determined by three aerial surveys (1982, 1983, 1984). The estimated averages during the study were 4156 elk and 3065 moose.

Statistical analysis of the mean number of elk and moose recorded per survey block was also used to estimate total populations with 95% confidence limits. (Five hundred and seventy five of 2326 blocks, or 24.7% of the park was sampled.) The estimates for elk were 4996 ± 706, 4142 ± 496, and 3482 ± 373, for 1982, 1983 and 1984, respectively, and for moose, 3178 ± 296, 3332 ± 308 and 2798 ± 251. These values are similar to those simply estimated, although in all cases slightly higher.

The statistical analysis was extended to the counts conducted from 1976 to 1981 (Fig. 7). Elk numbers have shown a recent downward trend from the peak reached in 1979. The 1984 population of 3482, a 34% drop from 1979, is the lowest recorded since annual surveys began.

Moose numbers formed a plateau from 1979 to 1981. Since then numbers have declined by 29% from a high of 3927 to a



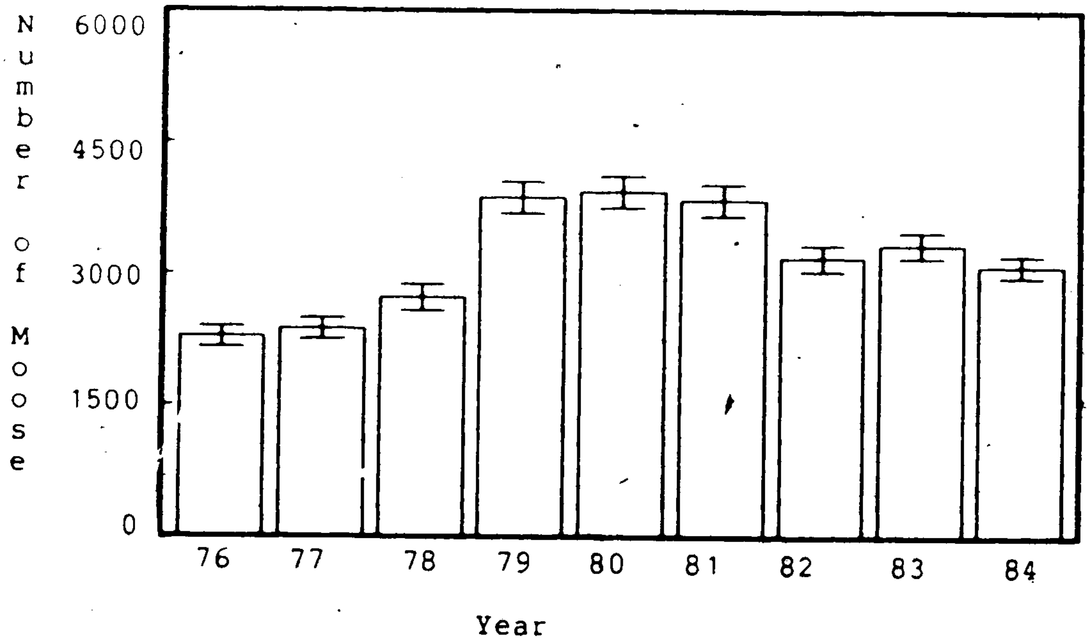


FIG. 7. Population estimates of elk and moose. Bars indicate 1 S.E. on either side of mean.

low of 2798. The 1984 population is the lowest recorded since 1978. The estimated densities were 1.7 elk and 1.1 moose per km^2 in 1982, 1.4 elk and 1.1 moose per km^2 in 1983, and 1.2 elk and 0.9 moose per km^2 in 1984.

Overall there is a significant correlation between elk and moose numbers since 1976 ($r=0.67$, $df=7$, $p < 0.05$). In general, numbers increased until the late 1970s, levelled off for a few years and then declined.

Examination of the confidence limits for the 1982, 1983 and 1984 elk and moose counts did not suggest much significant variation (i.e. only the 1981 and 1983 confidence limits for elk did not overlap). An ANOVA was carried out to examine the overall trends. All years from 1976 to 1984 inclusive were considered in the analysis. For both ungulate surveys, the mean number of animals seen per sampling unit for the different surveys, were not all the same ($F = 14.01$ and $F = 3.89$, for moose and elk, respectively, $p < 0.05$). Multiple comparisons among all possible pairs of means within each set of surveys, was carried out using the Welsch method (Sokal and Rohlf 1981). For elk, the peak value reached in 1979 was significantly different from the lower values recorded in 1977, 1978 and 1984 (Fig. 8). The second and third highest estimates, recorded in 1982 and 1981, respectively, also differed significantly from the results from 1984. The comparisons of 1977 and 1978 with 1982 were both close to being significant.

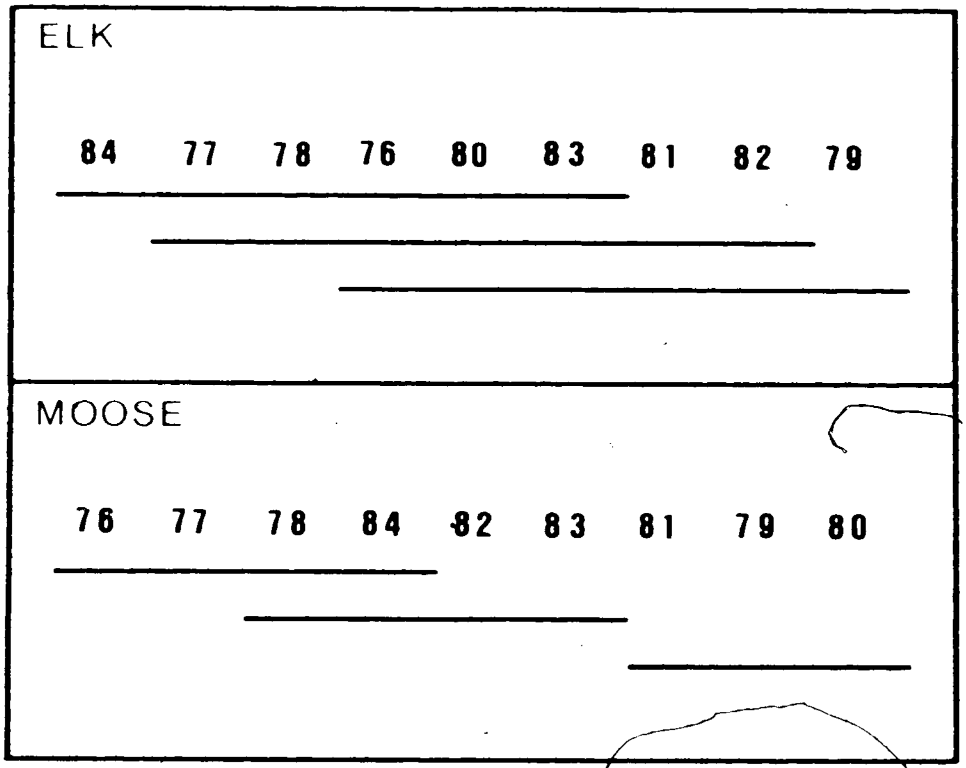


FIG. 8. Results of all pairwise comparisons of the yearly mean number of elk/moose per survey block using the Welsch method. Means are arranged in order of increasing magnitude with lines beneath the years representing nonsignificant sets of means.

Results for moose were similar (Fig. 8). The estimated population sizes for 1979, 1980 and 1981, were significantly greater than those for all other years. In addition, the 1982 and 1983 estimates were significantly greater than the estimates for 1976 and 1977.

Overall, these statistical results may be interpreted as indicating that the trends seen were valid. In particular, both ungulate populations reached a peak in the late 1970s, before undergoing a decline to 1984.

The distributional relationships of elk and moose were examined using the results from the 1983 and 1984 surveys (Figs. 9-12). Of the 266 quadrats (10.2 km^2) crossed by the aerial transects, elk occupied 64% in 1983 and 73% in 1984, for an average of 69%. Moose were present on 78% of the quadrats in 1983 and 79% in 1984, for an average of 78.5%. The combined populations occupied 91% and 92% of the quadrats during the two years. The distribution of all four populations differed significantly from a Poisson distribution and hence were non-random (χ^2 =159 and 87 for elk; 59 and 37 for moose).

Mean centers of areal distributions can be used either to trace any change in distributional patterns over time or to compare two or more distributions in the same area (Taylor 1977). Standard distances are analogous to standard deviations and serve to indicate dispersion around the areal mean (Taylor 1977). The mean centers and standard distances for the four populations clearly indicated distributional

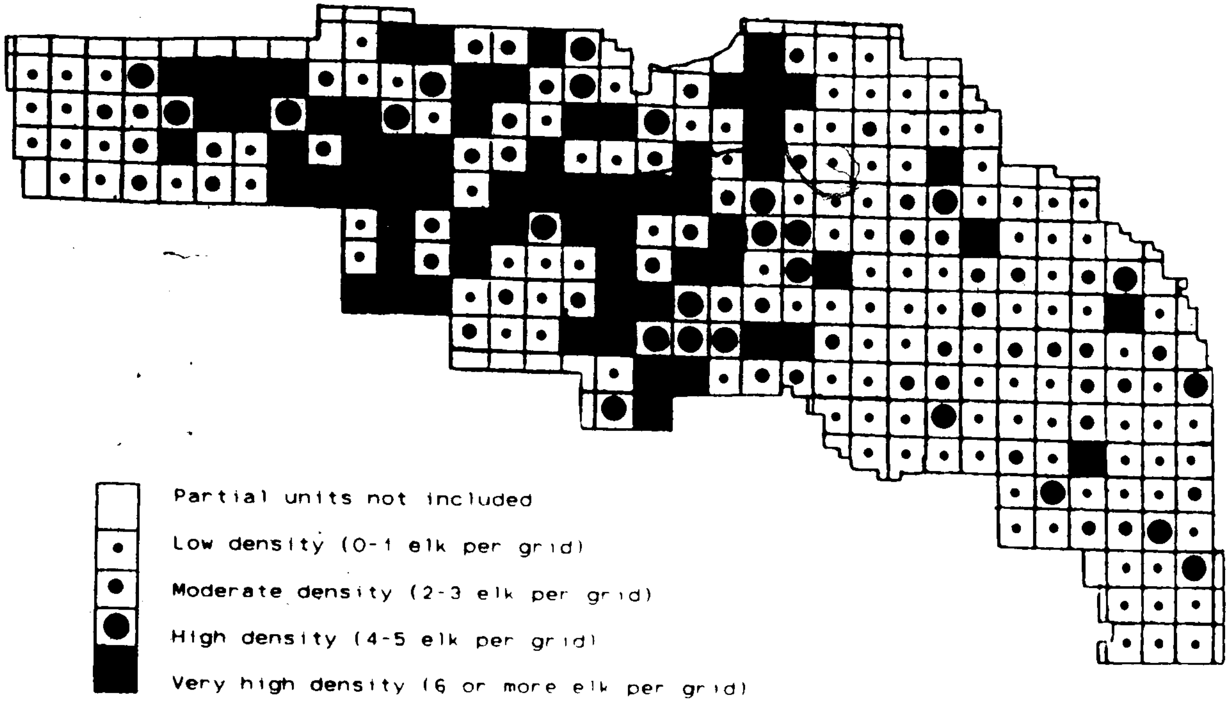


FIG 9 Density class categories for elk, 1983

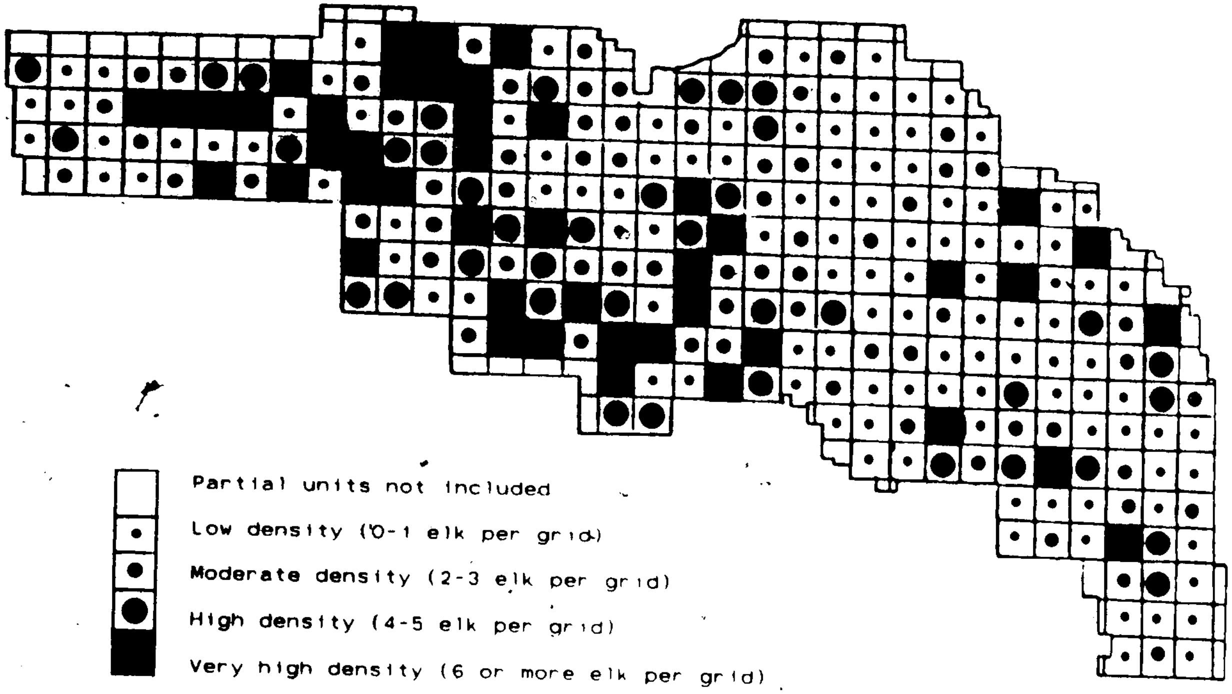
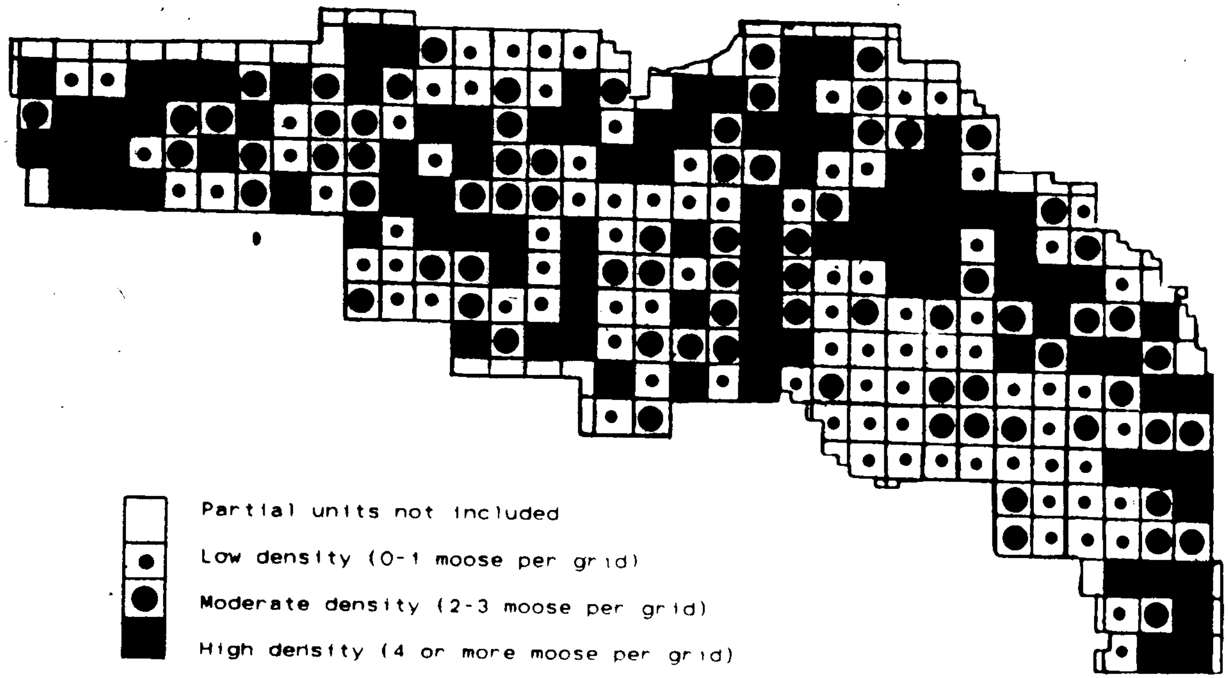


FIG. 10 Density class categories for elk, 1984


□ Partial units not included

● Low density (0-1 moose per grid)

⬤ Moderate density (2-3 moose per grid)

■ High density (4 or more moose per grid)

FIG. 11 Density class categories for moose, 1983

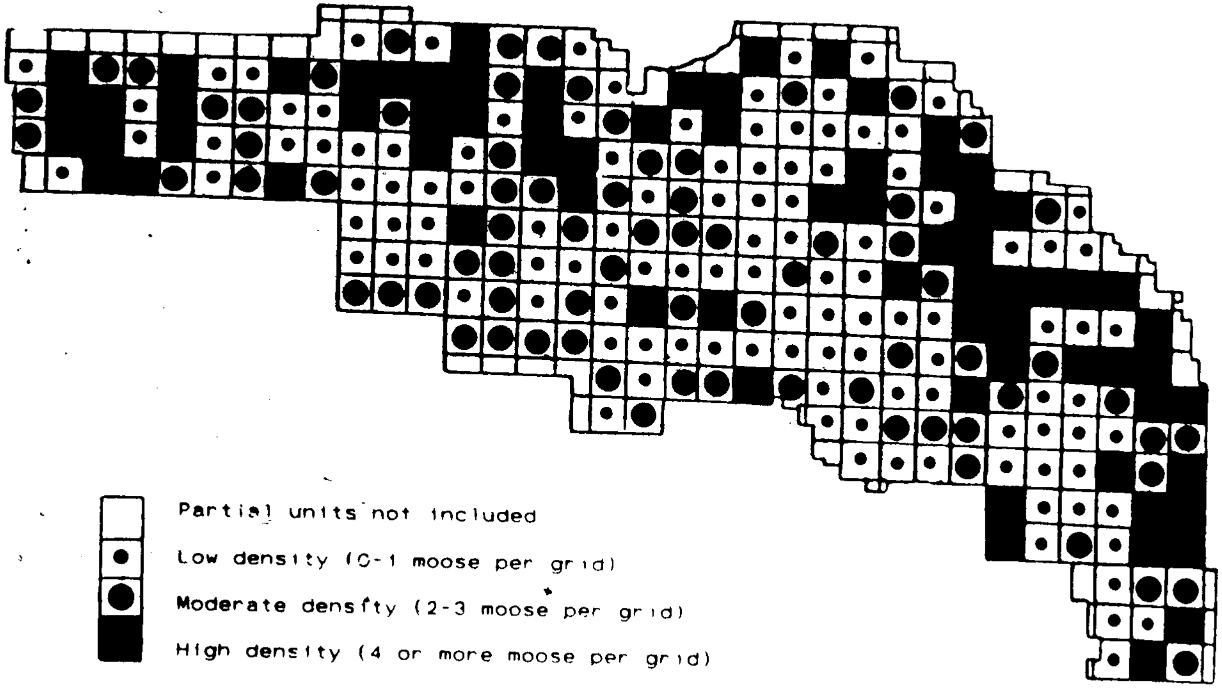


FIG 12. Density class categories for moose, 1984

differences between them (Fig. 13).

The results above indicate that:

1) Moose were more widely dispersed than elk,

2) Elk were more oriented to the western end of the park than moose, and

3) Individuals within a population were not randomly distributed in regard to conspecifics; more so for elk.

To investigate this last point further, variance to mean ratios were calculated. Ratios greater than one, equal to one and less than one indicate clumped, random and regularly dispersed populations, respectively. For elk the ratios were 6.17 and 4.30, and for moose 2.29 and 2.11, in 1983 and 1984, respectively. These results clearly indicated clumped distributions for both prey species.

Interspecific association was examined by means of Cole's (1949) coefficient of association. The value for 1983 was 0.04 and for 1984 0.09, indicating a very weak positive association. Chi-squared values, however, were not significant ($\chi^2 = 0.16$ and 1.62) indicating random distribution of elk and moose populations with respect to each other.

H. Beaver densities

Aerial counts of beaver caches have been conducted each fall from 1976 to 1983, except for 1978 (Fig. 14). The 1984 survey team experienced logistical problems and the survey

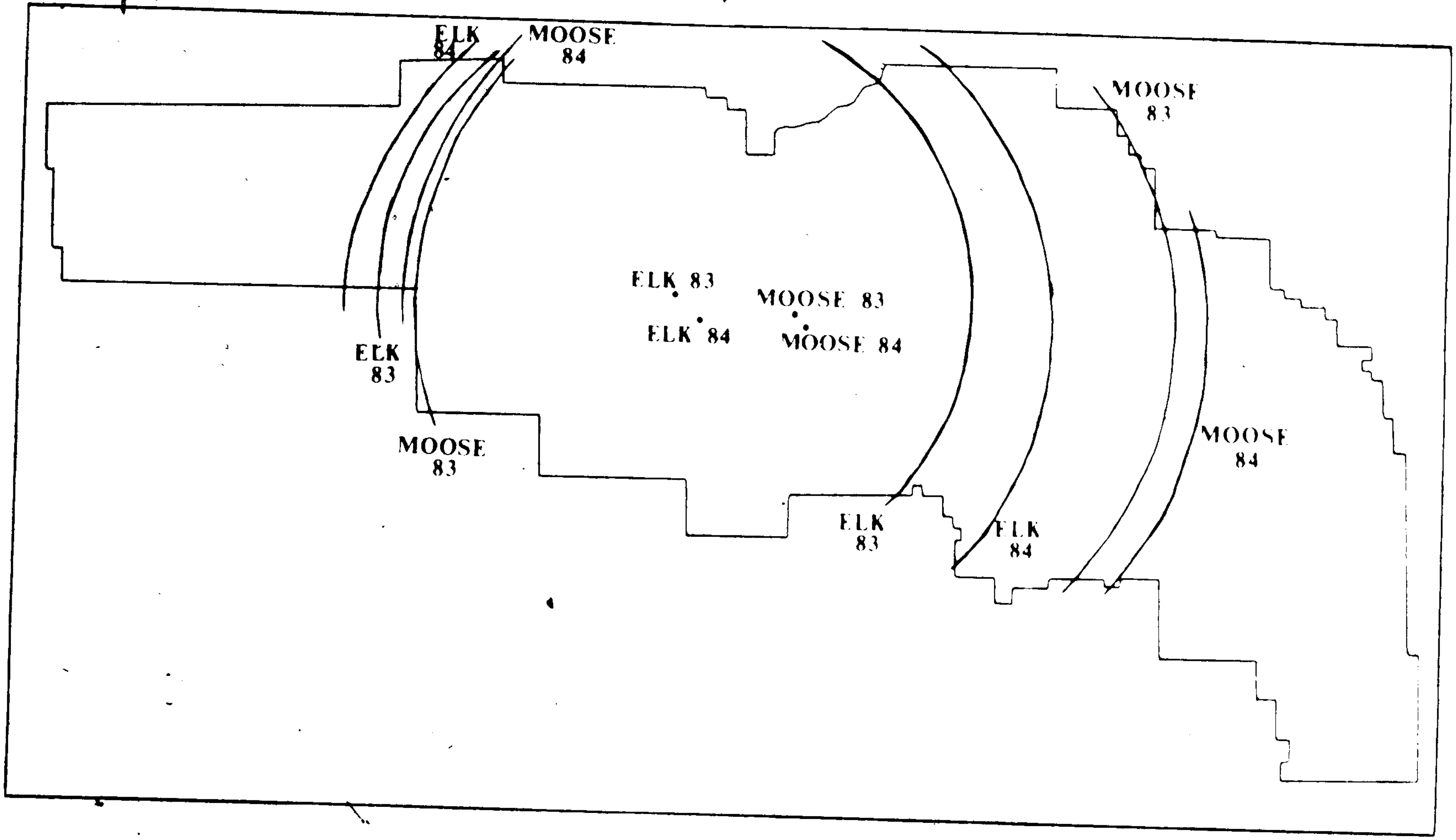


FIG 13 Mean centers of distribution and standard distances for elk and moose based on the 1983 and 1984 mid-winter surveys

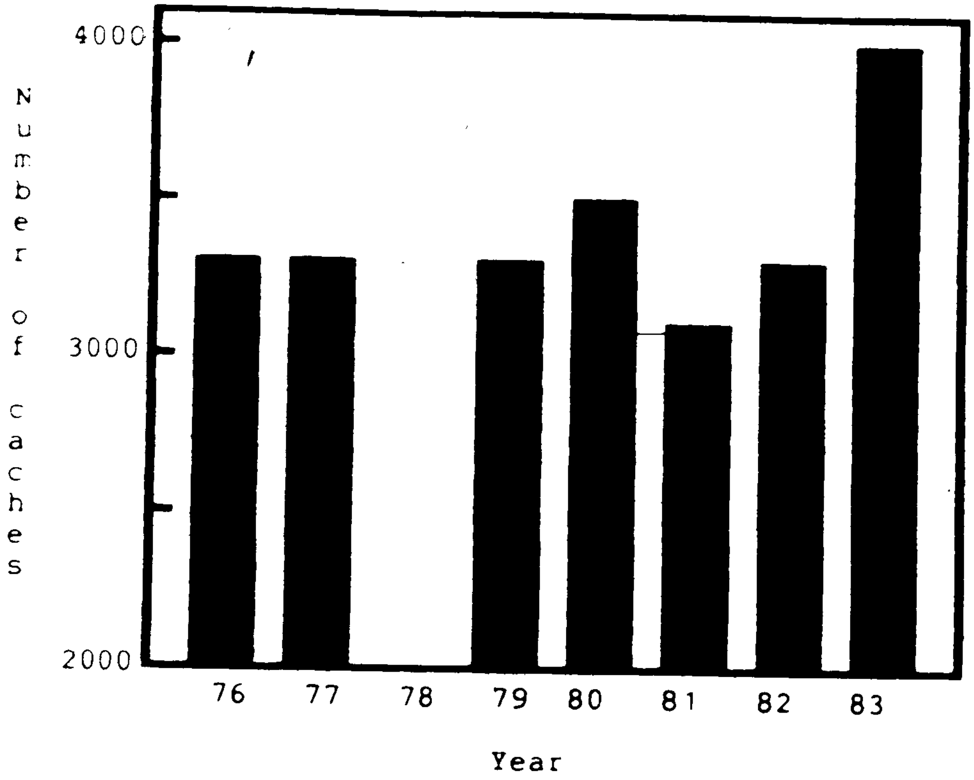


FIG. 14. Annual estimates of the number of beaver caches in R.M.N.P.

was not completed, hence only partial results for that year are available. The number of colonies for years 1982 and 1983 were 3316 and 3967, which, given an average of 5 beavers per colony, resulted in an average population during the course of the study of 18,210 beavers.

The number of caches increased by 5.5% from 1981 to 1982, and then by 19.6% from 1982 to 1983. The 1983 survey gave the highest estimate of caches since the survey began. The 95% confidence limits suggest that the true population for 1983 was between 3283 and 4650. Partial results from the 1984 survey indicated generally lower values for each quadrat sampled compared with the previous year. That result suggests that either the population for 1983 was overestimated, with the true and unknown value perhaps lying in the lower range of the confidence interval, or that the population was for that year only at a much higher level than previously.

Correlation analysis indicated no significant relationship between beaver numbers and elk ($r=-0.345$, $p > 0.05$) or moose numbers ($r=0.110$, $p > 0.05$) since 1976. There was also no correlation between beaver numbers and summer rainfall from the previous year ($r=-0.056$, $p > 0.05$).

I. Other prey populations

Because of their inconspicuous nature from the air, white-tailed deer could not be adequately counted during the moose and elk survey. Pellet count surveys were not deemed efficient or reliable enough to give valid population estimates. No deer activity was recorded during the 1983/84 winter survey of snowshoe hare.

The best estimate available came from winter sighting ratios of the three ungulate species. Over the course of the study the ratios were 1.0 deer: 3.0 moose: 3.7 elk. In other words, the deer population was approximately 27% of elk numbers and 33% of moose numbers. (Assuming the sightability of the three species to be approximately the same.)

Carbyn (1980) considered deer to follow the same population trend as elk. A composite index derived from both sighting ratios and ground surveys in a 150 km^2 study area (Trottier et al. 1983) gave a ratio of 1.0 deer: 4.0 elk, or about 25% of the elk population. This value is in close agreement with my own result, and owing to the larger sample size of the former and the desirability of maintaining consistency, the 25% value will be used. Hence, given the mean elk population of 4156, the mean deer population was estimated at 1039. This is a crude and qualitative estimate, but it was considered sufficient for use in certain calculations.

The snowshoe hare population crashed during the winter of 1981/82 after having reached a peak in 1980/81 (Carbyn et al. 1985). A snowshoe hare activity survey was conducted in the winter of 1983/84, with the resulting index being markedly lower than those recorded earlier in the park (Fig 15). During this study, the hare population was in the decreasing phase of the cycle, with the summer of 1982 possibly containing a slightly greater population than that of 1983 since it takes two to four years for hare populations to reach a minimum after passing a peak (Keith and Windberg 1982). In contrast, Carbyn's study took place during the increasing phase of the hare cycle.

J. Age and sex classification of elk and moose

Unlike the early winter counts flown in November, the late winter count conducted in March 1984, did not allow for adequate discrimination between cow and calf elk; hence a detailed analysis of data from that survey was conducted only on the moose sightings. The areas searched were chosen according to the results of censuses (Figs. 9-12) to provide the most animals in the least amount of time as well as a representative sample of the various age and sex classes (e.g. bull elk ranges) (Fig. 16).

In all 1477 elk were sampled in the first survey (Table 8). Given a 1983 population of 4092, this meant a sampling proportion of 36%. Based upon the cumulative count, the calf-cow ratio became constant by the third day of the survey (six days were flown). Of the 423 bulls sighted, 37

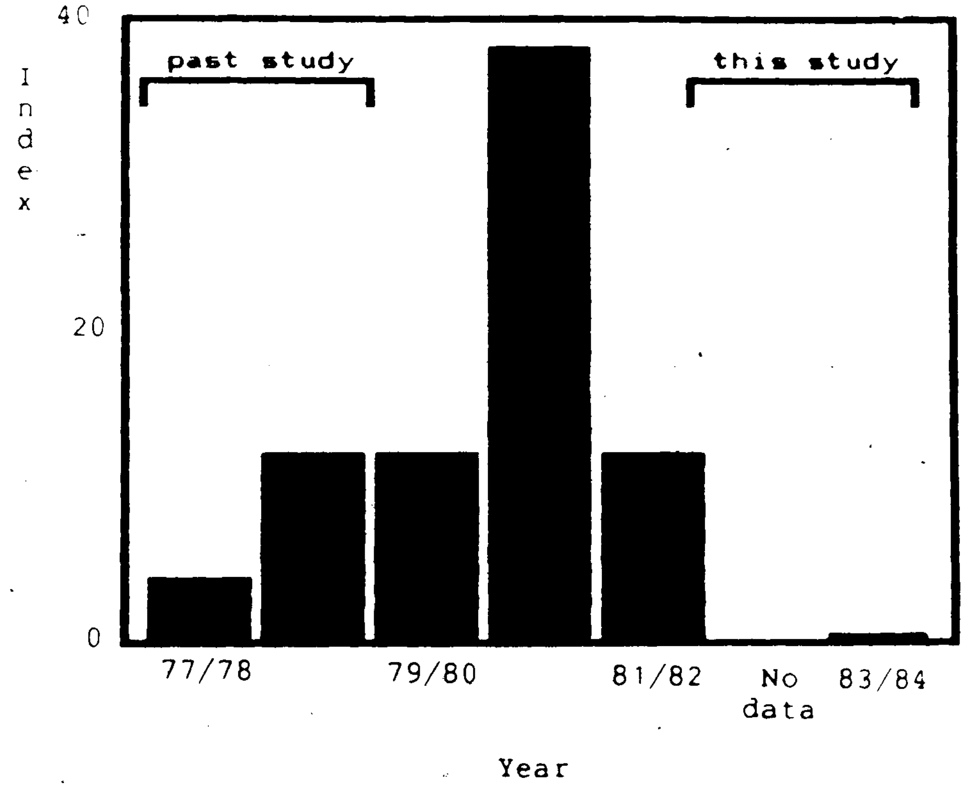


FIG. 15. Snowshoe hare abundance index (tracks/km) as related to R.M.N.P wolf studies.

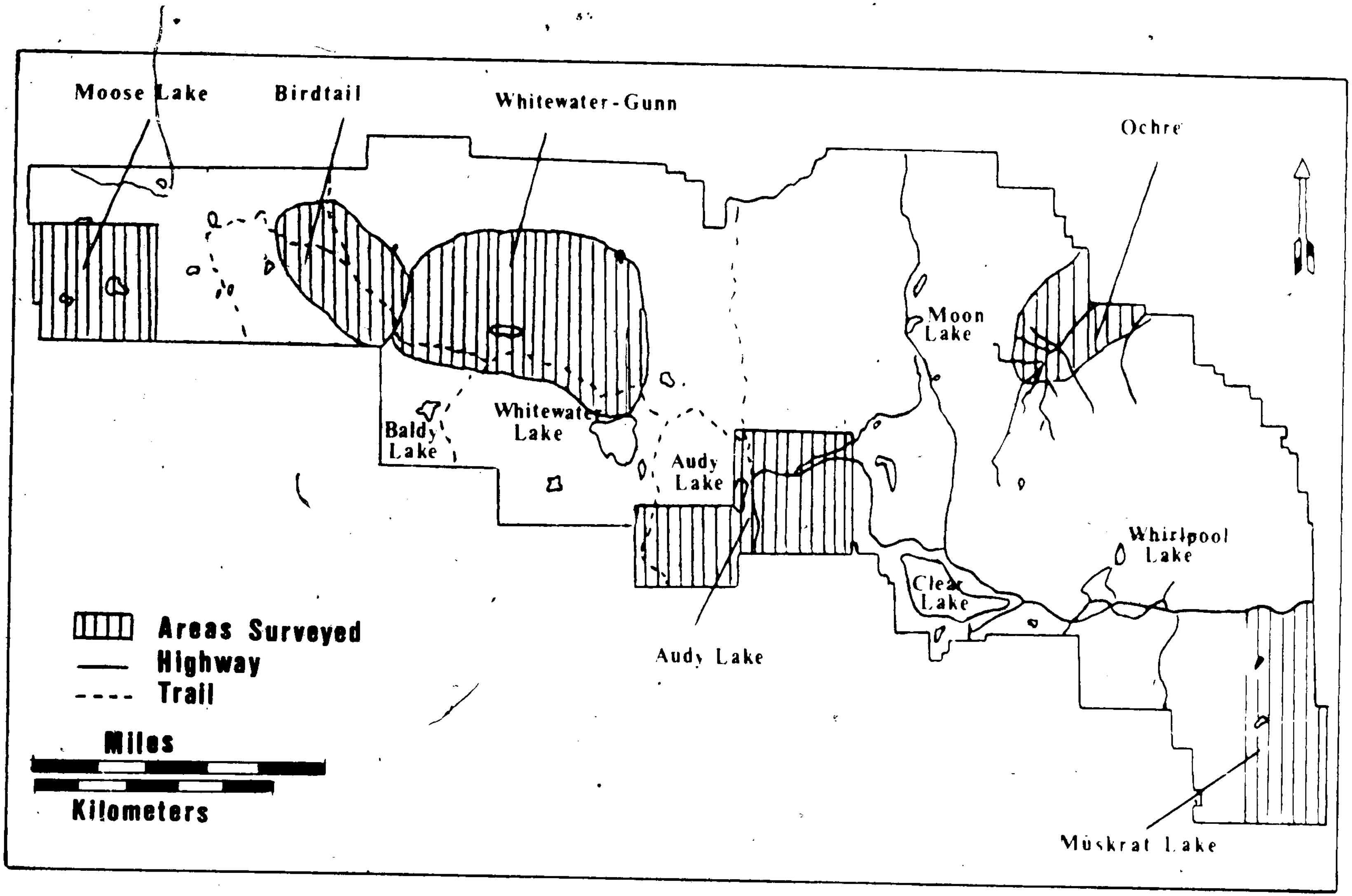


FIG 16. Areas surveyed for age and sex classification of elk and moose

TABLE 8. Age and sex classification of elk and moose in R.M.N.P.

Survey	Bulls	Cows	Calves	Calves/ 100 Cows	Bulls/ 100 Cows
November 1983					
Moose	207	418	135	32.3 ± 4.2[1]	49.5 ± 6.0
Elk	423	863	191	22.1 ± 2.2	49.0 ± 3.5
March 1984					
Moose	133	271	68	25.1 ± 5.1	49.1 ± 6.9
Elk	162	381[2]	-	-	
		331[3]	50	15.1 ± 2.9	49.0 ± 5.9
November 1984					
Moose	61	255	130	51.0 ± 7.1	23.9 ± 4.9
Elk	385	636	114	17.9 ± 2.5	60.5 ± 4.9

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[1] Confidence intervals from Czaplewski et al. (1983).
[2] Antlerless elk.
[3] Assuming a bull/cow ratio the same as early winter.

or 9% were classified as yearlings.

Based upon a 1983 population of 3292, 23% of the moose population was sampled in November 1983. A constant ratio of calves per 100 cows was reached before the end of the survey. A twinning rate of 1.5% was observed. The 207 bulls included 8 (4%) spiked or yearling males.

Altogether, 162 bulls and 381 antlerless elk were seen during the March 1984 survey. In order to get some estimate of the number of calves, it was assumed that the bull-cow ratio had remained constant from the early winter. Hence the antlerless animals would have included 50 calves, giving a ratio of 15[illegible] + 2.9 calves per 100 cows. This result should be treated with caution; it is likely an overestimate since bulls usually suffer more mortality than cows during the winter (Peek 1982).

The moose calf-cow ratio decreased by 7.2 calves per 100 cows from November 1983 to March 1984; however the confidence limits of the two surveys overlap and therefore the decrease may not be significant. The bull-cow ratio was almost identical to that seen in November.

Based on the February 1984 ungulate survey, only 16% of the elk and 17% of the moose populations were sampled in the March count although the amount of flying time was about the same as in the November survey. There were at least three reasons for the decrease:

1) Populations, especially of elk, were more dispersed in March than in November.

2) A longer time was required to classify each animal (moose drop their antlers in mid-winter, so the presence of a white vulva patch or a light coloured nose had to be used to discriminate between the sexes).

3) Observability was poorer because of more severe winter conditions (e.g. frosting up of airplane windows, poorer light conditions).

The November 1984 elk calf-cow ratio was lower than that of the previous year, but the confidence intervals overlapped. The bull-cow ratio showed a significant increase from 49.0 ± 3.5 to 60.5 ± 4.9. Thirty-three percent of the park population was sampled.

The moose calf-cow ratio showed a significant increase, to a value of 51.0 ± 7.1. The bull-cow ratio also differed significantly, dropping to 23.9 ± 4.9 from 49.5 ± 6.0 a year earlier. Only 16% of the park population was sampled.

The data for the three surveys were classified into sex-age groups (Appendix 4). Moose cow-calf groups (2.1 and 2.0) were significantly larger than cow-calfless groups (1.4 and 1.1) in both November 1983 ($t=12.28$, $n=377$, $p < 0.01$) and March 1984 ($t=22.50$, $n=211$, $p < 0.01$). This relationship did not hold for elk ($t=0.96$, $n=277$, $p > 0.20$).

K. Prey selectivity by wolves

Survey data were combined with scat content data to derive an estimate of large prey selection by wolves (Table 9). Mean population sizes of moose and elk were taken as the averages of the 1982, 1983 and 1984 mid-winter ungulate surveys, while the fall surveys of 1982 and 1983 were used to estimate beaver numbers. Deer were assumed to follow the elk population pattern and were calculated as one-quarter that of elk. Given an estimate of the total biomass of a species and considering the relationship between weight and collectible scats for that species as derived from the equation of Floyd et al. (1978), a value representing the potential collectible scats can be calculated. Taking all four species into consideration an expected scat collection was calculated and then compared with actual scats collected to derive an estimate of selectivity.

Moose was the least taken or preferred species of the three ungulates. Summer use was particularly low with a selection of use of only 27%. Overall, elk was clearly the preferred species, with both summer and winter selection rates more than twice what would be expected from random selection. The deer population, although sustaining relatively little predation in summer, had the highest selection rate in winter (over 3 times what would be expected if predation were random). The selection rate for deer would be higher if the population was overestimated and lower if it was underestimated. Beaver use was overall less

TABLE 9. Prey selectivity as determined by scat analysis and population estimates

	Moose			Elk			Deer			Beaver			Total		
	SUMMER	WINTER	YEARLY	SUMMER	WINTER	YEARLY	SUMMER	WINTER	YEARLY	SUMMER	WINTER	YEARLY	SUMMER	WINTER	YEARLY
Mean population			3065			4156			1039			18210			
Weight (kg)			302			247			64			125			
Total biomass, thousands (kg)			926			1027			66			228			
Dead Weight Biomass, thousands (kg)			695			770			50			205			
kg per collectible scat			6.42			5.32			1.66			0.63			
Potential collectible scats, thousands			108			145			30			325			608
% of potential collectible scats			18			24			5			53			100
Actual scats collected	15	28	43	165	161	326	12	40	52	87	12	99[1]	279	241	520
Expected collection	50	43	93	67	58	125	14	12	26	148	128	276	279	241	520
Actual as percentage of expected (selectivity index)	30	65	46	246	278	261	86	333	200	59	9	36			

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[1] Estimated using same ratio (0.25 deer/elk) as from Carbyn (1980)

than half of that expected.

L. Impact of wolves on elk

Losses of elk to wolves in the whole park were calculated primarily by using data from this study. Estimates of daily consumption by wolves in summer were taken from the literature (Kuyt 1972, Mech 1977) while winter kill rate and proportion of elk calf hair among cervid young were taken from the earlier R.M.N.P. study (Carbyn 1980, 1983).

Starting in the spring period, the 3-year average population of 4156 would consist of 2681 cows given a 2-year average ratio of 55 bulls to 100 cows. Data collected by the province from hunter kills around the park, indicated a pregnancy rate among cow elk of 69% (n=71) (D. Davies pers.comm.), giving a potential production of 1850 calves. (This is likely a minimum pregnancy rate, since some hunters would be likely not to report killing a pregnant cow.) Thus the late spring minimum population would be 6006.

The 1983-84 winter wolf population was estimated to consist of 59 adults and 16 pups divided among 12 packs (P. Paquet pers. comm.). The adult food requirement from 1 May to 30 September, assuming an average of 1.7 kg/day/wolf (Mech 1977), would be 15,346 kg. Pups would need 1541 kg from 15 June to 30 September, assuming a requirement of 0.9 kg/day/pup (Kuyt 1972). This dead weight can be converted to a live weight estimate by considering the former to be equal to 0.75 times the latter. Therefore the total summer requirement for wolves in the park would be 22,516 kg.

Assuming that 79% of cervid young hair was from elk calves (Carbyn 1980), then by weight elk calves were 4.5% of the diet (1013 kg) and adult elk were 79% (17,788 kg) of the requirement. Given average weights of 247 kg/elk adult and 30 kg /elk calf, 72 adults and 34 calves would have been lost to wolves.

In the fall-winter period, 12 packs with an assumed relatively high kill rate of one ungulate per 2.7 days (Carbyn 1983) would have required 942 ungulates over the course of the 212 days. The numerical ratios calculated from biomass equivalences in winter of 1.0 elk per 0.17 moose, per 0.30 deer, would result in 641 elk kills. (Recent results, suggesting a more moderate kill rate of one elk per nine days (P. Paquet pers. comm.), would result in only 283 kills.)

Hence the year end population, given only losses to wolves would be 5259 animals (6006-747 kills), a 27% increase from the starting population. Wolves by themselves could not depress elk numbers.

M. Weather data

Since weather conditions can play a role in predator-prey relationships (Peterson 1977), summer precipitation levels and winter snow and temperature conditions were analyzed (Tables 10 and 11).

Summer precipitation levels were below the 11 year average in 1983 and 1984. In contrast, 1982 levels were somewhat above average.

Totals of mean monthly snow depths for the winters of 1981/82 and 1982/83 were 76.0 cm and 113.5 cm, respectively; well below the 7-year average (77/78-83/84) of 149.3 cm. The winter of 83/84 had about 18 cm more snow than average. Unusual snow conditions occurred in the late winter of 1983. An ice-rain storm in early March left an icy-crusty snow cover.

Temperatures have generally been near average. The 9-year (75/76-83/84) mean daily temperature throughout the winter (November-March) was -12.1 °C. The readings from 81/82 to 83/84 were -12.6, -11.6 and -12.9 °C, respectively.

Monthly and total winter severity indexes were calculated for the last three winters of the study and compared with results available from previous years (Table 12). The data indicate that winters in the 1980s have been generally less severe than those from the 1970s.

The total winter severity indexes were compared to elk and moose numbers. Neither ungulate population was significantly correlated with the index ($p > 0.05$). To test

TABLE 10. Summer precipitation recorded at Clear Lake, R.M.N.P., 1974-1984[1].

Year	May	June	July	August	Sept.	Oct.	Total
			Precrptitation (cm)				
1974	8.0	2.5	8.1	6.4	5.7	0.2	30.9
1975	3.4	10.7	10.5	19.5	12.5	-	60.3
1976	1.1	15.5	1.1	2.3	1.1	1.5	22.6
1977	12.8	10.9	13.7	4.4	9.8	3.1	54.7
1978	6.0	9.6	5.8	6.6	9.4	1.3	38.7
1979	6.6	5.9	4.8	4.0	5.6	2.5	29.4
1980	1.5	5.5	9.5	14.9	7.8	3.3	42.5
1981	6.1	6.9	5.5	8.0	6.9	3.9	37.3
1982	5.2	4.7	14.9	5.3	5.7	6.4	42.2
1983	2.4	7.9	10.8	1.4	1.1	2.7	26.3
1984	3.0	10.0	2.2	3.0	7.3	6.9	32.4
11-year mean	5.1	8.2	7.9	6.9	6.6	3.2	37.9

[1] Extracted from park records.

TABLE 11. Winter weather data collected from various weather stations within R.M.N.P.[1]

	Nov.	Dec.	Jan.	Feb.	March
Mean Minimum °C					
81/82	-4.3	-17.6	-31.0	-20.6	-14.0
82/83	-15.3	-17.2	-18.6	-16.9	-12.9
83/84	-7.8	-29.4	-23.7	-14.2	-20.3
Mean Maximum °C					
81/82	3.8	-9.6	-20.3	-9.1	-2.9
82/83	-4.9	-9.0	-9.3	-8.1	-4.3
83/84	-2.6	-19.6	-12.1	-2.6	-6.8
Daily Mean °C					
81/82	-0.3	-13.6	-25.7	-15.0	-8.5
82/83	-8.9	-13.3	-14.1	-12.6	-8.9
83/84	-5.4	-24.2	-17.7	-7.6	-9.4
Mean(75/76-83/84)	-5.3	-16.0	-18.3	-13.3	-7.7
Mean Snow Depth					
81/82	0.0	0.0	21.6	27.1	27.3
82/83	3.2	15.7	25.3	29.2	40.1
83/84	28.7	31.0	32.3	33.0	42.3
Mean(77/78-83/84)	14.4	25.3	33.7	38.0	37.9
Mean Snow Density					
81/82	-	-	.09	.12	.15
82/83	.19	.14	.14	.15	.22
83/84	.12	.18	.18	.17	.18

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[1] Extracted from park records.

TABLE 12. Winter Severity Indices For R.M.N.P.[1]

Mean Monthly Severity	77/78	78/79	79/80	80/81	81/82	82/83	83/84
November	33	48	35	46	2	32	45
December	78	66	73	66	38	54	68
January	89	81	90	65	55	61	73
February	93	100	96	66	51	68	60
March	83	105	93	6	42	93	70
April	-3	70	-8	-3	42	39	-5
Total	376	470	381	246	230	3[illegible]7	311
Green-up[2]	-6	34	-16	12	-4	4	-22
Winter Severity	370	504	365	258	226	351	289

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[1] Extracted from park records.

[2] Calculated as difference between green-up date and mean green-up date multiplied by two. The value is added when green-up occurs after the mean date, subtracted when it occurs before.

for delayed effects of winter conditions, the index values were shifted up to 5 years forward and correlated with elk and moose numbers. None of the resulting correlation coefficients was significantly negative.

V. DISCUSSION

A. Canid feeding habits

Wolf: general characteristics

The results of this study were consistent with those from similar research carried out in the park from 1975-79 (Carbyn 1980). The consumption of the major prey species, elk, was up slightly although not significantly, from the past study. The average population of 4156 elk for this study was comparable to the 4-year average of 4160 for the earlier study. Elk has beem an important food item in Jasper National Park, with frequency values of 47% (Cowan 1947) and 30% (Carbyn 1974). Elk used to be the main food item for wolves in Yellowstone National Park (Weaver 1979b). On Vancouver Island, Roosevelt elk at 18% was second in importance to mule deer at 80% (Scott and Shackleton 1980). Elk, was and clearly still is, the most important prey item for wolves in R.M.N.P.

Beaver consumption ranked second in importance. Many other studies including those by Voigt et al. (1976) and Peterson (1977) have commented upon the significance of beaver in the diet of wolves. They found that as the primary prey decreased in abundance (moose on Isle Royale, white-tailed deer in Ontario), use of beaver increased markedly. Fuller and Keith (1980) also related beaver use to relative availability; however, they noted that even if beaver numbers were high, adult moose were still preferred if they were also abundant. Use of beaver was numerically greater, although not statistically so, in the second year of this study. As beaver numbers increased (Fig. 14), elk and moose numbers declined (Fig. 7). Although this suggests that wolves in R.M.N.P. responded to changes in relative availability of beaver, other explanations cannot be ruled out. For example, vulnerability of beaver is likely to increase when beaver forage great distances away from water (Peterson 1977), which may occur because of food shortages or low water levels owing to low precipitation. The latter factor may have been of importance in the non-winter months of 1983 when total rainfall was only 26.3 cm, well below the 11-year average (1974-1984) of 37.9 cm.

Both moose and white-tailed deer were numerically minor food items. In areas where the larger moose is the only ungulate prey available to wolves (e.g. parts of Alaska, Quebec, Alberta and Isle Royale), they experience heavy predation (Peterson 1977, Messier 1985, Fuller and Keith 1980, Peterson et al. 1984). In northern Minnesota and Ontario, where both moose and deer occur, the latter is the primary prey of wolves (Pimlott et al. 1969, Mech 1977). On Vancouver Island, mule deer are taken more than Roosevelt Elk by a factor of four to one (Scott and Shackleton 1980). Clearly in R.M.N.P. in both 1975-79 and this study, moose and deer were used much less than elk.

There was no difference in the use of snowshoe hare between the two studies. The overall use of 7.3% occurred during a period of low hare abundance; the declining phase of the hare cycle.

Although consumption of cricetids was statistically less in this study than in that of Carbyn (1980), the difference could possibly be explained by annual variation in vole numbers (Southern 1979). Unfortunately it was not possible to obtain trend information by snap trapping in the park. However, a close look at the yearly frequency data for the 1975-79 period is consistent with the view that cricetid numbers undergo significant annual variation. In the summer of 1977, wolf use of this minor prey resource, as indicated by frequency in scats was 19.6%, giving an overall summer average of 10% (Carbyn 1980). When 1977 data were deleted, the average for the remaining summers was 3.3%; which was only slightly more than the 3.2% obtained for this study. Therefore, if wolves take more cricetids when they are more abundant and if voles undergo a standard 4-year cycle (Southern 1979), then the relatively low use in this study compared with the previous one may be because no scats were collected during a peak year (i.e. 1981 or 1985).

No occurrence of cattle hair was noted in this study. This could perhaps have been a result of a sampling bias, since few scats were picked up on the periphery of the park. However since wolves can travel long distances after feeding, some cattle hair would be expected if they used livestock to a significant degree.

Overall the high frequency of mammalian items and the low use of vegetation, invertebrates and birds, agrees with the results from most other studies. Consumption of large prey, that is ungulates, occurred at a frequency of 55.5%. I suggest that these results and those from the 1975-79 study, indicate that wolf feeding habits have not changed in recent years.

Coyote: general characteristics

The frequency of occurrence of elk hair in coyote scats was significantly higher in this study than in the 1975-79 study. However, the overall value of 27.9% cannot be viewed as excessively high or without precedent. Bowen (1981) found use of elk in Jasper National Park to be as high as 29% in winter and 26% in summer. Weaver (1979a) not only found a frequency of occurrence of 74% between January and March, but related coyote numbers to the abundance of elk carrion in Jackson Hole, Wyoming. Murie (1945) determined that elk in Montana made up 20% of the diet and Bekoff and Wells (1980) indicated that ungulate carrion, particularly elk, was of great importance in the winter for coyotes in Grand Teton National Park. There is little evidence in the literature that coyotes kill elk (Weaver 1979a), so it must be assumed that the majority of elk hair in coyote scats came from carrion. In R.M.N.P. there are four potential sources of winter carrion: 1) hunter kills, 2) wolf kills,

3) winter kills, and 4) other natural mortality. Hunter kills occurred only around the edge of the park and actually decreased in numbers in the 1983-84 hunting season (Appendix 5). Wolf kills, as suggested by hair frequency in scats, did not increase significantly in comparison with 1975-79. With the decreasing elk population, it is conceivable that the number of winter kills was large and increasing. If that were true, however, one would expect an equivalent increase in elk use by wolves, which is not supported by the data. This seeming paradox could perhaps be explained by a greater functional response by coyotes to increasing carrion. In other words, coyotes may be more actively searching for both winter and wolf kills, than they did previously. In addition, wolves may maintain a preference for killing their food and hence not respond immediately to increasing carrion.

The greatest statistical difference between coyote use of elk in this study and the previous one, however, occurred in summer. Again elk carcasses from wolf kills or die-offs would be the major source for coyotes.

Coyotes occur in packs in areas such as Wyoming and Jasper National Park where they use elk (Camezind 1978, Bekoff and Wells 1980, Bowen 1981). Although there is some indication of pack formation among coyotes that kill deer in R.M.N.P. (P. Paquet pers. comm.), singles and pairs (as indicated by tracks) are the norm. In Riding Mountain elk are non-migratory and well-dispersed in winter relative to elk populations in mountainous areas. Hence the carrion resulting from winter kills is not concentrated and there is little advantage for packs to form to defend large scavenged carcasses. Time spent at carrion resulting from wolf kills would be much less than that spent at winter kills since wolves may have consumed much of the carcass before its discovery by coyotes.

Few studies have indicated the importance of beaver in the diet of coyotes. Most other studies in regions where beavers and coyotes are common, took place in winter when beaver are at low risk. Berg and Chesness (1978) found winter frequency of occurrence of beaver hair to be less than 1% in northern Minnesota. In the Adirondacks, use throughout the year was less than 0.5% in occurrence (Hamilton 1974). Young and Jackson (1951) provided anecdotal evidence of coyotes killing beaver in Colorado. Hilton (1978) considered beaver to be an unusual prey item of coyotes and suggested that the occurrence of beaver in coyote scats from Maine (18% in spring, 8% in fall) reflected the recent development of a searching image for beaver. Coyote use of beaver has increased since the 1975-79 study (Carbyn unpubl. data), particularly in the fall and summer. Most of the increase occurred in the second year of the study when frequency of occurrence was 23.1%, triple that of 1983. This suggests the possibility of a functional response by coyotes to changes in beaver numbers and/or increased vulnerability to predation owing to low water levels and possibly a greater number of beavers occurring in marginal habitat.

Deer use also increased from the earlier study, particularly in the summer. Whether that change resulted from changes in the deer population is unknown since no censuses of deer were taken. If observational ratios are valid, then the average deer population from 1982-1984 was similar to that present during the previous study. Coyotes can kill deer as well as use them in the form of carrion. In Minnesota, Berg and Chesness (1978) reported frequencies of occurrence of 55% in winter and 27% in summer and concluded that most use was as carrion. In northern Wisconsin, frequency of deer hair in spring scats appeared to be related to the severity of the preceding winter. A severe winter produced much carrion and a frequency of use of 62%, an increase of 27% over a mild winter (Niebauer and Rongstad 1977). Huegel and Rongstad (1985) found a definite shift from snowshoe hare to the killing of deer in late winter in Wisconsin under conditions of deep and crusty snow. These snow conditions give coyotes an advantage in mobility over deer, since they are often able to run on top of the snow while deer break through the crust, which slows them down. A similar preponderance of late winter kills has been noted in R.M.N.P. by Paquet (unpubl. data). Use of deer by coyotes in this study, as indicated by scat analysis, was greatest in 1983 which correlates with the March 1983 crusty snow conditions when a large number of deer killed by coyotes were found. Hamlin et al. (1984) found mortality of deer fawns in Montana to be lowest when the microtine population was high. In Maine and South Dakota, Hilton (1978) and MacCracken (1984) found deer to be the primary food in winter, whereas cricetids were in summer. The last two studies cited suggest a possible explanation for the increased summer use of deer in this study compared with the previous study in the park (Carbyn unpubl. data). Both cricetid and hare numbers were low in 1983 and 1984, which may have resulted in a greater dependence of coyotes on deer.

Cricetids, muskrats and miscellaneous items were of less importance in this study than in the 1975-79 study. As for wolves, deletion of data for summer 1977 from the analysis resulted in closer agreement of cricetid frequencies between the two studies. Correlations between small rodent populations and their use by coyotes have been reported (Pastuck 1974, Niebauer and Rongstad 1977). The drop in muskrat use was significant for all four seasons and hence the simplest explanation could be a lower muskrat population. The drop in miscellaneous items occurred in the winter. The first study in R.M.N.P. found greater use of items like porcupine, squirrel, birds and fish than this study. There is no obvious explanation why this was so.

The frequency of occurrence of snowshoe hare did not differ significantly from that recorded in 1975-79. Neither study took place during the peak of the local hare cycle which occurred in 1980/1981 (Fig. 15). An obvious question is how would coyote use of hare in R.M.N.P. change during peak levels of snowshoe hare? Pastuck (1974) working in Harcus and Spruce Woods, Manitoba, observed from the peak to non-peak years, a 10- to 15-fold decrease in hare numbers along with a 33% decrease of hare in the scats of coyotes. In South Dakota, MacCracken (1981) found that when abundant, leporids were preferred over rodents and went on to suggest that when abundant, leporids would dominate in the diet over rodents, deer, livestock and vegetation (MacCracken 1984). Berg and Chesness (1978) however, found low predation on an abundant hare population in a situation where deer carrion was abundant. Korschgen (1957) described a simple direct relationship between hare abundance and percentage in scats. In R.M.N.P., although snowshoe hare use would likely go up with increases in the hare population, the degree to which it would do so is not predictable. Other food items, including ungulate carrion and beaver, would likely influence any changes.

Compared with the first study, coyotes used large prey more and small prey less. The swing of about 25% further suggests that environmental conditions differed enough between the two studies to result in significant functional shifts by coyotes in their feeding habits.

B. Seasonal similarities and differences

Both canids displayed higher occurrences of ungulate hair in their winter and spring scats than in fall. Although elk remained important for wolves in summer, their use by coyotes declined significantly from winter and spring (although by weight it remained the number one item). I believe this indicates that coyotes experience difficulty in finding summer carcasses (which are fewer in number than in winter) and need to rely more on alternate food items. In winter, coyote tracks can often be seen in the snow following wolf tracks, a behaviour that may help coyotes to find wolf kills. Winter use of elk by wolves is likely influenced by winter severity. Deep snow can restrict elk movements, making them more vulnerable to wolves, and, where elk are abundant, may result in higher than normal predation rates because of the ease of killing (Carbyn 1983).

Wolf and coyotes made greater use of moose in winter and spring, and deer in winter than in the other seasons. For wolves, the high use of moose in spring agreed with concurrent kill data for the park (P. Paquet pers. comm.). For both ungulates, coyote use was low in fall while for wolves it was high. Again, low use of moose in the non-winter months indicates that coyote have difficulty in acquiring carrion at that time. The advantages that coyotes have over deer under snowy conditions are not present in the fall. For both canids, low summer use of moose and deer was a reflection of the seasonal availability of a number of m[illegible] easily ob[illegible]ned alternate food sources (e.g. beaver and cervid young).

Greater use of deer by wolves in winter than in summer has been observed in many areas (Thompson 1952, Pimlott et al. 1969, Van Ballenberghe et al. 1975, Theberge et al. 1978). Fritts and Mech (1981) observed a significant drop in deer consumption from winter to summer, with moose being the most important food in April and May. The high incidence of moose was believed to be a result of increased vulnerability caused by significant winter parasitism.

Cervid young are an important summer food source. Because of their vulnerability, elk calves, moose calves and deer fawns would be an attractive food item, particularly to wolves. Unfortunately it is not possible to rank, from scat contents, the importance of young of the year during winter months. However kill data for the winter of 1983-84 (Paquet unpubl. data.) indicated that 7 out of 27 (26%) kills were of calves. An estimate of the contribution of cervid young individuals derived from biomass equivalences, suggests that 34% of the cervid kills in summer are of calves and fawns. Biomass contribution of cervid young in summer is about 5%, compared to 88% for adults. Hence simple frequency data can be misleading with regard to the significance of the prey item to wolves, although the relative losses of young and adults can be significant to the prey population.

Cervid young, which ranked sixth in summer use by coyotes during the 1975-1979 study, comprised a frequency of occurrence of 24% deer fawn and 76% elk calf (Carbyn unpubl. data). There is evidence of coyotes killing elk calves in R.M.N.P. (Paquet pers. comm.) and hence that figure would not necessarily represent only carrion consumption.

Beaver is a good example of a seasonally available item. Biomass estimates indicated that in winter, 1 beaver was eaten by wolves for every 7 elk taken. However, compared with other seasons, winter use was insignificant for both canids; the few occurrences in scats likely represented beaver taken in either early or late winter when freeze over on ponds was incomplete. Previous mid-winter tracking of a pack of wolves in the park indicated no use of beaver over a 19-day period (Carbyn 1983). For both canids, frequency of occurrence is numerically greatest in fall, significantly so for coyotes. Peterson (1977) suggested that predation on beaver by wolves on Isle Royale should be greatest in the fall when beavers are vulnerable owing to their activity on land to cut trees for winter storage. Such may be the case in R.M.N.P., particularly for coyotes in which the switch over, primarily from cervid young, appeared to be quite distinct.

In the previous study in R.M.N.P., high levels of beaver consumption by coyotes occurred in the spring (Appendix 3), which coincides with the time of dispersal of young beaver, supposedly another situation of great

Seasonality in wolf diets has most often been related to summer time shifts to cervid young (Pimlott et al. 1969, Carbyn 1974, Frenzel 1974, Van Ballenberghe et al. 1975, Peterson 1977) and beaver (Voigt et al. 1976, Theberge et al. 1978, Fuller and Keith 1980). However those shifts do not necessarily alter the ranking of prey species so much as they serve to lessen the impact on the primary prey species. In R.M.N.P., the summer and fall consumption of beaver may lessen the impact on elk calves, which are most vulnerable during those periods. By weight, summer contribution of beaver was 4%, approximately equal to that of cervid young. Hence in the absence of beaver, consumption of elk calves could be as much as doubled. However if alternate prey are not available, high reliance on the primary prey may occur year-round (Peterson et al. 1984).

Snowshoe hare use displayed no seasonal trend whatsoever. Niebauer and Rongstad (1977) found that during a high in hare numbers, use was greatest in spring when many immature hares were taken by coyotes. Data presented here suggest that at low levels of abundance of hares, both wolves and coyotes are completely opportunistic in their use of this food item.

For both canids, occurrences of smaller items were greater in the summer and fall than in winter. Muskrats, cricetids and miscellaneous items all occurred in insignificant amounts for both canids in the winter. A good the number of species eaten increases and the average size of prey taken decreases in the summer. The same statement can likely be made about wolf habits in areas where prey diversity is moderate to large.

Over the eight seasons of the study, both canids displayed a similar pattern in the four associations examined. The strongest association for both was between the amount of elk and the amount of moose consumed. They varied directly, emphasizing the similar response by each canid to the two large ungulates. When conditions are favourable for wolves to hunt elk, they are also favourable for hunting moose. When conditions favour use of smaller, alternate prey, both moose and elk are used less. For coyotes, this trend supports the view that they rely on the existence of moose and elk carrion, whether they be wolf kills or supplied by other means (e.g. winter kills under severe snow conditions).

An inverse relationship between deer and beaver was more clearly indicated for coyotes than for wolves. In the second year in general, and both falls together in particular, increased use of beaver paralleled decreased use of deer. Presumably, as beaver became more available or vulnerable either through increased numbers or increased presence on land or in marginal habitat, coyotes switched from killing deer to killing beaver. Implicit in this is the assumption that beaver were easier to obtain than deer at that time.

The regression equation of Floyd et al. (1978) although derived from wolves was also applied to coyote data in this study on the assumption that differences in digestive processing of large prey items would be minor. However it is not known if the relationship holds for items that are primarily scavenged. It is reasonable to suggest that consumption of the latter stages of a carcass will increase the ratio of hair digested to meat consumed, thus overemphasizing the item in the diet. In particular, coyote use of both elk and moose may be exaggerated.

The relative number of prey items consumed by coyotes gives some indication of the relative importance of prey killed and food scavenged. If elk and moose are considered to be scavenged items, then in the summer, only 10.4% of the items eaten were scavenged. In winter, scavenging became more frequent, having occurred 30.0% of the time.

For coyotes, seasonal variation appears to be primarily a function of availability. In some areas, invertebrates and vegetation are of maximum importance in the summer when they are more abundant (Fichter et al. 1955). High use of invertebrates and vegetation coincides with a reduction in mammalian food items that typically occur at peak frequencies in scats during the winter (Pastuck 1974, Bowyer et al. 1983). MacCracken (1984) found grasshoppers and fruit to be of greatest importance in the fall when their availability was greatest. Fichter et al. (1955) in Nebraska, found seasonal differences in use of leporids, insects, fruit and mice. Carrion, be it from elk, moose or deer winter kills, is often a local, abundant food item in winter and early spring (Murie 1940, Berg and Chesness 1978, Bekoff and Wells 1980). Ozoga and Harger (1966) believed that the few deer killed were the most vulnerable, being small and weak. The results from those studies parallel those from this study; in particular, the high mammalian component of the winter diet, the greater summer diversity and the response in consumption to the relative availability of many food items.

All values of Morisita's coefficient of similarity were relatively high indicating further the relatively similar percentage use of the food categories held in common. The smallest value of 0.87 in summer indicates the increased diversity and decreased similarity of diets between the species during that season. It is also suggestive of less scavenging of wolf kills by coyotes at that time. The fall, winter and spring values are relatively close indicating greater dietary overlap during those seasons.

Over the course of the study, wolves and coyotes displayed similar patterns in use of the ungulate species. The relatively high correlations of use over the eight seasons could be a result of:

1) coincidence owing to small sample sizes,
2) environmental factors, e.g. prey abundance, and
3) canid interactions.

Since coyotes must be scavenging elk, the high correlation coefficient of 0.91 is consistent with the idea that they are scavenging wolf kills, although it doesn't rule out collateral responses to environmental conditions (e.g. severe winter die-offs). A similar argument, although supported by much lower correlations, may be made for moose and deer. In the latter instance, environmental factors likely play a more important role.

Surprisingly, use of beaver by wolves and coyotes was not correlated.

C. Wolf-coyote competition

Two types of competition are generally recognized (Krebs 1978:208). Resource competition occurs when two or more species use a common resource that is in short supply. Interference competition occurs when one species harms the other in the process of using a resource (i.e. aggressive behaviours become more evident than those designed for more efficient use of a resource). Common and obvious resources that may come under competition are habitat and food.

Wolves formed a stable breeding population on Isle Royale, an area that formerly contained coyotes. MacCracken (1984) considered that coyotes in the Black Hills of South Dakota filled a niche that was vacated relatively recently by the extirpation of wolves. Coyotes currently overlap with wolves in northern Minnesota and a number of areas in northern Canada and Alaska. The overall distribution of coyotes is far more extensive than that of wolves in areas that have moderate to high densities of man.

Negative interactions, possibly representing interference competition between the two canids have been recorded on Isle Royale (Krefting 1969), in northern Alberta (Fuller and Keith 1980), and in R.M.N.P. (Carbyn 1982). Krefting suggested that the loss of coyotes from Isle Royale was due to the actions of wolves, including killing of coyotes by wolves. Evidence of this behaviour has been observed in R.M.N.P. (Carbyn 1982, Paquet unpubl. data).

To demonstrate resource competition one has to show first that the two species use the same resource, and second that it is in short supply. Even if the same resource is used, different species may use it in different ways. For example, Trottier et al. (1983) found that although moose, elk and deer often browsed on the same species of shrubs, separation occurred owing to the use of different portions (i.e. heights) of the stems.

Similarity in wolf and coyote feeding habits is indicated by both the common occurrence of major food categories used and the overall Morisita similarity value of 0.92. Conversely, differences in relative use exist; wolves use the larger food items (moose, deer and elk), more than coyotes do and coyotes rely more upon smaller items such as snowshoe hare, cricetids and muskrats. In food requirements, coyotes can be considered to be much more generalist than wolves.

The smaller items are likely not restrictive since they do not make up a significant proportion of either canid's diet and hence even if they (e.g. porcupines, muskrats and squirrels) are in short supply at some time, they are not likely to influence behavioural interactions between wolves and coyotes. Beaver is an item with a frequency of occurrence around 20% for both wolves and coyotes, who are both quite capable of killing them on land. However, owing to the widespread distribution of a dense population of beavers, there is little reason to expect competition for that resource. Similarly neither canid depends upon snowshoe hare to any large extent during its cyclic lows. Indeed there is reason to suspect that during a peak, coyotes would increase use of this resource much more than wolves, which would contribute to a greater separation in feeding niches.

Owing to their large biomass contribution to both diets, particularly in winter, cervids are more likely to represent a limited resource. Data on frequency of occurrence indicate elk to be the most important food for both canids. Clearly, if elk were in short supply and one or both predators had difficulty sustaining population levels on alternate prey, then competition could occur.

The impact of wolves on elk, although significant, is not enough alone to limit the elk population. Since coyote predation on elk is rare, any additional direct impact on the elk population is minor, likely limited to a few instances of predation on calves.

In R.M.N.P. coyotes are known to follow wolf tracks to kills, and wolves often abandon incompletely consumed carcasses. (All wolf-killed ungulates examined in the winters of 1982/83 and 1983/84 had been visited by coyotes (P. Paquet pers. comm.). Similar results were obtained in 1979 (Carbyn pers. comm.).) Both these observations suggest use of wolf-killed elk by coyotes in non-competitive circumstances. The frequency with which wolves abandon kills suggests that further kills can be made easily owing to a relatively abundant prey population and/or favourable hunting conditions. Hence the data support the suggestion that under present circumstances, wolf and coyote do not usually compete for the use of food resources.

However if the elk population continues to decrease, the chance of competitive interactions could increase. Under conditions whereby elk are more difficult for wolves to kill, such as decreased elk numbers or mild winter weather, use of carcasses by wolves is likely to be more complete. If wolves then spend more time at kills the chance of interspecific aggression between the two canids may increase. Even under the current conditions of "abundant" large prey, interference competition occurs. Eight coyotes killed by wolves have been found in the park, at least three of which died near wolf-killed elk (Carbyn et al. 1985). The long-term result for coyotes might be a shift to alternate prey or a lowering of coyote numbers or both. Carbyn (1982) noticed an inverse relationship between howling indices for the two species (Appendix 6). This could mean that when wolf numbers are relatively high compared to coyotes, there is less carrion available to coyotes and the final result may be a lowering of their numbers. Todd and Keith (1976), Weaver (1979) and Todd (1985) noticed the effect of carrion in maintaining coyote populations; the less carrion available, the fewer the coyotes.

D. Wolf-prey relationships

Prey population trends

Kingsley and Smith (1981), using statistical models, showed that the moose counts are precise. The question of the degree of accuracy of the counts remains unanswered. (Attempts to derive a correction factor for the park based on sightability from the air failed because of logistical and financial considerations.) It is however, almost certain that the counts underestimate the true numbers because of animals present on the transects that are missed by the observers.

Both elk and moose numbers have been declining in recent years. Year to year variation may not be significant as indicated by the 95% confidence intervals, but the results of the ANOVA suggest overall trend information to be valid. By way of comparison with other areas, the elk density can be considered moderate while that for moose is moderately high. Elk in Elk Island National Park, may reach densities of up to 3.1 or more animals per km² (Telfer and Cairns 1979, J. Welman pers. comm.), but in the Spruce Woods Forest Reserve in southern Manitoba the density is less than 1 per km² (Hornbeck 1985). Moose in Quebec typically occur in densities ranging from 0.04 to 0.26 moose per km² (Brassard et al. 1974), while in interior Alaska, values ha~~ve~~T ranged from 0.06 to 1.5 moose per km² (Gasaway et al. 1983). Some habitat on the Kenai peninsula in Alaska, has supported 6.6 moose per km² (Bailey 1978).

Elk and moose distributional patterns have not changed over recent years. Variance/mean ratios and chi-squared values were in the ranges of those obtained by Rounds (1982) for the period between 1969 and 1978. Group size data (Appendix 4) were also consistent (Rounds 1978, 1980). These data indicate that elk are available to predators as a more clumped food resource than moose.

The mean centers of distribution and standard distances obtained further validate Rounds's (1982) claim that those values vary little with changes in the numbers of the two ungulates. Rounds went on to suggest that this result supports the view of collateral responses by elk and moose to severe winter weather.

The absolute accuracy of the classified counts can be questioned. The aerial surveys involved much circling and shifting of altitude, factors that contribute to observer fatigue and the likelihood of misidentification and incorrect counting. However, in a number of cases, constant ratios were obtained before the end of the flights, suggesting consistency in identification and counting. Hence, although biases undoubtedly exist, the calf/cow ratios are considered to be relatively accurate. Less confidence in the bull/cow ratios can be expressed, especially for elk, since they are sensitive to unrepresentative sampling of the sex-segregated ranges.

One possible source of bias for calf counts was suggested by Van Ballenberghe (1979). From his own moose research he concluded that cows without calves occurred in larger aggregations than cows with calves in the fall and *vice versa* in the spring. Hence calf/cow ratios would be underestimated in fall and overestimated in spring. Such, however, was not the case in this study for moose populations sampled in early and late winter. In both cases, groups of cows with calves were larger in size than groups of cows without calves. For elk there was no significant difference in size.

A review of past studies indicates the calf/cow ratios that were obtained were relatively low. In his survey of the literature on early winter elk calf counts, Peek (1982) reported a range of 18 to 71:100 among populations and 18 to 45:100 within a population over different years. For moose, Crichton (1977) reported a range during the 1970s of 40 to 79:100 on Hecla Island, Manitoba, while in the Nelchina Basin of Alaska, early winter ratios ranged from 18 to

90:100 (Bishop and Rausch 1974). The low values in this study suggest that summer losses of calves could be the main factor driving the two ungulate populations down. A low birth rate is also possible, but owing to the suggestion of a moderate pregnancy rate and a lack of severe winters in recent years, that appears unlikely.

Deer numbers in areas outside the park have been relatively stable in recent years (Manitoba Department of Natural Resources, unpubl. data). Judged by sighting ratios, deer numbers in the park remain low, and there is no evidence of any drastic increase or decrease from the population of the late 1970s.

The beaver population has been relatively stable over the last few years. The increase in 1983 if real, may be just a temporary, minor fluctuation.

Possible causes of the elk decline

The results of the calf/cow surveys indicate a significant loss of elk calves during summer and fall. A population of 4156 with a 69% pregnancy rate and an average bull/cow ratio of 55/100 should produce 1850 calves. An early winter count of 22 calves/ 100 cows means that about 590 calves survived or approximately 1260 calves were lost in the summer and fall. (This calculation assumes no summer losses of cows. Hence 1260 is a minimum estimate of the number of calves lost.)

Wolves occupy homesites during a sizeable portion of the early summer, when elk calves are likely most vulnerable. *A priori*, one might predict heavy predation upon young calves at that time. The collection of scats from homesite locations, however did not confirm the prediction. Rather, the abundance of beaver in scats from homesites was significantly greater than that from the overall summer collection. This result further indicates the possible role beaver may have in buffering predation upon elk calves. Carbyn (1980) obtained a similar result. Theberge et al. (1978) also found more beaver in scats located at homesites, while Fuller and Keith (1980) noted that dens were often located near beaver lodges.

Impact calculations based upon a first approximation of the relevant biological parameters, indicated that wolf predation would, over the year, account for about 17% of the starting spring elk population. Assuming production of 1850 calves, an elk population that remained stable would have losses of an additional 27%, or 1103 individuals (i.e. 1850 - 747 wolf kills) to be accounted for (Table 13). Losses to hunters during the study averaged 283 elk, or 7% of the spring population. A natural or base mortality rate (that excludes losses to predators and hunters) of approximately 20% would not be unrealistic (Kimball and Wolfe 1974). Addition of these last two mortality factors would be enough to offset recruitment to the elk population.

Table 13. One-year growth of an elk population under various conditions of wolf predation

Parameters			
Constants			
Starting spring population	4156	No. wolf adults	59
% cows	65	No. wolf pups	16
Pregnancy rate	69	No. of packs	12
% hunting mortality	7	% natural mortality	20

Variables	Cases[1]						
	1	2	3	4	5	6	7
Consumption rate (kg/wolf/day): adult	1.7	3.4	1.7	1.7	1.7	3.4	1.7
: pup	0.9	1.7	0.9	0.9	0.9	1.7	0.9
Summer diet % of: adult elk	79	79	90	45	0	0	79
: elk calf	4.5	4.5	10	55	100	100	4.5
Winter kill rate (no. kills per day per pack)	0.25	0.25	0.25	0.25	0.25	0.25	0.11
Year-end population	4137	4033	4086	3789	3493	2750	4496
% change	0	-3	-2	-9	-16	-34	8

1 Description of cases: 1- a first approximation of parameters in R.M.N.P.; 2- summer consumption rate doubled; 3-5- variation in proportions of elk adults and calves in summer diet; 6- an extreme case with double the base consumption rate and complete use of elk calves in summer; 7- as for case 1 with the exception of a more moderate kill rate

Considering wolf predation alone, increases in the summer consumption rates and/or the proportions of adult elk and calves in the summer diet of wolves, could significantly alter the impact on the elk population (Table 13). An extreme case where summer consumption rates are doubled with total dependence at that time on calves, could cause a 7% decrease in the elk population even before considering other sources of mortality.

However, even the first case considered may overestimate the contribution of wolf predation to elk mortality. The kill rate used of 0.25 kills per day per pack (i.e. 1 ungulate kill per 2.7 days with 68% of the kills being elk), comes from data collected during a severe winter (Carbyn 1983). A more moderate rate of 0.11 kills per day per pack, suggested by recent data for the park (P. Paquet pers. comm.), would decrease the effect of wolves and hence increase the year-end elk population by about 8% (Table 13). Furthermore, the assumption of a 69% pregnancy rate is a conservative estimate; an additional 27 calves being produced for every increase of one percentage point in the rate.

The important conclusion from this analysis is that although wolf predation alone could be of primary significance under "extreme" conditions, in actuality it is one of several factors that together limit the elk population in R.M.N.P. Bear predation on calves, hunter losses (including legal, illegal and native hunting) and natural mortality (e.g. disease, old age and winter die-off), in conjunction with losses to wolves, are all factors whose cumulative effect may be to cause the elk population to decline. The model considered above does not take into account the effect on the population of unbalanced losses of bulls and cows. Recent data indicate a greater loss of bulls than cows from wolf predation and winter stress (P. Paquet pers. comm.). Over the short term, the elk population should be able to sustain major losses of bulls much more readily than of cows.

The low early winter calf count recorded from aerial surveys is consistent with the recent annual population declines. If one adds to the calculated summer calf losses of 1260 the additional winter losses to wolves (641 animals, from case 1) and hunters (283 animals), one has a year-end population of 3823, an 8.0% decrease from the start of the year. An annual population decrease of approximately 17% would be realized with a further 9% loss because of natural mortality.

A possible additional source of summer losses is that of bear predation. Schlegel (1976) reported that most of his radio-collared elk calves were killed by black bears during summer. Other telemetry studies have reported black bear predation on moose calves (Franzmann et al. 1980) and white-tailed deer fawns (Ozoga and Verme 1982). In this study, the frequency of hair in bear scats was low (Table 6), suggesting that bear predation on cervid young was insignificant. However, M. Wilton (unpubl. paper) in a survey of the literature, found the results of many studies to have had similar low frequencies of animal material in bear scats. He concluded that this type of evidence is inconclusive since there is evidence from Alaska that bears there often evert the hide of their kills, so that little hair gets into the scats. It is not known whether this occurs in R.M.N.P. Hence it would be premature to rule out bear predation on elk calves as a significant factor.

Weather can also influence calf survival. Taber et al. (1982) commented on the effects of stressful winters on pregnant elk cows and their subsequent young. Small calves may be less likely than large ones to survive the rigours of the environment. None of the winters in the previous three years has been as severe as the winter of 1978/79 (Table 12). Park records indicated that while wardens found 32 winter-killed ungulates in the winter of 1978/79, they only discovered 9 winter-kills in total for the winters of 1981/82 to 1983/84. However, although the above suggests an immediate effect of winter severity on individual ungulates, the data give no indication of any immediate or delayed effect upon the population as a whole. Furthermore, even if there is an inverse relationship between severity and ungulate numbers, the last three winters have been near average in temperature and snow depths, and hence are unlikely to have had any major effect on elk numbers.

Relationships with other ungulates

Moose contribute much less to the diet of wolves than do elk. Selectivity values of 27% and 58% for summer and winter respectively indicate the low preference of wolves for moose. Distributional patterns for moose, indicate high densities on the eastern and northern edges of the park, areas where few scats were picked up. Since wolves using those areas may consume more moose than wolves elsewhere in the park, the selectivity values of wolf preference for moose may be underestimated. The magnitude of this bias is unknown.

Moose are considered to be 'r-strategists' relative to other North American ungulates (Trottier et al. 1983). With [illegible]ning, reproductive potential is typically higher than that for elk. Hence the calf count in early winter was higher for moose than for elk, but significant summer losses may still occur. Nevertheless, overall wolf use of moose is relatively minor compared to use of elk, and hence other factors must play a more important role in limiting the moose population.

Impact of wolves (and coyotes) on white-tailed deer is hard to determine owing to lack of adequate census data. Most impressions of seasonal distribution would indicate higher densities in summer. In the winter many deer have been seen leaving the park and yarding up in nearby agricultural lands. Wolf (and coyote) predation is high in winter as indicated by selectivity values. However summer predation seems particularly low. As indicated earlier, severe winters can play an important role in affecting the interactions of deer and predators. Even unborn young can be affected. Frenzel (1974) believed that the high proportion of deer fawns taken in spring was due to poor viability of the cohort as a result of *in utero* winter stress. Although canids in the park may exert an important influence on deer, clear knowledge of the relationship will only come about by a study on deer movements and population levels.

VI. CONCLUSION

Currently, in R.M.N.P., competition for food between wolves and coyotes is of little significance. Examples of interference competition, namely the killing of coyotes by wolves, do occur and may be related to incidents of coyotes following wolves to kills. Resource competition appears mostly inoperative. Although there is broad overlap in food items eaten, in general it is probably offset by the wide diversity and abundance of prey in the park. Furthermore, separation along the niche axis of prey size does occur, with wolves, as expected, taking more larger prey than do coyotes.

Winter, with its lesser diversity of prey, offers the greatest possibility for competitive interaction. A number of factors suggest that coyotes scavenge wolf kills and other sources of winter carrion. As long as winter food sources remain relatively abundant, competitive interactions should remain minimal. Lower levels of elk and deer, and/or higher wolf numbers could have an impact on the coyote population.

Wolf feeding patterns exhibited only minor differences from the 1970s study. In contrast, coyote food habits displayed significant changes from the past study, which may indicate a greater degree of opportunistic feeding behaviour by coyotes than wolves when faced with changes in environmental conditions (e.g. changing prey population levels, wolf population changes and/or increases in winter carrion). Coyote use of large prey has increased since the 1970s.

Both canids demonstrated responses to availability and vulnerability of food items. Muskrat, mice, beaver and some miscellaneous items were taken in the summer and fall, but use was much less in winter when they were for the most part not available. Snowshoe hare use over the two years of the study may reflect cyclic changes in hare numbers. Use of cervid young in summer and the greater use of all three ungulates in the winter corresponded to their times of greatest vulnerability. An increase in beaver use by coyotes in 1983 may reflect both availability and vulnerability. A slight increase in beaver numbers was accompanied by the lowest level of summer precipitation recorded since 1976.

The effect of wolves on the elk population has not changed significantly since earlier work in the park (Carbyn 1980). Scat analysis indicated significant use, but not enough in itself to cause a decline in elk numbers. The same is true for moose. Weather and hunting appear not to be major factors in recent years. Calf counts indicated that major losses occurred in the summer and fall months. The impact of black bear predation on elk remains in doubt. That elk and moose populations have been in synchrony since annual surveys started in 1976, suggests collateral responses to environmental conditions. Changing vegetation patterns may be of importance.

Other studies have demonstrated the importance of prey diversity in moderating the effect of predators on their prey. In simpler biotas, influences of predators on prey and prey on predators are very dramatic. Such examples come from Isle Royale for wolves (Peterson 1977) and from Utah for coyotes (Clark 1972, Wagner and Stoddart 1972). Where prey diversity is much greater, Jasper National Park for wolves (Carbyn 1974) and northwestern Wisconsin for coyotes (Niebauer and Rongstad 1977), prey populations do not seem to be related to predator numbers. Canid-prey relationships in R.M.N.P. appear to be an example of the latter category.

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APPENDIX 1. Characteristics of scats collected from a captive wolf pack.

Four deer fawns were fed in separate trials to a captive wolf pack housed at Dalhousie University. Prior to each feeding, the enclosure was cleared of any old scats. During the trial, scats were collected once a day until deposition ceased; usually after four days.

All scats collected were characterized as to colour, consistency and day of deposition. The colour categories were dark brown, brown, gray, yellow, white and green. Consistency classes were firm, semi-firm, crumbly, diarrhea, clay, fresh and hairy. If a scat was described as containing two colours or two consistencies, or if it had an intermediate consistency, then a score of one was added to each individual category. Hence the frequency totals were necessarily larger than the number of scats collected (n=361). G-test analyses were done on colour versus day (n=428) and consistency versus day (n=445). The contents of 28 scats were examined microscopically.

Both sets of classifications varied significantly with the time in days of deposition (colour: G=147.14, consistency: G=266.96, $p < 0.01$). Individual categories were examined separately. Scats classified as brown or green, occurred randomly throughout the pickup period. All other classes varied significantly. Dark brown scats occurred most often during the first two days. Gray coloured scats were uncommon in the first day. Scats classified as white or yellow were to be found more often in the last two days of collecting.

Thirty-five percent of the scats deposited the first day had a diarrhetic consistency. Semi-firm scats occurred more often in the first two days than the last two. Scats in which the hair content was quite evident, occurred mostly in the latter two days. Firm and crumbly scats occurred mainly during the last three days. Only fresh scats showed no significant variation.

Examination of the different types of scats indicated that those classified as firm or hairy, brown, dark brown or yellow, generally provided good hair samples that could be used for microscopic identification. However scats that were crumbly and/or white, often provided either no hair sample or a very poor one for identification purposes. Scats deposited early after feeding, which were diarrhetic or semi-firm in consistency, were variable in the quality of hair remains they contained.

These relationships need further study. Different food items should be fed to captive wolves (and coyotes) and similar analyses carried out. This information could supplement other methods for dating kills and estimating frequency of feedings.

APPENDIX 2. Percent seasonal frequency of occurrence of food items in wolf scats (1975-1979)[1].

Food item	Summer N=1196	Fall N=118	Winter N=525
Elk	27.1	34.7	51.8
Moose	2.0	9.3	12.6
Deer	3.2	13.6	16.0
Cervid Young[2]	13.8	1.7	
Beaver	20.9	15.3	4.4
Snowshoe Hare	7.0	0.8	4.6
Muskrat	4.3	3.4	1.5
Cricetidae[3]	10.0	5.1	2.3
Porcupine	2.8	0.0	1.0
Squirrel	3.2	9.3	0.4
Canid	1.9	0.0	1.5
Insects	0.3	0.0	0.0
Vegetation	0.7	5.1	0.8
Avian	1.2	1.7	0.6
Others	1.6	0.0	2.7

1 Extracted from Carbyn (1980)
2 Indistinguishable from adults after early fall
3 Excluding Muskrat

APPENDIX 3. Percent seasonal frequency of occurrence of food items in coyote scats (1975-1979)[1].

	Summer	Fall	Winter	Spring
Food item	N=820	N=202	N=178	N=65
Elk	8.5	8.9	29.8	16.9
Moose	1.3	1.0	6.2	4.6
Deer	1.6	1.0	8.4	3.1
Cervid Young[2]	8.3			
Beaver	10.5	9.9	17.4	29.2
Snowshoe Hare	18.0	22.8	5.1	7.7
Muskrat	12.6	16.3	8.4	24.6
Cricetidae[3]	19.3	21.8	5.1	4.6
Porcupine	2.8	2.5	6.7	1.5
Squirrel	4.8	2.5	2.2	1.5
Canid	0.7	1.5	0.6	1.5
Insects	2.7	2.0	0.0	1.5
Vegetation	4.3	2.0	1.1	0.0
Avian	3.5	4.0	3.9	0.0
Others	1.1	4.0	5.1	3.1

1 Carbyn unpubl. data.
2 Indistinguishable from adults after early fall
3 Excluding Muskrat

APPENDIX 4 Average size of elk and moose groups classified by sex and age from the 1983 and 1984 aerial surveys (Number of groups for each category are in parenthesis.)

Survey	Bulls Only	Bulls-Cows	Cows-Calves	Cows Only	Bulls-Cows-Calves	Total
November 1983						
Moose	1.4 (106)	2.9 (36)	2.0 (128)	1.1 (208)	3.2 (5)	1.6 (483)
Elk	1.7 (209)	4.7 (20)	4.4 (102)	2.2 (138)	16.8 (17)	3.0 (486)
March 1984						
Moose	1.1 (113)	2.5 (6)	2.0 (167)	1.0 (190)	3.0 (1)	1.3 (377)
Elk	1.6 (97)					2.1 (256)
November 1984						
Moose	1.3 (26)	2.5 (4)	2.0 (128)	1.7 (74)	4.2 (5)	1.9 (237)
Elk	4.1 (66)	3.7 (17)	4.1 (65)	3.7 (99)	6.2 (11)	4.0 (258)

APPENDIX 5. Hunter kill data for hunting zone bordering on R M N P

	Sex	Mean Age	Mean Age yearling & older	Oldest Age	Sample Size of aged kills	Total kills
Moose						
1982/83	M	5.8	6.4	10.5	18	210
	F	5.2	6.1	10.5	19	
1983/84	M	5.6	6.4	12.5	49	149
	F	5.4	6.4	16.5	49	
Elk						
1982/83	M	7.1	8.4	17.5	36	399
	F	6.7	7.1	19.5	77	
1983/84	M	8.3	9.3	15.5	18	166
	F	5.8	6.1	16.5	48	

Appendix 6. Estimates of Canid Numbers in R.M.N.P.

Winter estimates of wolf numbers based upon warden track surveys have been carried out since 1982/83. The three surveys have given estimates of 78 (1982/83), 60 (1983/84) and 65 wolves (1984/85), for an average of 68.

Carbyn (1980) used the number of wolves in radio-collared packs to extrapolate a figure for the whole park. His "best" estimates gave values of 120 (1975/76), 73 (1976/77), 52 (1977/78) and 63 wolves (1978/79) for an average during his study of 77. Opinions of a number of park personnel were that wolf numbers have been lower in recent years compared with the late 1970s.

Qualitative indices of coyote numbers have been obtained for both studies by comparing howling responses of both canid species during summer nocturnal surveys. Carbyn (1982) traced a roughly inverse relationship between estimates of wolf numbers and the number of coyote responses and sightings from 1975 to 1979. Compared with 1983, responses in 1984 increased for coyotes and decreased for wolves. The 30 coyote responses (both group and single) of 1984 were the second highest total recorded since surveys began. The 1977/78 total of 32 responses occurred during a low in wolf numbers (52).