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ASPECTS OF WINTER FORAGING IN LYNX AND COYOTES FROM SOUTHWESTERN YUKON DURING AN INCREASE IN SNOWSHOE HARE ABUNDANCE

BY

DENNIS L. MURRAY

A THESIS

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

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

SPRING 1991

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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 "Aspects of winter foraging in lynx and coyotes from southwestern Yukon during an increase in snowshoe hare abundance" submitted by Dennis L. Murray in partial fulfilment of the requirements for the degree of Master of Science.

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ABSTRACT

Lynx (Lynx canadensis) and coyotes (Canis latrans) were studied during two winters in southwestern Yukon to examine how differences in morphology and behavior interacted with snow conditions and prey density to affect habitat use and foraging in each species. Coyotes had 4.1 to 8.8 times the foot-load of lynx, but a similar chest height. Predators were tracked in snow for 645 km to determine their use of snow conditions, response to an increase in abundance of snowshoe hare (Lepus americanus), and habitat selection. Coyotes used primarily the low elevation region of the study site where there was less snow, and areas within both high and low elevation regions where snow was shallower and harder than average. Conversely, lynx selected the high elevation region where snow was deeper, as well as areas within both high and low elevation regions where snow was deeper than average. Further, lynx were less prone to travel on snow-packed trails than coyotes. Hare densities doubled between years of study, and both predators increased their kill- and scavenging rates by 1.6 and 2.2 fold respectively. Both predators selected spruce forests and avoided shrub and open areas but lynx traveled more in areas of low spruce cover. Lynx did not select habitats with highest hare densities or with the lowest snow depth, and their ability to detect hares at long distances may have influenced their strong selection for open spruce forests. Coyotes chased hares a shorter distance than did lynx, and success rates were higher in areas of dense cover. Coyotes did not select dense cover areas, though most kills occurred therein. This study confirms that differences exist in the foraging patterns of two similarly-sized sympatric carnivores.

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Finally, thanks must also be extended my longstanding friend K.T., as well as to The Chief, W.F., and The Zim, for providing me with solace and clemency as I sought "shelter from the storm".

ASPECTS OF WINTER FORAGING IN LYNX AND COYOTES FROM SOUTHWESTERN YUKON DURING AN INCREASE IN SNOWSHOE HARE ABUNDANCE.

CHAPTER 1: THE INFLUENCE OF SNOW ON LYNX AND COYOTE MOVEMENTS IN SOUTHWESTERN YUKON: DOES MORPHOLOGY AFFECT BEHAVIOR?

CHAPTER 2: WINTER DIETS AND CONSUMPTION RATES OF LYNX AND COYOTES IN SOUTHWESTERN YUKON, DURING AN INCREASE IN SNOWSHOE HARE ABUNDANCE.

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GENERAL INTRODUCTION

The relationship between a carnivore and its prey depends upon a number of factors. Two groups of carnivores, the felids and canids, have long had separate evolutionary histories which has resulted in each group having distinct adaptive strategies for the pursuit and capture of prey (Kleiman and Eisenberg 1973). Felid morphology is adapted for short, high-speed pursuit of prey, while that of canids is primarily designed for long-distance chases (Taylor 1989). Felids utilize cover as concealment when ambushing or stalking prey (Sunquist and Sunquist 1989), while canids typically run down their prey in relatively open habitats (Kleiman and Eisenberg 1973). Vision is the primary sense used by felids in hunting (Leyhausen 1956, cited in Kleiman and Eisenberg 1973), while olfaction and audition are the main senses used by canids when locating prey (Osterholm 1964; Kleiman and Eisenberg 1973; but see Wells and Lehner 1978). Further, felids are regarded as specialized predators, while canids are usually considered generalist predators, feeding on a wide array of foods (Kruuk 1986).

In addition to these differences between canids and felids, there may be a number of more proximate, environmentally governed factors that affect foraging by species from each group. These include the effects of snow conditions on movements (Parker 1981; Halpin and Bissonette 1988), effects of relative prey density on foraging patterns (Keith et al. 1977), the specific hunting behavior employed by individuals of the same species (Corbett 1979), and habitat use by different species (Schaller 1972; Elliot et al. 1977).

Despite the differences that exist between canids and felids, and the factors described above which may increase dissimilarities between both groups, it remains unclear how felids and canids differ in foraging behaviors under similar environmental conditions. Indeed, few studies have compared simultaneously, aspects of foraging behavior and/or relationships with prey in sympatric populations of felids and canids (Kruuk and Turner 1967; Iverson 1978; Toweill 1986; Witmer and deCalesta 1986; Major and Sherburne 1987; Litvaitis and Harrison 1989).

Lynx (*Lynx canadensis*) and coyotes (*Canis latrans*) are similarly-sized carnivores that occur sympatrically over much of the boreal forest biome, including areas of southwestern Yukon (Quinn and Parker 1987, Voigt and Berg 1987). Lynx have long been present in this geographical area (Repenning 1967), and are thought to be well adapted for residence in regions where snow is present, given their low foot-load (Parker et al. 1983). They are thought to rely heavily on snowshoe hare (*Lepus americanus*) (Brand et al. 1976), and appear to exhibit a Type II functional response to a change in hare density (Keith et al. 1977), where there is a relative deceleration in predation rate as prey density increases (Taylor 1984).

Coyotes are believed to be more recent immigrants to high latitude areas, having migrated northward from the midwestern United States earlier in this century (Nowak 1979). Their morphology appears to be poorly adapted for moving in snow (Todd and Keith 1976). However. it has been suggested that they may use behavioral modifications to alleviate the adverse effects of snow on their winter movements (Keith et al. 1977). In the boreal forest, coyotes appear to rely on snowshoe hare as food (Theberge and Wedeles 1989). Keith et al. (1977) suggest that the species undergoes a Type III functional response to a change in hare density, whereby predation rates do not decrease, relative to an increase in prey (Taylor 1984).

This study addresses several potentially important factors affecting foraging patterns of sympatric species by comparing the movements and hunting tactics of lynx and coyotes from southwestern Yukon. In Chapter 1, I examine morphological and behavioral adaptations of both predators to snow, and document the influence of snow on the vulnerability of snowshoe hare to predation. In Chapter 2, I examine the effect of an increase in snowshoe hare abundance on winter diets and consumption rates of both predators, and compare the functional response of the two species over a 2 year period. In Chapters 3 and 4, I describe habitat selection patterns of coyotes and lynx, and examine the effects of some external factors on the patterns that I recorded.

REFERENCES

Brand, C.J., Keith, L.B., and Fischer, C.A. 1976. Lynx responses to changing snowshoe hare densities in central Alberta. J. Wildl. Manage. 40:416-428.

Corbett, L.K. 1979. Feeding ecology and social organization of wildcats (Felis sylvestris) and domestic cats (Felis cattus) in Scotland. Ph.D. thesis, University of Aberdeen, Aberdeen, Scotland. 296 pp.

Elliot, J.P., Cowan, I.M., and Holling, C.S. 1977. Prey capture by the African lion. Can. J. Zool. 55:1811-1828.

Halpin, M.A., and Bissonette, J.A. 1988. Influence of snow depth on prey availability and habitat use by red fox. Can. J. Zool. 66:587-592.

Iverson, J.B. 1978. The impact of feral dogs and cats on populations of the West Indian rock iguana, Cyclura carinata. Biol. Conserv. 14:63-73.

Keith, L.B., Todd, A.W., Brand, C.J., Adamcik, R.S., and Rusch, D.H. 1977. An analysis of predation during a cyclic fluctuation of snowshoe hares. Proc. XIII Int. Cong. Game Biol. pp. 151-175.

Kleiman, D.G., and Eisenberg, J.F. 1973. Comparisons of canid and felid social systems from an evolutionary perspective. Anim. Behav. 21:637-659.

Kruuk, H. 1986. Interactions between felidae and their prey species: a review. In: Miller, S.D., and Everett, D.D. (eds.), Cats of the world: biology, conservation, and management. Nat. Wildl. Fed., Washington, D.C. pp. 353-374.

Kruuk, H., and Turner, D. 1967. Comparative notes on predation by lion, leopoard, cheetah and wild dog in the Serengeti area, East Africa. Mammalia 31:1-27.

Leyhausen, P. 1956. Verhaltensstudien an katzen. P. Parey-Verlag, Berlin.

Litvaitis, J.A., and Harrison, D.J. 1989. Bobcat-coyote niche relationships during a period of coyote population increase. Can. J. Zool. 67:1180-1188.

Major, J.T. and Sherburne, J.A. 1987. Interspecific relationships of coyotes, bobcats, and red foxes in western Maine. J. Wildl. Manage. 51:606-616.

Nowak, R.M. 1979. North American quaternary Canis. Monograph No. 6, Museum of Nat. Hist., University of Kansas, Lawrence, Kan. 154 pp.

Osterholm, H. 1964. The significance of distance receptors in the feeding behaviour of the fox, Vulpes vulpes L. Acta Zool. Fenn. 106:1-31.

Parker, G.R. 1981. Winter habitat use and hunting activities of lynx (Lynx canadensis) on Cape Breton Island, Nova Scotia. In: Chapman, J.A, and Pursely, D. (eds.), Proc. World. Furb. Conf., Frostburg, Md. (1980). pp. 221-248.

Parker, G.R., Maxwell, J.W., Morton, L.D., and Smith, G.E.J. 1983. The ecology of the lynx (Lynx canadensis) on Cape Breton Island. Can. J. Zool. 61:770-786.

Quinn, N.W.S., and Parker, G. 1987. Lynx. In: Novak, M., Baker, J.A., Obbard, M.E., and Malloch, B. (eds.), Wild furbearer management and conservation in North America. Ont. Min. Nat. Res., Toronto, Ont., pp. 683-694.

Repenning, C.A. 1967. Palearctic-Nearctic mammalian dispersal in the late Cenozoic. In: Hopkins, D.M. (ed.), The Bering land bridge. Stanford Univ. Press, Stanford, Calif. pp. 288-311.

Schaller, G.B. 1972. The Serengeti lion. Univ. Chicago Press, Chicago, Ill. 48 pp.

Sunquist, M.E., and Sunquist, F.C. 1989. Ecological constraints on predation by large felids. In:

Gittleman, J.L. (ed.), Carnivore behavior, ecology and evolution. Cornell Univ. Press, Ithaca, N.Y. pp. 283-301.

Taylor, M.E. 1989. Locomotor adaptations by carnivores. In: Gittleman, J.L (ed.), Carnivore behavior, ecology, and evolution. Cornell Univ. Press, Ithaca, N.Y. pp. 382-409.

Taylor, R.J. 1984. Predation. Chapman & Hall, New York, N.Y. 166 pp.

Theberge, J.B., and Wedeles, C.H.R. 1989. Prey selection and habitat partitioning in sympatric coyote and red fox populations, southwest Yukon. Can. J. Zool. 67:1285-1290.

Todd, A.W., and Keith, L.B. 1976. Responses of coyotes to winter reductions in agricultural carrion. Wildl. Tech. Bull. No. 5. Alta Rec., Parks and Wildl., Edmonton, Alta. 32 pp.

Toweill, D.E. 1986. Resource partitioning by bobcats and coyotes in a coniferous forest. Ph.D. thesis, Oregon State University, Corvallis, Or.

Voigt, D.R., and Berg, W.E. 1987. Coyote. In: Novak, M., Baker, J.A., Obbard, M.E., and Malloch, B. (eds.), Wild furbearer management and conservation in North America. Ont. Min. Nat. Res., Toronto, Ont. pp. 345-356.

Wells, M.C., and Lehner, P.N. 1978. The relative importance of the distance senses in coyote predatory behavior. Anim. Behav. 26:251-258.

Witmer, G.W., and deCalesta, D.S. 1986. Resource use by unexploited sympatric bobcats and coyotes in Oregon. Can. J. Zool. 64:2333-2338.

CHAPTER 1

THE INFLUENCE OF SNOW ON LYNX AND COYOTE MOVEMENTS IN SOUTHWESTERN YUKON: DOES MORPHOLOGY AFFECT BEHAVIOR?

INTRODUCTION

Snow may hinder the movement and activity of animals inhabiting temperate and arctic environments. The specific effect of snow on locomotion in terrestrial mammals depends not only on depth and bearing strength, but also on the animals' height, weight, and foot morphology (Formozov 1946). Mammals may also alter behavior to cope with snow, and some species use behavioral adaptations to offset morphological disadvantages. Telfer and Kelsall (1984) subjectively classified behavioral adaptations to snow by ungulates, but no study has examined behavioral adaptations of mammals quantitatively in a field setting.

Behavioral adaptations may include either adaptations expressed directly as a response to snow, or those which have evolved in response to other conditions, but which facilitate survival when snow is present (Telfer and Kelsall 1984). They may consist of selection of favorable snow conditions by a) residing in certain regions, b) travelling in specific areas within regions, or c) using specific travel routes within areas. The use of hard snow and animal trails and food acquisition methods that reduce

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the potential negative effect that snow has on food gathering, may also be considered behavioral adaptations.

Lynx and coyotes are mid-sized carnivores that range from 11 to 15 kg in weight (Stanley et al. 1983), and have overlapping distributions over much of the boreal forest of North America (Voigt and Berg 1987; Quinn and Parker 1987). Both predators appear to have different levels of morphological adaptation to snow, lynx being well adapted given a low body weight to foot surface ratio (Parker et al. 1983), and coyotes poorly adapted, because of their high foot-load (Todd and Keith 1976). Keith et al. (1977) suggest that coyotes may be forced to follow snowshoe hare (Lepus americanus) trails and Ozoga and Harger (1966) propose that coyote movements may be restricted to specific habitats when snow conditions are unfavorable. Therefore, coyotes may use behavioral adaptations in winter, to cope with snow.

For the purpose of this study, an adaptation was defined as a trait (either morphological or behavioral) which appeared to alleviate the potential adverse effects of snow on movement. I studied lynx and coyotes in southwestern Yukon to examine the following aspects of their winter ecology: 1) what was the magnitude of difference in morphological adaptation to snow between predators? 2) did morphological differences translate into a proportional difference in sinking depth in snow? 3) did the morphological disadvantages of coyotes force them to select regions, areas, or travel routes that differ from those used by lynx? and 4) do coyotes show other behavioral adaptations to cope with snowcover, as suggested by the literature?

STUDY AREA

Lynx and coyotes were studied in a 175 km^2 area of the Kluane Lake region of southwestern Yukon (61^oN, 138^oW). The study site was located in a broad valley running in an east-west direction. I worked from the base of the valley (830 m) to an altitude of 1169 m, which was near the base of the mountains. The altitude of the valley floor also differed with the central area, being up to 215 meters higher than that of either end. The entire area was part of the northern boreal forest zone (Douglas 1974), and white spruce (*Picea glauca*) was the dominant tree. Canopy cover ranged from 0 to 100% in the valley, and a strong negative relationship between elevation and spruce cover was evident. Other winter habitat types available to predators included deciduous (*Populus* spp.), shrub (*Salix* sp.), and completely open areas which included frozen waterways, meadows, and alpine tundra. Snowfall was directly related to altitude in the study site, and total snow accumulation for the entire site during the year of study averaged 65 cm, which was typical for that region (Krebs et al. 1986). I estimated that there were at least

16 lynx and 12 coyotes residing in the area during winter 1988-89, based on known locations of radio-collared animals, and associated tracks in localized areas. Other less abundant terrestrial predators included red fox (Vulpes vulpes), wolf (C. lupus), and wolverine (Gulo gulo). Snowshoe hare (Lepus americanus) was an important prey item for both lynx and coyotes in the southwest Yukon, and densities in the study site during winter 1988-89 were approximately .77 +/- .10 (mean +/- SD) hares per hectare (Chapter 2).

METHODS

Morphology

Skinned lynx and coyote carcasses were obtained from local trappers within a radius of 50 km of the study site, during winter 1988-89. All lynx were trapped whereas all coyotes were shot along the Alaska Highway. I recorded the weight, sex and ageclass (subadult or adult, according to skull size and tooth wear) of each lynx. Age was not estimated for coyotes. Carcasses were examined for chest height and foot-loading, two indices of morphological adaptation to snow (Telfer and Kelsall 1979; Telfer and Kelsall 1984).

Chest height of lynx and coyotes was measured from the distal tip of toes to midline of the brisket (Kelsall 1969). Foot-loading ratio was calculated by dividing carcass weight by the total area of unskinned paws. This involved severing a single fore and hindlimb from each carcass, thawing it completely, and placing the sole of the foot on a sheet of paper and tracing its contour. Because lynx paws have laterally flexible digits and retractile claws, all toes were compressed against each other and all claws were retracted before tracing, which produced a minimum estimate of print area. Print area was measured with a digital planimeter. Parker et al. (1983) found that skinning lynx carcasses reduced carcass weight by 10%; I assumed the same reduction for coyotes.

To determine how foot-loading of lynx and coyotes compared with that of their principal prey, I obtained foot-loads of snowshoe hares shot in the study site during December 1989. Hares were skinned, weighed, sex was determined, and foot-loading ratios of each carcass were measured as described above. Hares were not aged, and skinning reduced the weight of hare carcasses by 10%.

General Snow Conditions

Mean snowfall and snow hardness values for a representative of the entire study area were obtained along a 30 km snowmobile trail that ran along the valley floor, and bisected our study area. Snow depth and snow hardness were measured at 16 sites at a distance of 20 to 40 m from the snowmobile trail in 5 habitat types; the number of sites in each habitat type was proportional to the availability of each habitat, as determined by a LANDSAT image (Chapter 3). For analysis, I divided stations into high and low altitudes of the study area; there were 9 low altitude sites (837 m - 887 m) and 7 high altitude sites (935 m - 1035 m), and each of these was visited approximately every 2 weeks (total of eight times). At each site, four measures of snow depth and snow hardness (measured by the sinking depth of a penetrometer, see below for details) were taken at a distance of 1 m on each side of the stake. These were averaged prior to analysis.

Track Counts

As an index of relative abundance of each species at different altitude levels of the study area, I snowmobiled on trails in the study site between November 1988 and April 1989, and recorded the location of all lynx and coyote tracks that I observed crossing the trail. Tracks were grouped into high and low altitude levels for analysis. Tracks were usually noted up to 8 days after a snowfall, and an average of 30 km of trails were checked each day. Juvenile lynx travel and hunt with their mother throughout most of their first winter (Parker 1981), and kitten movements are not independent of those of the mother. Therefore, lynx families were recorded as a single animal crossing.

Predator Snowtracking

During winter 1988-89, I followed fresh predator tracks in snow (208 km for lynx and 188 km for coyote). Tracking was undertaken daily after snowfall, and continued until fresh tracks could no longer be differentiated from older trails (usually 7-10 days). Frequent snowfall permitted me to track from early November through March, with no inactive period longer than 5 days. Tracks were usually encountered along a network of snowmobile trails within the study area, though on occasion I followed tracks crossing the Alaska Highway, which bisects the study area. I tried to spread tracking sessions throughout the study area by rarely initiating track searches from the same point of departure on consecutive days, and by choosing tracks to be followed from all areas of the study site. Tracks were either back-tracked or, if their age was estimated as older than 24 hrs, foreward-tracked. If the animal being tracked was disturbed the session was immediately ended. Commonly, a track was followed until it was either lost or light levels and/or snow conditions made a track difficult to read. Distances tracked were obtained by counting paces (one pace was equal to two consecutive steps) with a hand counter and converting to kilometers (Parker 1981). The accuracy of the estimate was validated on several occasions, by counting the paces taken to traverse a known distance.

Snow Conditions

To measure use of specific snow conditions by predators, I made snow measurements at the beginning, end, and every 500 paces (approx. 600 m) of a tracking session. At these sites I measured snow depth between predator steps (on-track) and 1 m perpendicular to the track (off-track), and sinking depth of a single predator step (from top of snow to top of imprint; step sinking depth = SSD). In addition, I obtained an index of snow hardness by measuring the sinking depth of a penetrometer that was dropped from a height of 50 cm above the snow surface (penetrometer sinking depth = PSD). The penetrometer consisted of a soft-drink can filled with lead (total weight of penetrometer= 150g), and when dropped from a height of 50 cm, PSD was intermediate to that of lynx SSD and coyote SSD. The penetrometer was dropped between steps of the animal being tracked (on-track) and off-track. If the animal being tracked was following another track (trail), on-track PSD was measured on the trail itself. I also estimated the percent distance that a tracked animal spent on trails created by other animals within each block of 500 paces.

Predator-Prey Chases

All chases at prey by predators were recorded as they were encountered during a snowtracking session. I noted species chased and number of bounds in the chase, chase outcome (kill or attempt), snow depth and PSD on-track and off-track, and SSD. A scavenge was defined as any visit to a dead food item. At all scavenges I identified species scavenged, and where possible, original cause of death. I noted when chases or scavenges occurred on trails, however I did not determine if scavenges occurred on food items that had previously been killed by the animal being tracked.

Track Identification

Coyote and fox tracks were very similar in appearance in southwestern Yukon. To avoid mistaking them, I used a combination of track size, known home ranges of radio-collared animals, locations of visual sightings, and knowledge that spatial exclusion of foxes in coyote inhabited areas occurs (Voigt and Earle 1983, Major and Sherburne 1987, Sargent et al. 1987, Harrison et al. 1989).

Statistical Methods

ANOVA, G-test (with Williams' correction), and Student t-test were used to analyse snowtracking data (Sokal and Rohlf 1981), and P values less than .05 were considered significant. In order to maximize independence between observations, each tracking session was considered as the experimental unit. Thus, when I compared snow depth, PSD, and use of trails between species, I averaged all values obtained during one session. When I compared snow conditions on-track to those off-track, and SSD to PSD, I did not pool data from an entire session. This may have violated the assumption of independence, but all paired observations were separated by 500 paces, which suggests that consecutive observations on a single track were not strongly dependent. Data obtained for percent distance that tracked animals spent on a trail were normalized with an arcsin of the square root transformation (Krebs 1989). I divided the study period into 18-22 day intervals before analysis.

RESULTS

Morphology

Foot-loading for lynx (n=58), coyotes (n=10), and snowshoe hares (n=21) was calculated, and foot-load differed significantly among species (one-way ANOVA; F=354.6; df=2,86; P<.001). Foot-load of adult and subadult lynx, male and female adult lynx and coyotes, and snowshoe hares also differed (Table 1.1). The average foot-load of coyotes was between 4.1 and 8.8 times greater than lynx, and between 5.7 and 8.1 times greater than that of snowshoe hares. Chest height did not differ between species (two-way ANOVA; F=.000; df=1,64; P=.995), nor sex (F=.90; df=1,64; P=.3461), however differences in mean chest height of adult and subadult lynx were observed (Table 1.1).

Step Sinking Depth

The relationship between SSD and PSD was linear in the case of lynx, and curvilinear for coyote (Figure 1.1), and for this reason I did not perform an ANCOVA on these data. Instead, I grouped PSD into 5 cm increments and performed an ANOVA on species by PSD. This resulted in significant species (F=7.65; df=1,887; P=.006), and PSD (F=111.52; df=3,887; P=<.001) effects on SSD. A significant species by PSD interaction term was present in this analysis (F=6.49; df=3,887; P<.002), attributable to the difference in the relationship between PSD and SSD in both predators. For PSD values between 3 and 13 cm, coyotes sank 2 - 4 cm deeper than did lynx, while SSDs were not different at either extreme in snow hardness. Step sinking depths and PSDs almost never exceeded 20 cm, and this depth is well below chest height of either predator.

These results indicate that the morphological adaptation of the feet of lynx to snow, was much greater than it was in coyotes. However, despite this difference, coyotes sank a maximum of 73% deeper than lynx.

General Snow Conditions

Snowfall was highly variable within the study area, and depended primarily on altitude and time. Mean snow depth was significantly less at low altitude sites (two-way ANOVA on altitude level by time; F=66.63; df=1,112; P<.001; Figures 1.2, 1.3). Mean snow depth for the entire winter was 39.8 +/- 13.8 cm (n=72) at low, and 54.5 +/- 16.2 cm (n=56) at high altitude sites. There was significantly less snow in early winter (F=22.31; df=7,112; P<.001), where mean snow depth on 25 November 1988 was 21.2 +/- 9.2 cm (n=16), and 58.0 +/- 10.9 cm (n=16) on 24 March 1989.

However, rates of snow accumulation over the winter were similar between the two altitude levels (altitude level X time: F=.28; df=7,112; P=.960).

The PSD measured in the study area was dependent on prevailing weather conditions, and PSD was more variable than snow depth. Therefore, snow hardness values obtained at the snow stations represented conditions on that specific day rather than for that time period. I found that differences existed in mean PSD between high and low altitude sites (ANOVA; F=6.2; df=1,112; P=.014), however a significant altitude level X time interaction term was present in this analysis (F=10.11; df=7,112; P<.001). This suggests that the altitude level with lowest mean PSD varied among samples, as shown by Figure 1.4. Mean PSD for the 8 sampling days was 6.6 +/- 2.7 cm (n=72) at low, and 5.8 +/- 2.6 cm (n=56) at high altitude sites. I noted that snow generally became harder at both levels of the study site as winter progressed, an observation which was supported by the significant effect of time (ANOVA; F=10.11; df=7,112; P<.001). Mean PSD was 8.5 +/- 2.1 cm (n=16) on 25 November 1988, and 4.6 +/- 1.0 cm (n=16) on 24 March 1989.

Snow Conditions Associated with Predator Tracks

Use of Regions

Seventy-four percent (n=250) of lynx trails crossing the snowmobile trail were located in the high altitude level of the study site, compared to only 36% of coyote trail crossings (n=104); and results of a G-test indicated that species differed significantly in their use of altitude levels (G=44.67; df=1; P<.001).

Snow Depth

Use of Areas Within Regions

Lynx tracks occurred in snow of significantly greater depths than did those of coyotes (three-way ANOVA; F=15.71; df=1,293; P<.001); snow depth also differed between altitudes (F=19.43; df=1,293; P<.001), and winter periods (F=37.11; df=6,293; P<.001). Lynx selected deeper snow while coyotes selected shallower snow than at the snow sites (Figures 1.2, 1.3).

Travel Routes

Both predators travelled in areas where snow was shallower on-track than it was off-track. Mean snow depth on-track for lynx was 2.2 +/- 8.7 cm less than off-track (n=460; paired-t=5.41; P<.001), while for coyote on-track depth was 3.1 +/- 10.1 cm less than off-track (n=469; paired-t=6.73; P<.001).

Thus, movement patterns of both predators were influenced by snow: lynx selected deep snow regions, areas of deep snow within those regions, and travel routes of shallower snow, while coyotes selected shallow snow regions, areas of shallower snow within those regions, and travel routes of shallow snow.

Snow Hardness

Use of Areas within Regions

Snow used by coyotes was of lower PSD than that used by lynx (ANOVA, F=10.16; df=1,293; P=.002; Fig. 1.5). Altitude level did not affect PSD on predator tracks (F=.07; df=1,293; P=.798), but there was a significant time effect on PSD on predator tracks (F=8.07; df=6,293; P<.001), again attributable to the hardening of the snow as winter progressed.

Travel Routes

The PSD on a predator track was lower than it was off-track. The mean difference in PSD was 1.0 +/- 2.7 cm (n=454; paired-t=8.04; P<.001) lower on-track for lynx, and 1.7 +/- 3.3 cm (n=440; paired-t=10.88; P<.001) lower on-track for coyote.

Trail Use

I examined snow conditions on untracked snow and on trails for roughly one-third of the tracking sessions. An ANOVA on species by snow type (tracked or untracked) indicated that snow hardness was not different between snow used by each species (F=.99; df=1,156; P=.321), while hardness differed between tracked and untracked snow (F=7.87; df=1,156; P=.006). When on untracked snow, mean PSD on-track was 7.0 +/- 3.3 cm (n=50) for lynx, and 5.8 +/- 2.9 cm (n=58) for coyotes, while mean PSD on trails used by lynx was 4.9 +/- 3.4 cm (n=29), and 4.9 +/- 3.0

(n=23) on those used by coyotes. The higher mean PSD on fresh snow than on trails in both species clearly demonstrated the advantage of using the latter snow type for conserving energy, over the former.

Coyotes travelled on animal trails a greater percentage of the distance that I tracked them (52%), than did lynx (37%, t-test; P<.001). Both predators used snowshoe hare trails in similar proportions; however, overall use of trails created by animals other than hare was greater in coyotes (Table 1.2). Coyotes tended to use lynx trails more frequently than did lynx.

Predator Chases and Scavenges

All kills and most attempts by lynx and coyotes were on snowshoe hare (lynx= 32 of 32 kills and 48 of 52 attempts; coyote= 25 of 25 kills and 20 of 24 attempts). Characteristics of lynx and coyote chases of hare are given in Table 1.3. Snow depth at lynx chases was deeper than at those by coyote (ANOVA: F=11.51; df=1,87; P=.001), while snow depth at kills was similar to that at attempts (F=.023; df=1,87; P=.634). The PSD was greater at sites where lynx chased hares, than at those where coyotes chased hares (F=5.51; df=1,75; P=.022), and almost differed with chase outcome (F=2.91; df=1,75; P=.092), while the number of bounds was greater at lynx chases (F=10.85; df=1,127; P=.001), and at attempts by both species (F=57.03; df=1,127; P<.001). Although significant differences in snow depth and PSD between chase outcome were not detected, values for both species were always less for kills than for attempts (Table 1.3), suggesting that snow characteristics may to a certain extent influence the outcome of hare chases by both species.

I found 47 sites where coyotes scavenged food items with forty-five percent (n=21) of these occurring while coyotes were on predator trails (10 on coyote trails and 8 on lynx trails). Twenty scavenges made by lynx were encountered, and 25% (n=5) of these occurred while on lynx trails.

DISCUSSION

Morphological Adaptations to Snow

Coyotes are thought to have originated in areas where snowcover is negligible, and to have colonized the boreal forest only in the last century (Gier 1975; Nowak 1979). In contrast, lynx were present at high latitudes in pre-glacial times (Repenning 1967). Coyotes in the Yukon have morphological adaptations to snow similar to those of coyotes from central Alberta (Telfer and Kelsall 1984); but they are not nearly as well adapted morphologically to snow as are lynx residing in the same area. Coyote foot-load is 4.1 to 8.8 times greater, but chest height is similar, to lynx. However, foot-loads of lynx in the Yukon are similar to those reported for European lynx (Lynx lynx) (Formozov

1946). My results suggest that foot-load was probably the primary factor in morphological adaptation to snow in my study area, as predators were rarely found to sink to depths greater than 20 cm, which was much less than chest height of either species. However this condition may be specific to the Kluane area, where yearly snowfall is relatively light and comes in small increments, giving it a chance to harden before fresh snow falls. In other regions of the boreal forest where snowfall is more frequent and voluminous, snow may be softer and SSDs of these predators may be higher, making chest height more important in facilitating travel.

Though coyotes sank deeper than did lynx at most levels of snow hardness (PSD), the mean difference in step sinking depth (SSD) between species was never greater than 4.5 cm. I attribute this to the increasing snow density under foot as a predator limb entered the snow, and the eventual compression of the snow to a level beyond which further penetration was not possible. The SSD of lynx was never less than 60% that of coyote, despite the sizable difference in foot-load. Therefore, despite an apparently large morphological disadvantage, coyotes experienced a much smaller actual disadvantage in snow.

Behavioral Adaptations to Snow

Lynx selected deep snow regions and deep snow areas within regions, but also used travel routes of shallower snow. Coyotes frequented shallow snow regions and shallow snow areas within regions, as well as shallow snow travel routes. Though use of snow depths by both predators appeared designed to alleviate the adverse effects of snow depth and hardness on movement, that of coyotes appeared most strongly adapted to offset morphological disadvantages. To a degree, each species selected areas of different snow depth. Use of areas of low snow cover by coyotes may have facilitated winter movements, although snow depths greater than the sinking depth of a predator step do not directly affect an animals' ability to travel through an area. Although I did not consistently observe harder snow in low altitude regions, higher snow compression in sites of lighter snowfall probably exist, which could explain coyote preference for such locations. The surprising limited use of shallow and hard snow travel routes by lynx, and their use of high altitudes and deep snow, is difficult to explain. Factors that I did not measure quantitatively in this study, such as lynx avoidance of areas heavily used by coyotes, or the possibility that hare density and/or that hare vulnerability to lynx predation was higher in areas of deep snow, may have caused the lynx snow usage patterns that were observed.

Both predators travelled on snow that was shallower and harder than it was off-track, a trend that may be attributed to the use of "paths of least resistance" such as tree wells, and windswept areas. This phenomenon has been observed in winter movements of red fox (Henry 1979; Halpin and Bissonette 1988), and lynx (Parker 1981).

Despite a greater tendency to use behaviors apparently designed to reduce their sinking depth, overall SSD of coyotes was still greater than lynx (t-test, $P<.001$): coyotes sank a mean of 9.53 +/- 4.41 cm (n=186), but lynx sank only 7.72 +/- 3.24 cm (n=144) on average. These results suggest that strong morphological, and moderate behavioral adaptations of lynx outweighed strong behavioral adaptations expressed by coyotes. It thus would appear that coyotes were experiencing greater restriction to their movements when travelling through snow.

Trail Use and Scavenging

Keith et al. (1977) proposed that the creation of numerous hare trails near the peak of the hare cycle facilitates coyote movement through the forest, and may contribute to the Type III functional response expressed by coyotes as hare densities increase. My study was done 2 years before peak hare densities (C.J. Krebs pers. comm.), and the total proportion of time spent on hare trails was essentially the same for both predators. This suggests that either hare trails were equally selected by both predators in times of mid to high hare densities, or that each species used this trail type according to its overall availability. In contrast, distance travelled on other trails, either man- or animal-made, was higher for coyotes. Non-predator trails were usually devoid of scavengeable food items, and the use of these was probably strictly to facilitate winter movements. Consequently, the higher total use of non-predator trails by coyotes can be attributed to their selection of these, or an avoidance by lynx. However, high use of predator trails apart from facilitating travel, also increased the likelihood of finding scavengeable food items left behind by the animal being trailed.

Though not necessarily a direct adaptation to snow, scavenging may have facilitated coyote survival in winter. I frequently observed coyotes following lynx trails for several kilometers at a time, and scavenging leftover food items on these. However, lynx commonly travelled in open spruce forest, which was a habitat type with relatively low hare densities, and where coyotes exhibited a relatively poor success rate in capturing hares (Chapter 3). Consequently, coyotes opting to follow lynx may have foregone potential chases of hare, and reduced the probability that any chases would be successful, because of the strong selection for open forests by lynx; in exchange for a lowered energy expenditure per distance travelled, and an increased likelihood of finding scavengeable food items. However, the volume of food consumed at a scavenge was substantially less (9%) than that consumed at kills (Chapter 2), and rate of scavenging by coyote was not high enough to make net energetic intake higher by employing trails and scavenging. Therefore, coyotes clearly do not follow trails to increase their energetic intake, but probably to decrease energetic expenditure.

Relationship Between Predators and Principal Prey

Snowshoe hares were the most frequently taken food type of lynx and coyotes in southwestern Yukon, and hares were shown to have a lower foot-load than adult lynx, and one much lower than that of coyotes. As snow was present for over 6 months of the year in the study area, hare ability to travel in snow was certainly an important factor in determining predation rates of lynx and coyotes on hares. Considering exclusively foot-loads of the three mammals studied, the presence of snow should benefit hare over lynx, and particularly hare over coyote, in predator-hare chases taken during winter. However, the greater chest height of both predators, and their longer gait, may alleviate the advantage in foot-loading expressed by hares. Morphological indices obtained for wolf and its ungulate prey (Telfer and Kelsall 1984) indicated that predator foot-load was always less than twice that of prey. This result suggests that the behavioral adaptations which must be undertaken by wolves to allow for successful predation on ungulates may be roughly the same as for lynx on hare, but probably less than those necessary for effective coyote-hare predation.

The question of susceptibility of hares to predation is a complex one requiring further study; however, it is clear that more is involved than simply the differential between foot-load of predator and prey. Behavioral adaptations to snow for each predator presumably facilitated winter hare predation. However travelling in hard snow may have benefitted hare as well as predators, suggesting that other behavioral adaptations by predators are necessary for successful predation on hares to occur.

Hunting Tactics

I noted slight, though not significant, differences in snow depth and snow hardness at sites of kills and attempts by both predators, and snow conditions have been suggested as having an effect on the outcome of lynx chases of hare (Haglund 1966; Nellis and Keith 1968), though Parker (1981) found no sign of this phenomenon. Coyote chases usually consisted of fewer bounds than those of lynx, and the bounds of each species were roughly of the same length. Although coyotes are among the fastest carnivores (Bakker 1983), their speed was probably reduced in snow. Given this, it appears that coyotes must have initiated chases at closer range than did lynx. During the year of study, most hares killed by coyotes occurred in habitats with low visibility (dense cover), whereas lynx achieved similar predation success rates in all habitat types (Chapters 3, and 4). Thus, it may be that coyotes used concealment as a means of approaching hares, meaning the shorter the chase, the less chance for snow to determine the outcome the interaction. This certainly could be an important component of the predator-prey system, particularly when predator foot-load was 5.7 to 8.1 times greater than that of prey. In contrast, the longer chases of hare by lynx could be explained at least in part by the smaller difference in foot-load between the two. Because felids are typically sit and wait or stalking predators, and canids usually run down their prey (Kleiman and Eisenberg 1973; Bakker 1983), snow must be an important factor in determining the hunting tactics employed by each predator on snowshoe hare.

Lynx-Coyote Interaction

Lynx and coyotes did not appear to interact directly with each other during winters of moderate to high hare densities in southwestern Yukon. Although hare was the primary prey of both predators during this period, each frequented areas of different snow characteristics. Though coyotes followed lynx and scavenged their old kills, this relationship appeared to be strictly commensalistic in nature. Although Nellis and Keith (1968) found that lynx scavenged relatively frequently, the animals I studied rarely revisited their old kills. It therefore seems unlikely that, on my study area, lynx were affected by consumption of their prey remains by coyotes. Only in the instance where a coyote was able to displace a lynx from an unfinished kill would this trailing behavior be detrimental to lynx. Although I observed what I perceived as signs of lynx avoiding coyote inhabited areas (eg. lynx avoiding trap baits once they had been visited by coyotes, and lynx occasionally changing their direction of travel when they would intersect a fresh coyote trail), in no case did I see any evidence that suggested that a lynx had been usurped by a coyote at a lynx-killed hare. Therefore it appears that at the prey densities studied, lynx and coyotes were able to coexist in the same general area without agonistic interactions or direct competition.

Competition has been suggested as the result of interactions between coyotes and red fox in the Yukon (Theberge and Wedeles 1989), as well as between coyotes and bobcats in Maine (Litvaitis and Harrison 1989). However, most authors believe that food levels or resource overlap levels between coyotes and bobcats allow for coexistence (Toweill 1986; Witmer and deCalesta 1986; Major and Sherburne 1987). Though a change in hare densities can alter the food and habitat overlap levels between lynx and coyotes (Chapters 2, and 4), I do not know if different overlap values can catalyze interspecific competition between the two species.

Table 1.1: Mean weight, total foot area, foot-load, and shoulder height of skinned lynx, coyote, and snowshoe hare carcasses. Sample sizes are given in parentheses.

Species	Weight (kg) Mean	+/- SD	Total Foot Area (cm^2) Mean	+/- SD	Foot-Load (g/cm^2) Mean	+/- SD	Chest Height (cm) Mean	+/- SD
Lynx								
Adult								
M (30)	8.99	1.19	286.4	28.4	31.6	5.2	46.7	10.4
F (15)	7.08	1.36	275.6	27.7	25.9	5.5	42.2	6.3
Subadult								
M (7)	4.03	0.50	262.9	35.1	15.6	4.0	38.6	4.9
F (6)	4.32	0.50	265.0	23.8	16.5	2.9	35.5	5.5
Coyote								
M (5)	10.32	1.16	77.0	10.7	136.8	30.9	43.1	2.8
F (5)	8.00	0.58	75.8	5.2	106.0	11.1	42.3	4.0
Snowshoe Hare								
M (12)	1.60	0.13	92.2	10.5	16.8	1.4	-	
F (9)	1.65	0.15	87.9	6.8	18.4	1.4	-	

Table 1.2: Percent use of trails by single lynx and coyotes in southwestern Yukon. Number of tracking sessions are 102 for lynx and 144 for coyote.

Trail Type	Lynx Mean	+/- SD	Coyote Mean	+/- SD
Snowshoe hare	31.3	23.7	34.3	27.6
Lynx	2.60	5.93	6.87	20.4
Coyote	0.41	2.21	2.42	6.85
Wolf	0.28	1.57	1.86	8.67
Wolverine	0.59	3.62	0.96	4.75
Moose	0.37	1.61	0.89	5.15
Snowshoe	0.31	1.59	0.73	5.10
Snowmobile /road	0.59	2.18	3.60	15.5
Total	36.5	25.1	51.6	30.2

Table 1.3: Snow depths, penetrometer sinking depths (PSD), and number of bounds taken by lynx and coyotes at hare chases.

Characteristic	Lynx %	+/- SD	(n)	Coyote %	+/- SD	(n)
Snow Depth (cm)						
kill	55.2	18.2	(33)	40.9	23.6	(24)
attempt	63.1	20.8	(19)	44.0	29.4	(20)
Penetrometer Sinking Depth (PSD) (cm)						
kill	7.1	3.0	(20)	5.1	3.1	(19)
attempt	7.9	2.7	(30)	6.6	2.9	(11)
Bounds in the Chase (n)						
kill	2.21	1.89	(33)	0.48	1.05	(25)
attempt	5.92	3.46	(20)	4.35	2.85	(20)

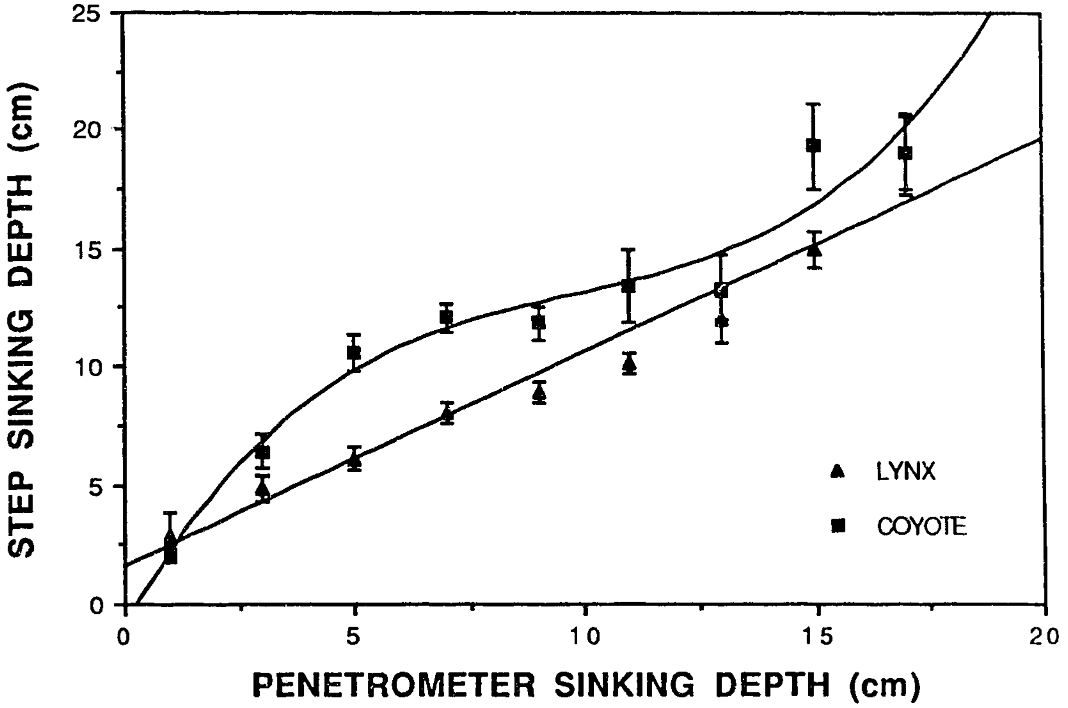

Figure 1.1: Mean step sinking depths (SSD) of lynx and coyotes as a function of penetrometer sinking depth (PSD). Vertical bars indicate standard errors, and consecutive PSDs have been pooled in increments of 2.

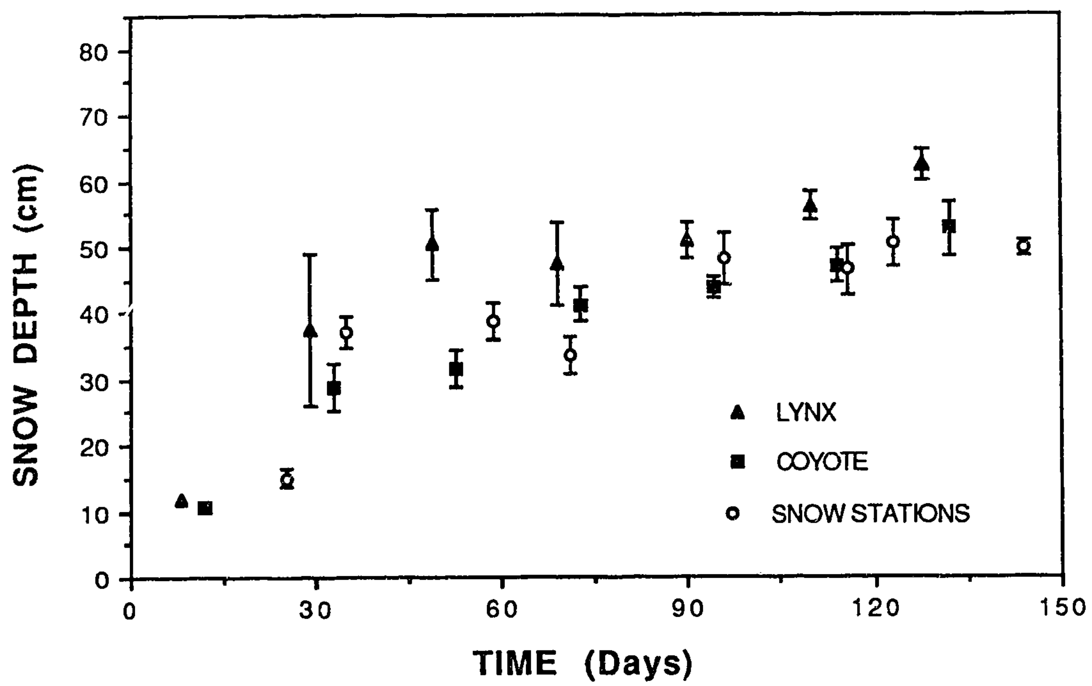

Figure 1.2: Mean snow depths on lynx and coyote tracks, and at snow sites, at low altitudes of the study area. Day 1= November 1. Vertical bars indicate standard errors.

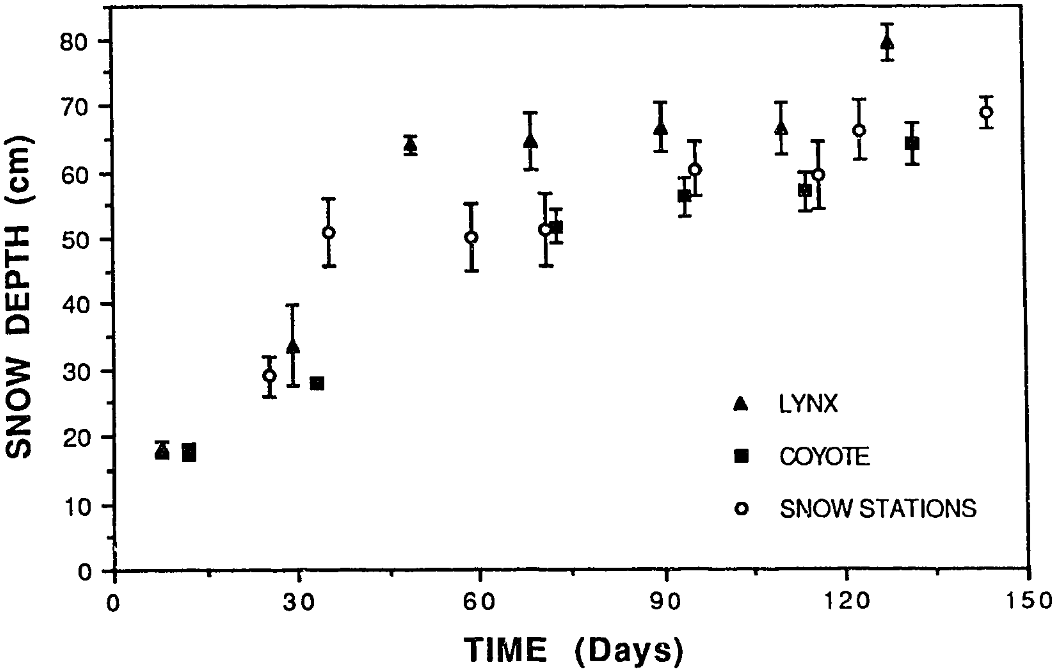

Figure 1.3: Mean snow depths on lynx and coyote tracks, and at snow sites at high altitudes of the study area. Day 1= November 1. Vertical bars indicate standard errors.

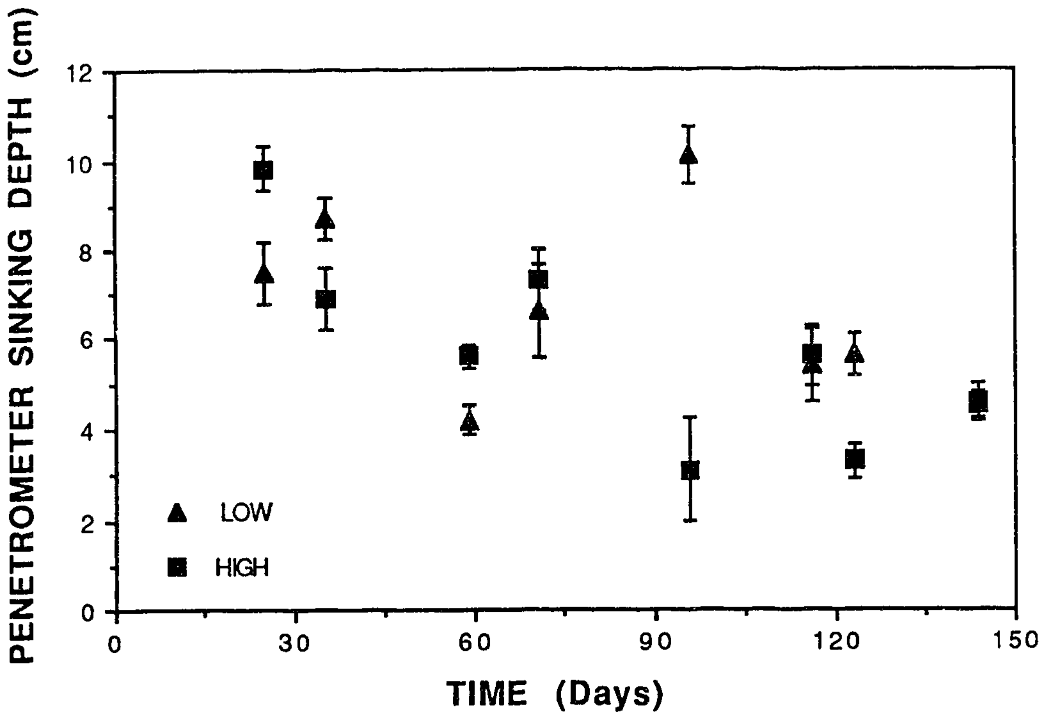

Figure 1.4: Penetrometer sinking depths (PSD) on 8 days during winter 1988-89 at low and high altitudes of the study site. Day 1= November 1. Vertical bars indicate standard errors.

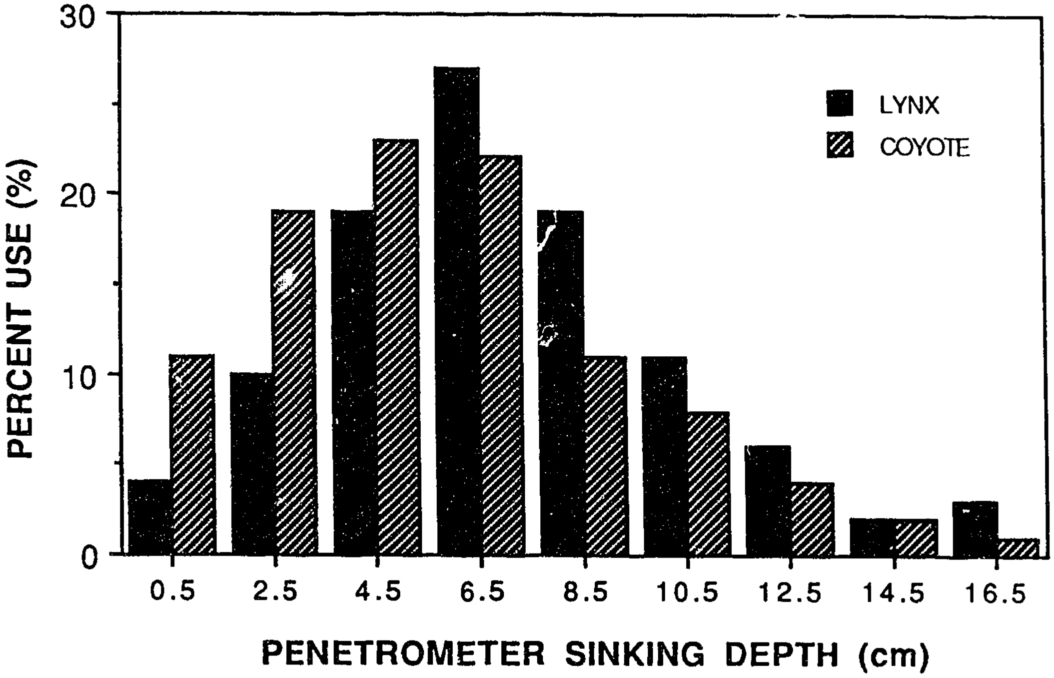

Figure 1.5: Distance travelled by lynx and coyotes on snow of increasing penetrometer sinking depths (PSD). Consecutive PSDs have been pooled in increments of 2.

REFERENCES

Bakker, R.T. 1983. The deer flees, the wolf pursues: incongruities in predator-prey coevolution. In: Futuyama, D.J. and Slatkin, M. (eds.), Coevolution. Sinauer Assoc., Mass., pp. 350-382.

Douglas, G.W. 1974. Mountain zone vegetation of the Alsek River region, southwestern Yukon. Can. J. Bot. 52:2505-2532.

Formozov, A.N. 1946. Snow cover as an integral factor of the environment and its importance in the ecology of mammals and birds. Materials for fauna and flora of the USSR. Zool. Sect., New Series No. 5. Moscow Society of Naturalists. (Translated by Prychodko, W. and Pruitt, W.O.. 1963. Univ. Alberta Boreal Inst. Occas. Pap. No. 1.)

Gier, H.T. 1975. Ecology and behavior of the coyote (Canis latrans). In: Fox, M. (ed.), The wild canids. R.E. Krieger Publ. Co. Inc., Malabar, Fl. pp. 247-262.

Haglund, B. 1966. Winter habits of the lynx (Lynx lynx L.) and wolverine (Gulo gulo L.) as revealed by tracking in the snow. (In Swedish; English summary.) Viltrevy 4:81-310.

Halpin, M.A., and Bissonette, J.A. 1988. Influence of snow depth on prey availability and habitat use by red fox. Can. J. Zool. 66:587-592.

Harrison, D.J., Bissonette, J.A., and Sherburne, J.A. 1989. Spatial relationships between coyotes and red foxes in eastern Maine. J. Wildl. Manage. 53:181-185.

Henry, J.D. 1979. The urine marking behavior and movement patterns of red foxes during a breeding and post-breeding period. In: Muller-Schwaze, D. and Silverstein, R.M. (eds.). Chemical signals in vertebrates and aquatic animals. Symp. Chem. Signals in Vert. and Aquatic Anim. State University of New York, Syracuse. Plenum Press, N.Y. pp. 11-27.

Keith, L.B., Todd, A.W., Brand, C.J., Adamcik, R.S., and Rusch, D.H. 1977. An analysis of predation during a cyclic fluxuation of snowshoe hares. Proc. XIII Int. Cong. Game Biol. pp. 151-175.

Kelsall, J.P. 1969. Structural adaptations of moose and deer for snow. J. Mammal. 50:302-310.

Kleiman, D.G., and Eisenberg, J.F. 1973. Comparisons of canid and felid social systems from an evolutionary perspective. Anim. Behav. 21:637-659.

Krebs, C.J., 1989. Ecological methodology. Harper & Row, New York, NY. 653 pp.

Krebs, C.J., Gilbert, B.S., Boutin, S., Sinclair, A.R.E., and Smith, J.N.M. 1986. Population biology of snowshoe hares. I. Demography of food-supplemented populations in the southern Yukon, 1976-84. J. Anim. Ecol. 55:963-982.

Litvaitis, J.A., and Harrison, D.J. 1989. Bobcat-coyote niche relationships during a period of coyote population increase. Can. J. Zool. 67:1180-1188.

Major, J.T., and Sherburne, J.A. 1987. Interspecific relationships of coyotes, bobcats, and red foxes in western Maine. J. Wildl. Manage. 51:606-616.

Nellis, C.H., and Keith, L.B. 1968. Hunting activities and success of lynxes in Alberta. J. Wildl. Manage. 32:718-722.

Nowak, R.M. 1979. North American quaternary Canis. Monograph no. 6, Museum of Nat. Hist., University of Kansas, [illegible] pp.

Ozoga, J.J., and Harger, E.M. 1966. Winter activities and feeding habits of northern Michigan coyotes. J. Wildl. Manage. 30:809-818.

Parker, G.R. 1981. Winter habitat use and hunting activities of lynx (Lynx canadensis) on Cape Breton Island, Nova Scotia. In: Chapman, J.A., and Pursely, D. (eds.), Proc. World. Furb. Conf., Frostburg, Md., (1980). pp. 221-248.

Parker, G.R., Maxwell, J.W., Morton, L.D., and Smith, G.E.J. 1983. The ecology of the lynx (Lynx canadensis) on Cape Breton Island. Can J. Zool. 61:770-786.

Quinn, N.W.S., and Parker, G. 1987. Lynx. In: Novak, M., Baker, J.A., Obbard, M.E., and Malloch B. (eds.), Wild furbearer management and conservation in North America. Ont. Min. Nat. Res., Toronto, On., pp. 683-694.

Repenning, C.A. 1967. Palearctic-Nearctic mammalian dispersal in the late Cenozoic. In: Hopkins, D.M. (ed.), The Bering land bridge. Stanford Univ. Press, Stanford, Calif. pp. 288-311.

Sargeant, A.B., Allen, S.H., and Hastings, J.O. 1987. Spatial relations between sympatric coyotes and red foxes in North Dakota. J. Wildl. Manage. 51:285-293.

Sokal, R.R., and Rohlf, F.J. 1981. Biometry. W.H. Freeman & Co. New York, NY. 859 pp.

Stanley, S.M., Van Valkeburgh, B., and Steneck, R.S. 1983. Coevolution and the fossil record. In: Futuyama, D.J., and Slatkin, M. (eds.), Coevolution. Sinauer Assoc., Mass., pp. 328-349.

Telfer, E.S., and Kelsall, J.P. 1979. Studies of morphological parameters affecting ungulate locomotion in snow. Can. J. Zool. 57:2153-2159.

Telfer, E.S., and Kelsall, J.P. 1984. Adaptation of some large North American mammals for survival in snow. Ecology 65:1828-1834.

Theberge, J.B., and Wedeles, C.H.R. 1989. Prey selection and habitat partitioning in sympatric coyote and red fox populations, southwest Yukon. Can. J. Zool.

67:1285-1290.

Todd, A.W., and Keith, L.B. 1976. Responses of coyotes to winter reductions in agricultural carrion. Alta. Wildl. Tech. Bull. No.5. 32 pp.

Toweill, D.E. 1986. Resource partitioning by bobcats and coyotes in a coniferous forest. Ph.D thesis, Oregon State University. Corvallis, Or. 155 pp.

Voigt, D.R., and Earle, B.D. 1983. Avoidance of coyotes by red fox families. J. Wildl. Manage. 53:852-857.

Voigt, D.R., and Berg, W.E. 1987. Coyote. In: Novak, M., Baker, J.A., Obbard, M.E., and Malloch, B. (eds.), Wild furbearer management and conservation in North America. Ont. Min. Nat. Res., Toronto, On. pp. 345-356.

Witmer, G.W., and deCalesta, D.S. 1986. Resource use by unexploited sympatric bobcats and coyotes in Oregon. Can. J. Zool. 64:2333-2338.

CHAPTER 2

WINTER DIETS AND CONSUMPTION RATES OF LYNX AND COYOTES IN SOUTHWESTERN YUKON, DURING AN INCREASE IN SNOWSHOE HARE ABUNDANCE.

INTRODUCTION

Lynx and coyotes are similarly sized carnivores that occur sympatrically over much of the boreal forest (Quinn and Parker 1987; Voigt and Berg 1987). Most canids are regarded as generalist feeders, while felids are considered specialized predators (Kruuk 1986). Prey populations are an important component of predator-prey relationships, and predators can respond to an increase in prey by increasing their own numbers and/or by increasing the number of prey consumed per individual predator (Taylor 1984). The latter response is known as a functional response, and is based on a reaction to proximate stimuli by an individual predator, through a direct effect of prey density on behavior (Hassel 1966).

Keith et al. (1977) suggested that the relationship between lynx (*Lynx canadensis*) and its principal prey, the snowshoe hare, (*Lepus americanus*) was different to that of coyote (*Canis latrans*) and hare. Lynx are thought to rely on hare at all hare densities, and to show a Type II functional response to changes in hare abundance; whereby there is a deceleration of predation rates as prey numbers increase. Conversely, coyotes are thought to prey on a variety of food items at low hare densities, and switch onto hares as numbers surpass a threshold; their response to changes in hare densities appears to follow a Type III response curve (Keith et al. 1977), where density-dependent acceleration of predation rates occur during a period of increase in prey density.

Lynx and coyotes rely heavily on hare in southwestern Yukon, and hare populations fluctuate widely in that area, with an approximate yearly doubling in density during the increase phase (Krebs et al. 1986). Though hare predation by lynx and coyotes has been studied previously, the effect of an increase in hare on diet and consumption rate of each predator has not been documented in detail. I therefore undertook this study to determine how sympatric populations of lynx and coyotes responded to a doubling in hare abundance, by monitoring the predators' food habits, kill-rates, and scavenging rates.

STUDY AREA

Lynx and coyotes were studied in a 175 km^2 area of the Kluane Lake region of southwestern Yukon (61^oN, 138^oW). The study site was located in a broad valley running in an east-west direction. I worked from the base of the valley (830 m) to an altitude of 1169 m, which was near the base of the mountains. The altitude of the valley floor also differed with the central area, being up to 215 meters higher than that of either end. The entire area was part of the northern boreal forest zone (Douglas 1974), and white spruce (Picea glauca) was the dominant tree. Canopy cover ranged from 0 to 100% in the valley, and a strong negative relationship between elevation and percent spruce cover was evident. Other winter habitat types available to predators included deciduous forests (Populus sp.), shrub (Salix sp.), and completely open areas, which consisted of frozen waterways, meadows, and alpine tundra. Snowfall was directly related to altitude in the study site, and total snow accumulation for the entire site during both years of study averaged 65 cm, which was typical for that region (Krebs et al. 1986). I estimated that there were at least 10 lynx and 8 coyotes residing in the area during winter 1987-88 (Year 1), based on known locations of radio-collared animals and associated tracks in localized areas. In winter 1988-89 (Year 2) my estimate was of 16 lynx and 12 coyotes. Other less abundant terrestrial predators included red fox (Vulpes vulpes), wolf (C. lupus), and wolverine (Gulo gulo).

METHODS

Predator Snowtracking

I followed fresh predator tracks in snow during two winters (378 km for lynx and 268 km for coyote). Tracking was undertaken daily after snowfall, and continued until fresh tracks could no longer be differentiated from older trails (usually 7-10 days). Frequent snowfall permitted me to track from early November through March, with no inactive period longer than 5 days. Tracks were usually encountered along a network of snowmobile trails within the study area, though on occasion I followed tracks crossing the Alaska Highway, which bisects the study area. I tried to spread tracking sessions throughout the site, by rarely initiating track searches from the same point of departure on consecutive days, and by choosing tracks to be followed from all areas of the study site. Tracks were either backtracked or, if their age was estimated as older than 24 hrs, forward tracked. If the animal being tracked was disturbed the session was immediately ended; however more commonly a track was followed until it was either lost, or light levels and/or snow conditions made it difficult to read. Distances tracked were obtained by counting steps with a hand counter and converting to kilometers (Parker 1981). The estimate was truthed on several occasions, by counting the paces taken to traverse a known distance.

Diets and Foraging Rates

Diet of lynx and coyotes were determined by collecting scats encountered either on snowmobile trails, or while snowtracking predators, between November and March of both years of study. Scats were examined for presence of hair or feathers by the Composition Analysis Laboratory, Ft. Collins, Colorado, U.S.A. All scats from Year 1 were analyzed, while a random subsample of 51 coyote, and 52 lynx scats (9-11 scats/species/month) were examined from Year 2.

All predator chases of prey were recorded as they were encountered during a snowtracking session. I noted species chased, chase outcome (kill or attempt), and at kill sites I estimated percent of body left unconsumed. Sites where predators attempted to capture small mammals consisted of evidence of both pouncing and digging in the snow. At such sites it was impossible to determine if the attempt had resulted in a kill, thus all chases were classed as an attempt at a small mammal. A scavenge was defined as any visit to a dead food item, where sign of consumption (exposed flesh, pieces of fur, blood, etc.) was present. This definition excluded visits to food items which showed no sign of consumption, or those where all food had been consumed by the predator, and no signs of scavenging were apparent. At each scavenge I identified species scavenged, percent body remaining, and where possible, original cause of death. I did not identify if scavenges occurred on food items that had been previously killed by the same individual.

I also recorded the number and types of beds encountered during a tracking session. I grouped beds based on an index of the duration of their use: crouches (indentations consisting of soft snow), short beds (indentations consisting of hard packed snow), and long beds (indentations consisting of ice-encrusted snow).

Juvenile lynx travel and hunt with their mother throughout most of the first winter, and though a family usually travels in single file, group members may fan out when traveling in areas where hares are common (Parker 1981). When I tracked lynx family groups in Year 1, I attempted to track all branches of the track, while in Year 2, I only tracked the trail left by 1 individual. This may have caused some unsuccessful attempts on other track branches to be missed, therefore causing an underestimate of the attempt rate of lynx families in Year 2. However I found that family members converged at kills and scavenges, and communal beds were typical; thus the different tracking method employed for lynx family groups in Year 2 is unlikely to have caused a bias in kill-rates, scavenging rates, or bed-rates.

Track Identification

Coyote and fox tracks were similar in appearance in southwestern Yukon, and to avoid mistaking them I used a combination of track size, known home ranges of radio-collared animals, locations of visual sightings, and knowledge that spatial exclusion of foxes in coyote inhabited areas occurs (Voigt and Earle 1983, Major and Sherburne 1987, Sargent et al. 1987, Harrison et al. 1989).

Prey Density

Snowshoe hare densities within the study site were estimated by counting all fresh (less than 1 year old) hare turds along 480 transects, during June 1988 and June 1989, and extrapolating numbers of hare turds collected to an estimate of the number of hares per hectare (see Krebs et al. 1987). Turd transects were placed in a variety of habitats, in proportions that were roughly proportional to the availability of each type (Chapter 3).

Other prey items available to lynx and coyotes during winter in southwestern Yukon included red squirrel (*Tamiasciurus hudsonicus*), grouse (*Bonasa*, *Lagopus*, and *Dendragapus*), muskrat (*Ondatra zibethicus*), and various small mammals (*Microtus*, *Clethrionomys*, *Peromyscus*, *Sorex*, *Synaptomys*, *Lemus* , and others). Other food types available to lynx and coyotes, if scavenged, included ground squirrels (*Spermophilus paryii*), moose (*Alces alces*), and probably Dall Sheep (*Ovis nivicola*).

Statistical Methods

G-test (with Williams' correction) and ANOVA were used to analyze data (Sokal and Rohlf 1981), and P values less than .05 were considered significant. G-test was used to examine the change in proportion of kills, attempts, and scavenges on snowshoe hare between years, and differences in success rates on hare, between species. G-test was also used to analyse kill-rates, attempt rates, scavenging rates, and bed-rates, by using rate of encounter of each observation over total kilometers covered. Data in the form of percentages were subjected to an arcsin of the square-root transformation (Krebs 1989), prior to analysis.

RESULTS

Hare Density

Hare density almost doubled in the study area, as mean +/- SD went from .39 +/- .05 hares/hectare in Year 1 to .77 +/- .10 hares/hectare in Year 2.

Diets

Snowshoe hare was the most frequent (Table 2.1), and abundant (Table 2.2) item in both coyote and lynx scats. Despite the increase in hare density from Year 1 to Year 2, the frequency and abundance of hare decreased in the diet of lynx. The opposite was true for coyotes. Hare made up a greater proportion of lynx scats than of coyote (ANOVA: F=11.27; df 1,261; P<.001), and did not change between years (F=0.00; df=1,261; P=.962). However, an interaction term was present here (F=7.42; df=1,261; P=.007) because of the decrease in abundance of hare in lynx scats, but the increase in those of coyotes, observed in Year 2 (Table 2.2). Hair of snowshoe hare was the predominant type in scats, while hair of other prey usually comprised a small percentage of hairs in a scat. Combined percent occurrence of the 8 food types reported in Table 2.2 was 97.4% and 88.3% for lynx in Years 1 and 2, and 81.7% and 84.5% for coyote in Years 1 and 2.

Predator Kills, Attempts and Scavenges

Most kills, encountered during both years of snowtracking were of snowshoe hare (Table 2.3), and proportion of kills made up of snowshoe hare increased for both predators in Year 2 (lynx: G=6.893; df=1; P<.01; coyote: G=7.961; df=1; P<.005). Kills of prey other than hare in Year 1 consisted of red squirrels (n=3) and spruce grouse (n=1) for lynx, and muskrats (n=2) and red squirrel (n=1) for coyote. Proportion of attempts on hare was similar for lynx and coyotes for both years (lynx: G=.362; df=1; P<.90; coyote: G=1.975; df=1; P<.5). Attempts by lynx at prey other than hare were at red squirrels (n=7), and grouse (n=4), while for coyotes, non-hare attempts were at squirrels (n=7), and grouse (n=2). A total of 12 small mammal attempts were observed for coyote, but none were recorded for lynx. Most scavenges were on hares, and the proportion of scavenges increased only for coyotes (lynx: G=.506; df=1; P<.50; coyote: G=11.319; df=1; P<.005). Other than hare, lynx scavenged moose (n=1) and grouse (n=1), while coyotes scavenged moose (n=6), squirrels (n=2), grouse (n=2), and an unidentified bird (n=1).

Rates of Chases at Hare

The rate at which hares were killed per km tracked, was 1.6 times higher in Year 2 for single animals of both species (Table 2.4); however neither of these differences was significant (lynx: G=1.119; df=1; P<.50; coyote: G=.953; df=1; P<.50). The numbers of hares killed per km were similar for single animals of both species, during both years of study.

The rate of attempted kills of hare was slightly lower for coyote than for lynx (Table 2.5), and though the frequency of attempts increased 1.6 times for lynx and 1.2 times for coyotes, these differences were not significant (lynx: G=3.186; df=1; P<.10; coyote: G=.219; df=1; P<.90).

Scavenging was 2.4 times more frequent for single lynx (Table 2.6; G=2.448; df=1; P<.50), and 2.3 times more frequent for single coyotes (G=3.898; df=1; P<.05) in Year 2. On average, coyotes scavenged hares 3 times more frequently per distance than did lynx.

To summarize, I found that kill-rates, attempt rates, and scavenging rates on snowshoe hare increased for both predators in Year 2, but most of these differences were not significant.

Group Size

Groups of lynx had more snowshoe hare kills (G=6.483; df=1; P<.025) and attempts (G=8.879; df=1; P<.005) per km than did single animals, while scavenging rates were similar between group sizes (G=.000; df=1; P<.975). However on a per individual basis, fewer hare kills, attempts and scavenges occurred per km on group tracks than on those of individual lynx. During Year 2, kill-rates (G=.298; df=1; P<.90), and rates of both attempts (G=.010; df=1; P<.975), and scavenges (G=.123; df=1; P<.90), were similar between single coyotes and groups of 2 individuals. On a per individual basis, all rates were lower on group tracks than on those of single coyotes.

Hunting Success

Groups of lynx and coyotes generally had higher success at hunting hares than did single individuals of each species, however sample sizes were small, and a G-test showed no significant difference (Table 2.7; lynx: G=.928;

df=1; P<.50; coyote: G=.173; df=1; P<.90). Single lynx were not less successful at capturing hares than single coyotes (G=3.14; df=1; P<.10), despite an overall success of 32% (n=146 chases) in lynx and 47% (n=61) in coyotes. Success rate of single lynx was constant between years of study (G=.041; df=1; P<.90), whereas single coyotes showed a 1.4 fold increase in their success at capturing hare. This result was not statistically significant (G=.833; df=1; P<.50).

Bed-rates

Bed-rates of lynx and coyotes are shown in Table 2.8. Single lynx crouched more frequently (G=5.601; df=1; P<.025) in Year 2, while the frequency of short beds (G=.074; df=1; P<.90) and long beds (G=.052; df=1; P<.90) remained unchanged. Coyotes bedded for short periods more frequently in Year 1 (G=3.948; df=1; P<.05), while rates of crouches (G=1.877; df=1; P<.50) and long beds (G=.655; df=1; P<.50) remained unchanged.

Daily Hare Kill-Rates

Distance between consecutive ice-encrusted beds has previously been used as an index of daily cruising distance (DCD) in lynx (Brand et al. 1976, Parker 1981). Lynx bedded down in long-term beds more frequently than did coyotes (G=5.790; df=1; P<.025). As frequency of ice-encrusted beds did not differ between years for either species, I pooled rates from both years to calculate average DCD. My calculation yielded a mean DCD of 4.7 km for single lynx and 8.6 km for single coyotes. When I converted kill-rate to the number of hares killed/day, lynx killed 1 hare per 2.8 days in Year 1, and 1 hare per 1.8 days in Year 2, which was a 1.6 fold increase. Coyotes killed 1 hare every 1.5 days in Year 1, and a hare every .9 days in Year 2, which was also a 1.6 fold increase.

Daily Hare Scavenging Rate

When I converted scavenging rate to the number of hare scavenges per day, I obtained one hare scavenge per 6.3 days in Year 1, and 1 per 2.6 days in Year 2 for single lynx, while for coyotes I calculated 1 hare scavenge per 1.1 days in Year 1, and 1 per .5 days in Year 2.

Hare Consumption

Percent of hare kills consumed by each predator species was similar (ANOVA; F=.68; df=1,78; P=.413), as were differences in percent consumed in Year 1 and Year 2 (F=1.00; df=1,78; P=.314). Percent of kills that remained uneaten averaged 11.3 +/- 17.2% (n=18) and 7.5 +/- 11.6% (n=6) in Year 1, and 14.8 +/- 17.0% (n=33) and 14.6 +/- 16.8% (n=25) in Year 2, for lynx and coyote kills, respectively. Lynx left less than 5% of complete hare carcass at 64.7% (33/51) of kills, while coyotes left less than 5% at 58.1% (18/31) of kills.

The percentage of the carcass left behind when either predator species scavenged on remains of snowshoe hare was similar (ANOVA; F=2.60; df=1,72; P=.273). This was also the case between years (F=2.60; df=1,72; P=.111). Percent remaining uneaten was 2.6 +/- 2.2% (n=5) and 1.4 +/- 1.4% (n=8) in Year 1, and 7.3 +/- 11.8% (n=18) and 3.7 +/- 5.0 (n=44) in Year 2, for lynx and coyote respectively.

Though significant differences in percent consumption of kills and scavenges of snowshoe hare were not detected, lynx consumed less of kills and scavenges than did coyotes, and Year 1 consumption rates were greater for all categories than in Year 2.

An average of 86.3% of a hare carcass was consumed at kill sites (average remains= 13.7%). As lynx and coyotes may scavenge on hares killed either by themselves or by conspecifics, and coyotes frequently scavenge old lynx kills (Chapter 1), I estimated that, on average, 13.7% of a hare carcass was available for scavenging at all sites where predators visited dead food items. The percentage of a whole hare carcass remaining at a scavenge averaged 5.9%, and the difference between pre and post-scavenge remains (13.7-5.9=7.8%) was then divided by the average percentage consumed at kills (86.3%), to calculate percent of food consumed at kills that was consumed at scavenges. The result was that an average of 9.0% of the volume of that typically consumed at a kill, was consumed by a scavenger.

To summarize, lynx obtained 31% of a hare each day from kills and 1% from scavenges in Year 1, and 48% from kills and 4% from scavenges in Year 2. Coyotes obtained 58% of a hare from kills each day and 8% from scavenges in Year 1, and 92% from kills and 18% from scavenges in Year

2.

DISCUSSION

Responses of Predators to an Increase in Prey

Both predators responded to an increase in hare abundance by increasing kill-rate, and daily hare scavenging rates. Hare densities in the study area during Year 2 were 2.0 times greater than in Year 1, while increases in daily hare kill rates were 1.6 for both lynx and coyotes.

It would be presumptuous to attempt to explain the functional response of lynx and coyotes to an increase in hare abundance based on only 2 years of data; however comparisons of the observed responses are still interesting. If lynx have a Type II functional response and coyotes a Type III response, as suggested by Keith et al. (1977), the greatest difference in the response to changes in prey density should occur in the increase phase of prey densities (Murdoch 1973; Taylor 1984). In Type II responses, kill-rates per individual predator do not rise faster than do prey densities, while in a Type III response, for a period, kill-rates rise above the rate of increase in prey abundance. Given this, data from my study indicated that the functional response of the two predators was very similar, both predators appearing to follow a Type II functional response. However the effect of a single coyote on hare populations would be greater than that of a single lynx, given the apparently higher daily intake of hare by coyote than by lynx.

Predator Diets

Canids usually have more varied diets than felids (Kruuk 1986), however the diets of lynx and coyotes in southwestern Yukon appeared similar during the two years of study. Snowshoe hare was clearly the most important food type of both species when hare densities varied between .39 and .77 hares/ha. However, a variety of other foods were also taken by both species. An increase in hare abundance had a positive effect on snowshoe hare kills by both species, though an analysis of the number of lynx scats containing snowshoe hare fur showed a decrease in presence of hare in Year 2. Hair from snowshoe hare was present in higher proportions in lynx scats than in those of coyote. This phenomenon is perhaps attributable to the greater importance of hare scavenges in the diet of coyotes, and the smaller ration of food available at scavenges than at kills.

Other food types, and small mammals in particular, were frequently observed in scats, while attempts at small mammals were rarely encountered while tracking predators. This discrepancy suggests that a bias existed in my ability to detect small mammal kills, and that results from tracking studies may overlook the small mammal component of predator diets. Also, this suggests that average daily intake of food by both predators is higher than the values I calculated.

Hare Consumption Rates

The rate at which lynx killed hares increased from .36 to .56 per day (1 hare/2.8 days to 1 hare/1.8 days), and an estimate of 1 hare killed by single lynx per 2 days in Newfoundland (Saunders 1963), and 1 per 2.4 days in Alberta (Nellis and Keith 1968), are similar to my estimate. However Iurgenson (1955) suggested that European lynx (L. lynx) killed 1 hare (L. europeaus) every 4 days, while Parker (1981) proposed that lynx killed hares daily, during a period of decline in hare abundance (Parker et al. 1983). Thus there exists a wide variance in what authors have calculated as daily hare kill-rates of lynx.

Fasting metabolic rate of bobcats (L. rufus) was approximated by Mautz and Perkins (1989), and that value was used by Powers et al. (1989) to calculate that winter requirements of a resting bobcat were 1 snowshoe hare per 1.9 days. These authors also suggested that energy requirements of active bobcats may be 2-3 times higher than this level. As size of bobcats and lynx is similar (McCord and Cardoza 1982), the minimum daily requirements of lynx should also approach this value (1 hare per .95-.63 days), which is well above the actual kill-rate that I measured. Further, the partial consumption of hare that I observed at lynx kills would further accentuate the difference between required and actual daily intake estimates. Though other prey items, and occasional scavenges, supplemented lynx diet, it seems likely that I underestimated the daily intake of lynx in the study area, and that the source of this error is in the estimate of lynx DCD. If lynx rested for long periods more frequently than once per day, I would have calculated a shorter mean DCD than actually occurs. Daily Cruising Distances of single lynx have previously been reported as being 3.4 km or 7.0-8.0 km depending on method used (Parker 1981), 7.7 km (Iurgenson 1955), 8.0 km (Saunders 1963), and 8.8 km (Nellis and Keith 1968). Lynx DCDs' from this study are shorter than most other estimates, while daily kill rates are similar to those from 2 of 4 other studies. However, if I underestimated DCD, daily kill rates obtained here probably are a conservative estimate. Brand et al. (1976) suggest that DCD is a function of hunting success rather than hare density, and in this study beds were sometimes found to be associated with kill sites. Few of these appeared to have been used to ambush the hare, but rather seemed to be used for resting between feeding bouts, suggesting that lynx DCD may have been affected by hunting success. Therefore, I suggest that distance between ice-encrusted beds is not a suitable estimate of lynx DCD, and that other methods such as locating radiocollared lynx on consecutive days and snowtracking between locations to calculate distance covered, be examined more closely in the future.

Daily kill-rates of coyotes have not been calculated previously. However Perkins and Mautz (1990) estimated that free-ranging eastern coyotes needed the equivalent of 1.5 hares per day to satisfy energy requirements. This value is equal to my estimate of daily hare-kill rate for Yukon coyotes (smaller than eastern coyotes) in Year 1, and is less than my estimate of 1 hare / .9 days in Year 2. In addition to hare kills, coyotes supplemented their diets with other prey items, and scavenged other foods relatively often. Therefore, if distance to ice-encrusted beds is a reliable method to assess coyote DCD, in terms of energy coyotes were probably doing well in Year 1, and even better in Year 2. It is therefore possible that an overabundance of food may have existed for coyotes.

Daily Cruising Distance of coyotes in Oregon,as estimated by intensive 24 hr telemetry relocations during winter, was 12.8 km (Toweill 1986), which is greater than the estimate I derived using mean distance to long beds. Coyotes too, may have bedded down for long periods more frequently than once per day, which would have caused me to underestimate DCD. However coyotes use all types of beds less frequently than lynx, and did not bed down at kill sites, suggesting that resting time and prey handling time was lower than for lynx. Canids typically have a large stomach capacity and can consume substantial quantities at a single meal; most species rarely have several meals from one carcass in the same place (Kleiman and Eisenberg 1973). Hares killed by coyotes appeared to be consumed at one sitting, suggesting that coyote DCD is not strongly related to hunting success. I therefore feel that long beds may be more useful in calculating DCD of coyote than lynx, and that the margin of error is narrower for the former species. Nevertheless, if coyote DCD was underestimated, daily food consumption rate would be even higher than that which I calculated, suggesting that coyotes obtained more than adequate food during the study.

Other Responses

One assumption made by the model of a Type II functional response is that predator hunting success rate is independent of prey density (Abrams 1990), and I found that hunting success of single lynx was unaffected by an increase in hare abundance; thus lynx predation rates on hare do not violate this assumption. Conversely, single coyotes may have had a higher success rate in Year 2 (though sample size for Year 1 was small, and G-test detected no difference); and this type of response would be expected of a Type III predator. This phenomenon may have been attributable to the improvement of hunting skills by coyotes, such as through the development of a "search image" (Tinbergen 1960) for hares, as their densities increased.

Though both predators appeared to respond similarly to an increase in hare abundance with comparable increases in hare kill and scavenging rates, the effect of individual coyotes on hares would appear to be greater than lynx.

In summary, results from this study suggest that both lynx and coyotes have a Type II functional response to an increase in hare, which for coyotes is different than that reported by Keith et al. (1977). However, it will be necessary that other studies examine predation by both species over a larger gradient of hare densities before the functional response of both species has been fully examined.

Table 2.1: Frequency of occurence of food items in lynx and coyote scats collected during two winters in southwestern Yukon.

	Lynx		Coyote	
	Year 1 (n=62)	Year 2 (n=52)	Year 1 (n=100)	Year 2 (n=51)
Lepus	83.8	67.3	53.0	68.6
Peromyscus	25.8	13.4	27.0	9.8
Microtus	11.3	17.3	21.0	21.6
Clethryonomys	6.4	23.1	16.0	27.5
Spermophilus	12.9	17.3	19.0	13.7
Tamiasciurus	17.7	7.7	9.0	11.8
Eutamias	1.6	3.8	10.0	9.8
Sorex	11.3	13.5	10.0	9.8
Alces	4.8	0	6.0	2.0
Ovis	3.2	1.9	5.0	0
Synaptomys	4.8	3.8	5.0	3.9
Lemmus	3.2	0	3.0	3.9
Ochotona	3.2	7.7	1.0	7.8
Neotoma	0	9.6	1.0	5.9
Castor	1.6	0	2.0	3.9
Bonasa	1.6	3.8	1.0	2.0
Marmota	1.6	0	6.0	0
Zapus	1.6	0	0	0
Ursus	0	1.9	0	0
Martes	0	0	1.0	0
Phenacomys	1.6	0	0	0
Vegetation	11.3	36.5	56.0	39.2

Table 2.3: Mean volume of hair of the eight most common types in lynx and coyote scats collected during two winters in southwestern Yukon.

	Lynx				Coyote			
	Year 1		Year 2		Year 1		Year 2	
	%	+/- SD	%	+/- SD	%	+/- SD	%	+/- SD
<u>Lepus</u>	63.5	39.9	50.9	42.9	33.3	39.3	46.2	40.8
<u>Peromyscus</u>	10.4	22.6	4.8	15.5	9.9	19.6	3.2	11.9
<u>Microtus</u>	3.9	11.4	8.8	23.6	10.4	25.3	8.2	21.6
<u>Clethryonemys</u>	2.9	13.9	7.8	20.3	8.5	22.0	9.8	19.6
<u>Spermophylis</u>	6.9	18.7	11.4	27.8	8.5	21.0	7.0	21.4
<u>Tamiasciurus</u>	6.7	18.1	1.1	4.6	4.3	14.9	4.7	17.2
<u>Eutamias</u>	0.5	3.8	1.5	8.0	2.2	7.6	2.9	10.5
<u>Sorex</u>	2.6	7.6	2.0	7.1	4.6	16.8	2.5	9.1

Table 2.3: Percent of kills, attempts, and scavenges made by lynx and coyotes on snowshoe hare, during two winters in southwestern Yukon Attempts at small mammals are not included. Sample size is given in parentheses.

Species	Year	% Kills	% Unsucc. Attempts	% Scavenges
Lynx	1	81.8 (22)	87.8 (49)	83.3 (6)
	2	100 (33)	91.2 (57)	94.7 (19)
Coyote	1	66.7 (9)	66.6 (15)	50.0 (16)
	2	100 (25)	83.3 (24)	93.6 (47)

Table 2.4: Rates at which lynx and coyotes killed snowshoe hares, as determined by tracking during two winters in southwestern Yukon. Average size of lynx 2+ groups was 3.1 in Year 1, and 3.2 in Year 2.

	Group Size	km	Kills	Kills/km	Kill/km /Individual
Lynx					
Year 1	1	118.1	9	.076	.076
	2+	50.9	9	.177	.057
Year 2	1	160.2	19	.119	.119
	2+	48.0	14	.292	.091
Coyote					
Year 1	1	77.3	6	.078	.078
	2	2.2	0	0	0
Year 2	1	144.7	18	.124	.124
	2	43.0	7	.163	.082

Table 2.5: Rates at which snowshoe hares were chased by lynx and coyotes, as determined by tracking during two winters in southwestern Yukon. Average size of lynx 2+ groups was 3.1 in Year 1, and 3.2 in Year 2.

	Group Size	km	Attempts	Attempts /km	Attempts/km /Individual
Lynx					
Year 1	1	118.1	28	.237	.237
	2+	50.9	33	.648	.209
Year 2	1	160.2	60	.374	.374
	2+	48.0	25	.520	.163
Coyote					
Year 1	1	77.3	16	.207	.207
	2	2.2	0	0	0
Year 2	1	144.7	35	.242	.242
	2	43.0	10	.233	.116

Table 2.6: Rates at which snowshoe hares were scavenged by lynx and coyotes, as determined by tracking during two winters in southwestern Yukon. Average size of lynx 2+ groups was 3.1 in Year 1, and 3.2 in Year 2.

	Group Size	km	Scavenges	Scavs./km	Scavs./km /Individual
Lynx					
Year 1	1	118.1	4	.034	.034
	2+	50.9	1	.019	.006
Year 2	1	160.2	13	.081	.081
	2+	48.0	5	.104	.033
Coyote					
Year 1	1	[illegible]	8	.103	.103
	2	[illegible]	0	0	0
Year 2	1	[illegible]	35	.242	.242
	2	43.0	9	.209	.105

Table 2.7: Success rates of lynx and coyotes on snowshoe hare during two winters in southwestern Yukon.

	Group Size	Kills	Chases	% Success
Lynx				
Year 1	1	9	28	32
	2+	9	33	27
Year 2	1	19	60	31
	2+	14	25	56
Coyote				
Year 1	1	6	16	37
	2	0	0	-
Year 2	1	18	35	51
	2	7	10	70

Table 2.8: Rates at which lynx and coyotes bedded, as determined by tracking during two winters in southwestern Yukon. Average size of lynx 2+ groups was 3.1 in Year 1 and 3.2 in Year 2. Sample sizes are given in parentheses.

	Group Size	km	Crouch/km /Individual	Short/km /Individual	Long/km /Individual
Lynx					
Year 1	1	118.1	.398 (47)	.228 (27)	.220 (26)
	2+	50.9	.418 (66)	.240 (38)	.177 (28)
Year 2	1	160.2	.218 (35)	.256 (41)	.206 (33)
	2+	48.0	.156 (24)	.254 (39)	.065 (10)
Coyote					
Year 1	1	77.3	.013 (1)	.233 (18)	.091 (7)
	2	2.2	0	0	0
Year 2	1	144.7	.048 (7)	.111 (16)	.131 (19)
	2	43.0	.046 (4)	.151 (13)	.116 (10)

REFERENCES

Abrams, P.A. 1990. The effects of adaptive behavior on the Type-2 functional response. Ecology 71:877-885.

Brand, C.J., Keith, L.B., Fischer, C.A. 1976. Lynx responses to changing snowshoe hare densities in central Alberta. J. Wildl. Manage. 40:416-428.

Douglas, G.W. 1974. Mountain zone vegetation of the Alsek River region, southwestern Yukon. Can. J. Bot. 52:2505-2532.

Harrison, D.J., Bissonette, J.A., and Sherburne, J.A. 1989. Spatial relationships between coyotes and red foxes in eastern Maine. J. Wildl. Manage. 53:181-185.

Hassell, M.P. 1966. Evaluation of parasite or predator responses. J. Anim. Ecol. 35:65-75.

Iurgenson, P.B. 1955. Ecology of the lynx in forests of the central zone of the USSR. Zool. J. 34:609-620.

Keith, L.B., Todd, A.W., Brand, C.J., Adamcik, R.S., and Rusch, D.H. 1977. An analysis of predation during a cyclic flucuation of snowshoe hares. Proc. XIII Cong. Game Biol. pp. 151-175.

Kleiman, D.G., and Eisenberg, J.F. 1973. Comparisons of canid and felid social systems from an evolutionary perspective. Anim. Behav. 21:637-659.

Krebs, C.J., 1989. Ecological methodology. Harper & Row, New York, NY. pp. 653.

Krebs, C.J., Gilbert, B.S., Boutin, S., Sinclair, A.R.E. 1987. Estimation of snowshoe hare population density from turd transects. Can. J. Zool. 65:565-567.

Krebs, C.J., Gilbert, B.S., Boutin, S., Sinclair, A.R.E., and Smith, J.N.M. 1986. Population biology of snowshoe hares. I. Demography of food-supplemented populations in the southern Yukon, 1976-84. J. Anim. Ecol. 55:963-982.

Kruuk, H. 1986. Interactions between felidae and their prey species: a review. In: Miller, S.D., and Everett, D.D. (eds.), Cats of the world: biology, conservation and management. Nat. Wildl. Fed., Washington, D.C. pp. 353-374.

Major, A.R. 1989. Lynx Lynx canadensis canadensis (Kerr) predation patterns and habitat use in the Yukon Territory, Canada. M.Sc. thesis, State University of New York, Syracuse, N.Y. 75 pp.

Major, J.T., and Sherburne, J.A. 1987. Interspecific relationships of coyotes, bobcats, and red foxes in western Maine. J. Wildl. Manage. 51:606-616.

[illegible] W.W. and Perkins, P.J. 1989. Metabolic rate of bobcats as influenced by seasonal temperatures. J. Wildl. Manage. 53:202-205.

McCord, C.M., and Cardoza, J.E. 1982. Bobcat and lynx. In: Chapman, J.A., and Feldhammer, G.A. (eds.), Wild mammals of North America, biology, management, and economics. Johns Hopkins Univ. Press, Baltimore, Md. pp. 728-766.

Murdoch, W.W. 1973. The functional response of predators. J. Appl. Ecol. 10:335-342.

Nellis, C.H., and Keith, L.B. 1968. Hunting activities and success of lynxes in Alberta. J. Wildl. Manage. 32:718-722.

Parker, G.R. 1981. Winter habitat use and hunting activities of lynx (Lynx canadensis) on Cape Breton Island, Nova Scotia. In: Chapman, J.A., and Pursely, D. (eds.), Proc. World. Furb. Conf., Frostburg, Md., (1980). pp. 221-248.

Parker, G.R., Maxwell, J.W., Morton, L.D., and Smith, G.E.J. 1983. The ecology of the lynx (Lynx canadensis) on Cape Breton Island. Can. J. Zool. 61:770-785.

Perkins, P.J., and Mautz, W.W. 1990. Energy requirements of eastern coyotes. Can. J. Zool. 68:656-659.

Powers, J.G., Mautz, W.W., and Perkins, P.J. 1989. Nutrient and energy assimilation of prey by bobcats. J. Wildl. Manage. 53:1004-1008.

Saunders, J.K. 1963. Movements and activities of the lynx in Newfoundland. J. Wildl. Manage. 27:384-390.

Sokal, R.R., and Rohlf, F.J. 1980. Biometry. W.H. Freeman & Co. New York, NY. 859 pp.

Quinn, N.W.S., and Parker, G. 1987. Lynx. In: Novak, M., Baker, J.A., Obbard, M.E., and Malloch B. (eds.), Wild furbearer management and conservation in North America. Ont. Min. of Nat. Res., Toronto, Ont., pp. 683-694.

Sargeant, A.B., Allen, S.H., and Hastings, J.O. 1987. Spatial relations between sympatric coyotes and red foxes in North Dakota. J. Wildl. Manage. 51:285-293.

Taylor, R.J. 1984. Predation. Chapman & Hall, New York, N.Y. 166 pp.

Theberge, J.B., and Wedeles, C.H.R. 1989. Prey selection and habitat partitioning in sympatric coyote and red fox populations, southwest Yukon. Can J. Zool. 67: 1285-1290.

Tinbergen, L. 1960. The natural control of insects in pinewoods. I. Factors influencing the intensity of predation by songbirds. Arch. Neerl. Zool. 13:265-343.

Toweill, D.E. 1986. Resource partitioning by bobcats and coyotes in a coniferous forest. Ph.D thesis, Oregon State University. Corvallis, Or. 155 pp.

Voigt, D.R., and Earle, B.D. 1983. Avoidance of coyotes by red fox families. J. Wildl. Manage. 53:852-857.

Voigt, D.R., and Berg, W.E. 1987. Coyote. In: Novak, M., Baker, J.A., Obbard, M.E., and Malloch, B. (eds.), Wild furbearer management and conservation in North America.

Ont. Min. of Nat. Res., Toronto, Ont., pp. 345-356.

Witmer, G.W., and deCalesta, D.S. 1986. Resource use by unexploited sympatric bobcats and coyotes in Oregon. Can. J. Zool. 64:2333-2338.

Youngman, P.M. 1975. Mammals of the Yukon territory. Publ. in Zoology No. 10, Nat. Mus. of Canada, Ottawa, Ont. 192 pp.

CHAPTER 3

FACTORS AFFECTING WINTER HABITAT USE BY COYOTES IN SOUTHWESTERN YUKON.

INTRODUCTION

If food availability is heterogeneous an animal should spend its foraging time in areas where energetic returns per unit time are maximized (Stephens and Krebs 1986). Indeed, vertebrates use habitats according to profitability (Werner and Hall 1979), and though the most rewarding areas are usually those either with highest availability of food items, and/or most easily acquired food, other factors may contribute to selection of foraging areas (Pyke 1984).

Work with mammalian predators has usually stopped short of differentiating between influences of prey availability and prey vulnerability on foraging (Kruuk et al. 1990), and it is likely that in carnivores, foraging patterns are a direct result of the effects of a number of different stimuli on behavior of the predator. For example, factors such as hunting behavior (Kruuk 1986), morphology (Bakker 1983; Taylor 1989), avoidance of competitors (Major and Sherburne 1987; Litvaitis and Harrison 1989; Theberge and Wedeles 1989), or the effects of snow on movements (Henry 1979; Parker 1981; Halpin and Bissonette 1988), may all affect habitat use of terrestrial predators.

Coyotes are recent immigrants to the boreal forest of North America (Nowak 1979; Voigt and Berg 1987). Their morphology is poorly adapted for travel through deep snow, however they select snow conditions to alleviate their morphological disadvantages (Chapter 1). Though winter habitat use of coyotes in areas of snowcover has been described previously (Ozoga and Harger 1966; Toweill 1986; Witmer and deCalesta 1986; Major and Sherburne 1987; Litvaitis and Harrison 1989; McKinlay 1990), including in the Yukon (Theberge and Wedeles 1989), there is a lack of information concerning the factors which influence habitat use. I therefore undertook this study to examine the influence of a) habitat availability, b) snow conditions, c) presence of other predators, d) food availability, and e) prey vulnerability, on winter habitat use of coyotes from the Yukon.

STUDY AREA

Coyotes were studied during 2 winters in a 175 km^2 area of the Kluane Lake area of southwestern Yukon (61^{o}N 138^{o}W) previously described in detail (Chapter 1). The study site was located in a broad east-west valley within the boreal forest zone (Douglas 1974), where white spruce (Picea glauca) was the dominant tree. A strong altitudinal gradient existed in the study site, and I worked from the base of the valley (830 m) to an altitude of 1169 m, which was near the base of the mountains. The altitude of the valley floor also differed with the central area, being up to 215 meters higher than that of either end. Altitude was inversely related to canopy cover, and though spruce cover ranged from 0 to 100%, most areas in the valley had between 25 and 75% cover. Other winter habitat types available to predators included deciduous (Populus) forests, shrub (Salix), and completely open areas. Snowfall was proportional to altitude in the study site, and total snow accumulation for both years of study averaged 65 cm, which was average for that region (Krebs et al. 1986). I estimated that there were at least eight coyotes in the study area during winter 1987-88 (Year 1), based on track transects and known locations of radio-collared animals. Fourteen coyotes were thought to be present during winter 1988-1989 (Year 2). Lynx (Lynx canadensis) appeared to be slightly more numerous than coyotes in the study area (Chapter 4), and other less abundant terrestrial predators incuded red fox (Vulpes vulpes), wolverine (Gulo gulo), and wolf (C. lupus).

METHODS

Habitat Availability

The availability of the five predominant habitat types (Open Spruce, Closed Spruce, Deciduous, Shrub, Open) within the study area was estimated using LANDSAT imagery. To measure the similarity of the LANDSAT system and the habitat classification system that I used while tracking predators, LANDSAT was groundtruthed with the tracking method. The LANDSAT system was refined once, after which both methods classified habitats similarly.

Coyote Snowtracking

Coyotes were snowtracked during both years for a total of 268 km. Tracking was undertaken daily after snowfall, and continued until fresh tracks could no longer be differentiated from older trails (usually 7-10 days). Frequent snowfall permitted me to track coyotes between January and March during Year 1 and between November and March during Year 2, with no inactive period longer than 8 days. Tracks were usually encountered along a network of snowmobile trails within the study area, though on occasion I trailed tracks crossing the Alaska Highway, that bisected the study area. I tried to spread tracking sessions throughout the site by rarely initiating track searches from the same point of departure on consecutive days, and by choosing tracks to be followed from all parts of the study site. Tracks were either backtracked or, if their age was estimated as being older than 24 hrs, forward tracked. If the animal being tracked was disturbed, the session was immediately ended; however more commonly a track was followed until it was either lost, or light levels and/or snow conditions made it difficult to read. Distances tracked were obtained by counting steps with a hand counter and converting to kilometers (Parker 1981). The estimate was truthed on several occasions by counting the number of paces taken to traverse a known distance.

Habitat types encountered while tracking were recorded according to a four point classification system which estimated percent canopy cover in blocks of 50%, predominant canopy species, percent understory cover (in blocks of 25%), and predominant understory species. I recorded habitat changes on coyote tracks as they were encountered, however habitat types that were used for less than 10 consecutive meters of the predator track were not recorded.

Snow Conditions

The method used to obtain snow measurements on tracks, and in the study site, has previously been described in detail (Chapter 1). Snow depth was measured at the beginning, at the end, and every 500 paces (one pace= 2 consecutive steps; 500 paces= approx. 600 meters) of a tracking session, during both years of study. Snow hardness was measured in Year 2 by the sinking depth of a penetrometer (PSD), at the same locations where snow depth measurements were taken. Habitat type was noted at each site of snow measurements. General snow conditions (snow depth and snow hardness) in the study area were measured at 16 sites placed in all habitat types along the network of snowmobile trails. The distribution of sites among habitat types was roughly proportional to the availability of each type in the study area. At each site 4 measures of snow depth and snow hardness were taken, and averaged. The sites were visited 8 times between November and March of

Year 2.

Use of Altitude Levels by Coyotes and Other Predators

I documented regions of the study site used by coyotes and other predators by snowmobiling along a network of trails within the study area, and recording all predator crossings. At each location where a predator track crossed the trail, species and location (altitude level; see Chapter 1) were noted. Tracks were recorded along the transect for the first 4 to 6 days after snowfall, and an average of 30 km of trails were checked each day for predator tracks. Track crossings were recorded between November and April of both years.

Prey Availability

Snowshoe hare densities within the major habitats of the study site were estimated by counting all fresh (less than 1 year old) hare turds along 480 transects, during June 1987 and June 1988, and extrapolating numbers of hare turds collected to an estimate of the number of hares per hectare (see Krebs et al. 1987). Though transects were placed within major habitat types available in the study area, no turd transects traversed completely open areas. Hares tend to avoid open habitats (Pietz and Tester 1983), and turds were rarely observed in such locations; therefore I assumed that hare density was zero in that habitat type. The number of transects placed within each other habitat type was roughly proportional to its availability in the study area.

Other prey items in coyote diet were less important than hare during both years of study (Chapter 2). Therefore relative abundance of these species with respect to habitat type was not examined. Relative abundance of scavengeable food items was estimated by recording habitats in which coyotes scavenged food while I tracked them.

Hare Vulnerability

Hare vulnerability in a habitat was defined as the percent of coyote chases of hares within that habitat that resulted in a kill. Under this definition, vulnerability of hares could only be assessed once a chase had been initiated, and encounters with hare that did not result in a chase may have been excluded. Coyote chases of prey were recorded as they were encountered during a snowtracking session, and at these sites I recorded species chased, number of bounds in the chase, and chase outcome, while also observing standard habitat characteristics of the site.

Track Identification

Coyote and fox tracks were very similar in appearance in southwestern Yukon. To avoid confusing them, I used a combination of print size, home ranges of radiocollared animals, locations of visual sightings, and knowledge that spatial exclusion of foxes in coyote inhabited areas occurs (Major and Sherburne 1987; Voigt and Earle 1983; Sargent et al. 1987; Harrison et al. 1989).

Statistical Analyses

I used criteria outlined by Aldredge and Ratti (1986) to determine which analysis method was appropriate for most of the resource use-availability data; as the number of habitats was small (5), observations were numerous, and observations were independent (see below), the method proposed by Neu et al. (1974) was selected, though a G-test with Williams' correction (Sokal and Rohlf 1981) was used rather than a Chi-square. Probabilities less than .05 were considered significant, and proportional data were transformed prior to analysis, using the arcsin of the square root (Krebs 1989).

The way in which the snowtracking data were collected may have violated the assumption of independence which is implicit to both G-test and ANOVA. I therefore analysed the data in 3 ways: a) by randomly selecting 500 tracking paces for each year (out of 62250 in Year 1 (=.8%), and 156409 in Year 2 (=.3%)), and subjecting these to a G-test (this method maximized independence between observations), b) by using total kilometers tracked in each habitat in a G-test (minimum independence), and c) by using tracking sessions as experimental units, and calculating proportional use of each habitat per session, and subjecting each habitat to a separate ANOVA (independence between sessions but dependence within sessions). The proportional use of each habitat type as determined by each analysis method is given (Figure .1). All values are similar, which suggests that the 3 methods are representative of the overall habitat use patterns that I observed.

Effect of Session Length

Length of coyote tracking sessions varied from .03 to 5.8 km, and I was concerned that tracks of differing lengths may not produce similar interpretations when subjected to ANOVA. Therefore I divided sessions into 3 groups: less than 1 km, between 1 and 3 km, and greater than 3 km, and performed a one-way ANOVA for each of the 5 habitat types by session length groups. The analysis did not detect an effect on the frequency of use of any habitat types (lowest P value was in Open, where F=1.81; df=2,232; P=.165). A G-test on total kilometers tracked, also did not indicate any significant length effect (G=8.29; df=8; P<.50). Thus tracking sessions of all lengths were treated equally.

Effect of Winter Season

Winters were divided into 4 seasons: Early Winter (Nov. 1 - Dec. 14), Mid-Winter (Dec.15 - Jan.31), Breeding Season (Feb.1 - Mar.5), and Late Winter (Mar.6 - Mar.31). The number of km tracked in each season differed between years (Table 3.1), and this could have confounded comparisons. Therefore I examined the effect of winter season on habitat use by performing a contingency analysis of km tracked in each habitat, by winter season. Results indicated no differences between seasons (Year 1: G=3.0138;

df=4; P<.50; Year 2: G=13.5412; df=12; P<.50). I also performed an ANOVA on habitat use during winter seasons for each year, and found that coyote use of all habitats between seasons was similar in Year 1 (lowest P value was in Closed Spruce, where F=2.82; df=1,38; P=.101), but that use of only 4 of the 5 habitats did not differ between seasons in Year 2 (lowest non-significant P value was in Closed Spruce, where F=2.62; df=3,191; P=.052). The use of Open areas was significantly higher during the Breeding Season (F=5.03; df=3,191; P=.002; Figure 3.2). However overall use of that habitat by Yukon coyotes was found to be very low (7% of total in both years). Therefore I assumed that the seasonal change in the use of Open habitat was not an important component in the habitat selection patterns of Yukon coyotes. Thus all winter seasons were pooled when I analysed for yearly shifts in habitat selection.

RESULTS

Habitat Selection

Coyotes did not use habitats according to availability in either year of study (Year 1: G=175.9; (n=500); df=4; P<.001; Year 2: G=218.6; (n=500); df=4; P<.001). Selection of Closed Spruce (cover < 50%) in Year 1, and Open Spruce in Year 2, was observed (Figure 3.3), and overall use of spruce forests (Open Spruce + Closed Spruce) for both years was seventy-eight percent. Deciduous habitat was used slightly more than its availability in both years but total use of that habitat was relatively low (Year 1: 9% ; Year 2: 8%). Shrub and Open areas were avoided during both years.

Changes Between Years

I next analysed habitat use between years to determine if yearly effects existed in the patterns that I observed. A G-test detected a dependence of habitat use on year (G=46.789; df=4; n=500; P<.001). However a one-way ANOVA on use of each habitat by year did not detect a year effect (lowest P value was in Open Spruce and Closed Spruce where F=2.97; df=1,233; P =.087). In this case the G-test is more sensitive to subtle changes in yearly use, while the ANOVA is cruder and would only detect larger changes in the observed patterns. I suggest that given the complete independence between observations for the G-test, but not so for the ANOVA, the former test is the more accurate one in this case, and that coyotes did undergo a slight change in habitat use between the two years of study.

Use of Understory

A G-test on use of areas with thick understory (shrub cover > 75% ground cover) did not detect a difference in understory use between years (G=1.306; df=1; P<.50). However there was a significant interaction between winter season and year (year: F=4.65; df=1,229; P=.032; winter season: F=1.51; 3,229; P=.212; year by winter season interaction: F=9.17; df=1,229; P=.003). This phenomenon was a result of lower heavy shrub cover use during Mid-

Winter of Year 1 but higher use during Breeding Season of the same year (Figure 3.4). Overall use of thick shrub cover was (mean +/- SD) 16.1 +/- 31.2% (n=40) in Year 1, and 19.2 +/- 29.7% (n=195) in Year 2.

Snow Conditions

I performed an ANOVA on snow depth on coyote trails by habitat, year, and altitude level. This test resulted in significant differences in snow depths between habitats (F=4.63; df=4,348; P<.001); mean snow depth in Open habitat was less than in all other types (Table 3.2). However snow depth on coyote trails did not differ between years (F=.43; df=1,348; P=.512) or altitude levels (F=.000; df=1,348; P=.984).

A habitat by altitude level interaction term was found to be present in the analysis of snow depths in the study site (at the snow stations) (habitat: F=6.01; df=4,118; P<.001; altitude level: F=13.49; df=1,118; P<.001; habitat by altitude level interaction: F=4.69; df=4,118; P=.002). This result suggests that snow accumulation rates differed between habitats at different altitudes. However, on average, snow depth was shallower at low altitudes, and Closed Spruce and Open habitats had shallower snow than other habitat types (Table 3.3).

Snow hardness on coyote tracks in Year 2, differed between habitat types (ANOVA: F=3.55; df=4,248; P=.008), but was similar between altitude levels (F=.15; df=1,248; P=.628). Snow was harder on coyote tracks in Open habitat than in all other types (Table 3.2). However snow hardness in the study area (at the snow sites) did not differ either between habitat types (F=.13; df=4,118; P=.972) or between altitude levels (F=2.81; df=1,118; P=.096).

Use of Altitude Levels by Coyotes and Other Predators

Most coyote crossings occurred in the lower altitude level of the study site during both years, while most crossings by lynx, red fox and wolverine occurred at higher altitudes (Table 3.4). A G-test performed on km tracked at both levels found habitat use of coyotes to be similar at both altitude levels (G-test: G=4.046; df=4; P<.50). However a one-way ANOVA on each habitat type by altitude level indicated that only Closed Spruce was encountered at different rates at the low level (F=4.11; df=1,233; P=.044). However the availability of Closed Spruce habitat is greater at low altitudes, and a difference in usage between areas is to be expected. The fact that all other habitats were encountered at similar frequencies, and that the G-test detected no differences in usage, suggests that coyotes use habitats at low and high altitudes similarly.

Hare Density

Hare turds were most abundant in Closed Spruce forest and this difference translated into a significantly higher number of hares per hectare in that habitat type over all others (Figure 3.5). Open Spruce and Deciduous habitats were second, with roughly the same number of hares per area, while Shrub was third. Relative number of hare turds present in each habitat type was similar between Year 1 and Year 2, but were roughly double in Year 2. As a result, overall hare densities which were estimated at .39 +/- .05 hares/hectare (mean +/- SD) in Year 1, were at .77 +/- .10 hares/hectare in Year 2.

Rate of Coyote Chases of Hare

The rate at which coyotes chased hares in various habitats during both years of study, did not closely reflect the increase in hare abundance in all habitats in Year 2, nor the relative number of hares present in different habitat types (Table 3.5). Attempts in Year 1 were least frequent in Closed Spruce despite higher hare densities there. However sample size was small. In Year 2, chases in Closed Spruce were 4 times more frequent, while chases in Open Spruce and Other (Deciduous + Shrub + Open) habitats decreased. Distribution of chases among habitats did not differ between years (G=2.043; df=2; P<.50).

Kill-rates in different habitats did not reflect closely the relative increase in hares in Year 2. Kill-rate (kills/km) was .03 (n=1 kill) in Closed Spruce, .14 (n=4) in Open Spruce, and .06 (n=1) in Other habitats in Year 1. During Year 2, kill-rate was 7.6 times higher in Closed Spruce (.29 kills/km; n=13), while rates in Open Spruce (.10; n=10), and Other (.05; n=2) habitats decreased. The distribution of kills among the three habitat types was not significantly different between years

(G=2.2389; df=2; P<.50). The percentage of chases that occurred in thick understory was 19.7 (total number of chases= 61), which was similar to the average value for both years in use of dense shrub areas by coyotes (18.6 +/- 29.9%).

Scavenging Rates

A total of 63 sites where coyotes scavenged food were encountered while snowtracking. The proportion of scavenges occuring in Open Spruce, Closed Spruce and Other habitats changed between years (G=8.8123; df=2; P<.025), as scavenges in both types of spruce became more frequent in Year 2. In Year 1, the number of scavenges encountered per kilometer of trail was .12 (n=5) in Closed Spruce, .14 (n=4) in Open Spruce, and .40 (n=8) in Other habitats. In Year 2 rates were highest in Open Spruce habitat (.29; n=10), followed by Closed Spruce (.22; n=30) and Other habitats (.16; n=7). Most scavenges in both years were of snowshoe hare remains: 81.3% (n=16) in Year 1, and 95.7% (n=47) in Year 2, however scavenging rate within each habitat type was not directly proportional to relative hare densities therein.

Hare Vulnerability

While most hares were killed in Open Spruce in Year 1, Closed Spruce became the habitat from which most hares were taken in Year 2, with over half of the hare kills occurring there (Table 3.6). Overall success rates for both years was 73.7% (n=19 chases) in Closed Spruce, 40.0%

(n=35) in Open Spruce, and 42.9% (n=7) in Other habitats, and these differences are not significant (G=5.680; df=2; P<.10). However if success rate in Closed Spruce is compared to that in all other habitats combined (Open Spruce + Other), success rates in Closed Spruce is significantly higher than in other habitats (G=5.782; df=1; P<.025).

The percentage of hare kills occurring in thick understory areas was almost twice as high (25.8%; n=31 for all kills), as the number of attempts in the same understory type (13.3%; n=30 for all attempts). Though these differences are not significant (G=1.463; df=2; P<.50), it should be noted that average use of heavy understory for both years (1[illegible] +/- 29.9% ;n=235) was lower than proportion of kills occurring in that cover type, but higher than the percent for attempts.

The number of bounds in coyote chases was not affected by overstory type (ANOVA: F=.27; df=2,55; P=.767). However chase outcome (kill or attempt) did affect the number of bounds (F=28.3; df=1,55; P<.001; Table 3.7); whereby the average number of bounds for both years was 0.7 +/- 1.3 (n=31) at coyote kills and 4.2 +/- 2.5 (n=30) at attempts.

DISCUSSION

Habitat Selection of Coyotes

Coyotes did not use habitats according to their availability, but selected Closed Spruce habitat in Year 1 and Open Spruce in Year 2. Theberge and Wedeles (1989) examined coyote habitat selection in a study area 70 km from mine, and did not observe selection for spruce forests, but rather found a selection for open habitats. However my results indicated an avoidance by coyotes of both open and shrub habitats during both years of study. Avoidance of these habitats is not surprising, given the lack of hare and other prey in such habitat types, and it is difficult to explain why a population of coyotes studied by Theberge and Wedeles (1989) selected a habitat type where food was probably rare.

Snow Conditions

If habitat selection patterns of coyotes were affected by snow conditions, would have expected coyotes to select habitats where either snow depth and/or snow hardness were favorable for their movements, as observed by McKinlay (1990). Snow conditions appeared to be most favorable in Open habitat, but that habitat type was avoided during both years. Though habitat selection changed between years of study, snow depths on coyote tracks from both years of study appeared similar. Therefore snow conditions did not prompt this habitat change. Coyotes have a morphology that is ill-equiped to deal with unfavorable snow conditions (Todd and Keith 1976), and they restrict their winter movements to regions, areas, and travel routes where snow conditions are favorable (Chapter 1). In fact, snow was both harder and shallower in Open habitat. However coyotes strongly avoided this habitat type during all winter periods except Breeding Season in both years and this was probably due to the lack of food therein. Todd et al. (1981) also observed higher use of open habitats in Alberta coyotes in late winter, and they suggest that the occurrence of snow conditions favorable to movements in such habitats, caused this pattern. However, snow conditions between Breeding Season and Late Winter were similar in this study (Chapter 1), but coyotes still used Open habitat differently between these seasons. Therefore, I suggest that mate-seeking movements are a more likely explanation of this phenomenon in southwestern Yukon.

Use of Altitude Levels by Coyotes and Other Predators

If the presence of other species of predators affected habitat use of coyotes, I would have expected to observe different use patterns between altitude levels. The fact that coyotes employed habitats similarly between altitude levels suggests that the higher density of other species at high altitudes (as well as the deeper snow found there) did not greatly affect habitat use patterns of the coyotes that I studied. A shifting of habitat use as a direct result of interspecific competition has been demonstrated in fish (Werner and Hall 1977), and speculated upon in carnivores (Major and Sherburne 1987; Litvaitis and Harrison 1989; Theberge and Wedeles 1989).

Coyotes commonly follow predator trails for long distances during winter in southwestern Yukon (Chapter 1). However, this behavior would be maladaptive if coyotes were trying to avoid areas where other carnivores were present. Coyotes appear to displace red fox (Theberge and Wedeles 1989), and perhaps lynx (Chapter 1), in the Yukon, and the presence of these predators should not strongly alter the habitat use patterns of coyotes. While the relationship between coyote and wolverine is unknown, coyotes avoid areas in which wolves are present (Fuller and Keith 1981). However wolves were not common in the study area and they may have been too scarce to cause coyote habitat use to shift in this study.

Hare Density

Hare density was greatest in Closed Spruce, and relative numbers of hares varied directly with cover density of the 4 habitat groups examined. Visibility of hares to predators is lower in Closed Spruce than in all other habitats, and hares select areas of highest cover during winter partly by virtue of the greater concealment from predators provided by those areas (Litvaitis et al. 1985). Consequently heterogenous distribution of hares in the study area may be related, at least in part, to potential predator detection in each habitat type.

Hares are the primary food of coyotes in southwestern Yukon (Theberges and Wedeles 1989, Chapter 2). If availability of hares had an effect on habitat selection by coyotes, I would have expected to observe selection of Closed Spruce forests in both years of study. Yet Closed Spruce was only selected in Year 1, and used less than its availability in Year 2, at the expense of use of Open Spruce. Despite the fact that relative abundance of hare between habitats did not change between years, hares were more abundant in all habitats in Year 2. If coyote habitat selection works on a threshold system (i.e. a habitat is selected only if prey numbers within it surpass a certain threshold), this may have influenced the strong selection for Open Spruce that occurred in Year 2. However rates of both hare kills and hare chases were highest in Open Spruce in Year 1 and Closed Spruce in Year 2, and coyotes selected Closed Spruce in Year 1 and Open Spruce in Year 2. This result would not have occurred if hare density or hare vulnerability had prompted habitat use patterns of coyotes. Therefore, it seems unlikely that the shift in habitat use observed between years was a direct result of hare density, and the overall effect of hare density on habitat use does not appear to be strong.

Other Foods

Non-hare food items obtained strictly through predation were encountered only infrequently while tracking coyotes (Chapter 2), and the presence of these did not appear to strongly affect habitat selection of Yukon coyotes. Though coyotes consumed a variety of small mammals, the importance of these in their diet was substantially less than hare (Chapter 2), and seemed not to have greatly affected habitat selection patterns of the coyotes that I studied.

Coyotes were found to scavenge relatively frequently while they were tracked, and an increase in the use of Open Spruce in Year 2 coincided with a greater frequency of scavenges in that habitat type. Though most scavenges in both years were on hare, the distribution of scavenges among habitats did not closely reflect relative hare abundance. Coyotes often scavenged hares killed by other predator species (Chapter 1), and the availability of at least hares killed by lynx was greatest in Open Spruce habitat (Chapter 4). Similarly, most scavenges made by coyotes in Year 2 were in Open Spruce habitat. Though one might be tempted to attribute selection of Open Spruce habitat in Year 2 to the greater availability of scavengeable food items in that habitat, volume of food consumed at a scavenge is relatively small (9.0% of the volume consumed at kills; Chapter 2). Given this, it is clear that the total volume of food (kills + scavenges) consumed per km tracked in each habitat was higher in the spruce habitats that were not selected during each year (Open Spruce in Year 1, and Closed Spruce in Year 2). Therefore food availability does not seem to affect directly the habitat use of these coyotes.

Hare Vulnerability

Overall, coyotes achieved a higher success rate in

Closed Spruce habitat than in other types, thus making hare vulnerability once a chase had been initiated, highest within that habitat. However, coyotes did not select Closed Spruce in Year 2, despite the fact that most of their kills occurred there. The reductions in coyote chases at hare in Open Spruce and Other habitats in Year 2 are perhaps attributable to a decrease in hunting "interest", or food satiation when coyotes are outside of Closed Spruce areas, and the use of other habitats for non-foraging activities. Selection of habitats other than Closed Spruce suggests that other factors than simply those related to prey vulnerability may influence habitat use patterns that I observed.

Hunting Tactics

Canids are typically well adapted for running down prey over long distances (Kleiman and Eisenberg 1973), and Bakker (1983) provided evidence that coyotes are among the swiftest of carnivores. However, in southwestern Yukon, coyotes did not appear to rely on either stamina or running speed in their acquisition of hares, as the average number of bounds per kill was less than 1. Further, Gier (1975) suggests that coyotes have evolved for hunting in relatively open areas, but I found overall coyote predation rates on hares to be directly proportional to cover density. Coyotes are recent immigrants to the Yukon area (Nowak 1979; Voigt and Berg 1987), and I have shown that differences in morphological adaptation to snow between coyotes and hares are large (Chapter 1). To achieve successful predation on snowshoe hares during winter, coyotes may need to employ a flushing type of hunting tactic, where approach is slow, rather than a running approach typical of canids. Dense vegetation may have been used to approach hares to within a short striking distance, thereby reducing the potential negative effect of snow on the outcome of a chase. In more open habitats, coyotes may have been detected by hares before the distance between predator and prey had been sufficiently reduced to ensure an effective chase.

It has been suggested that hares can assess their vulnerability to predation, and that they seek areas of high cover to reduce their visibility (Litvaitis 1989). Further, the use of complex habitats by potential prey may be deleterious to predator hunting success (Werner et al. 1983). In the case of hares, distance of flight from an approaching predator may have been affected by cover density. For this reason, coyotes may have approached hares more easily in dense vegetation, as hares may have felt less visible to potential predators and may not have flushed at as great distances as they did in more open habitats. Another possibility is that hares used dense cover for resting, and were less attentive to the approach of a coyote in this type of habitat than in more open ones. Regardless of the mechanism governing hare behavior, the hunting tactic employed by Yukon coyotes appears to be adapted to decrease the initial chase distance, thus alleviating potential adverse effects of snow on the outcome of coyote-hare chase.

Canids typically have a well developed sense of olfaction (Kleiman and Eisenberg 1973), and coyotes have been shown to use smell when hunting, particularly if vision is obstructed (Wells and Lehner 1978). Coyotes should therefore be able to detect hares by smell when hunting in a habitat where dense cover exists and when visibility is substantially reduced.

It is conceivable that hare-predator interactions in the boreal forest evolved in the absence of a competent dense cover terrestrial predator. Lynx are important snowshoe hare predators (Parker 1981). However, they appear to prefer hunting hares in areas of low spruce cover (Chapter 4). Though red fox in the Yukon rely primarily on hare (Theberge and Wedeles 1989), success rates on hare relative to habitat type is unknown. Red fox have a lower foot-load than do coyotes (D. Murray unpubl.) and this may render possible higher success rates than coyotes, in habitats where visibility is high, and a chase through the snow might be necessary. This may allow red fox to prey on hare in Open Spruce forests. Avian predators are adept at capturing hares in more open forests, where visibility is high and they are able to swoop down onto their prey. Thus as a result of the immigration of coyotes to the Yukon, hares may have become more vulnerable to predation in a habitat where they were formerly more secure.

Optimal Habitat Choice?

It is unlikely that a single factor is entirely responsible for the habitat selection patterns of a terrestrial carnivore such as the coyote, and the patterns that I observed were likely the result of a number of factors. The study site consists of a mosaic of habitat patches of varying sizes ranging from .25 to 2 km^2 which is much smaller than the 2-9.5 km^2 size of coyote home ranges in Oregon, described by Witmer and deCalesta (1986). As the overall availability of Closed Spruce forest in the site is 26.0%, there is an upper limit to the possible use of this habitat, despite the greater hare availability and hare vulnerability to coyotes in that habitat. Given the distribution of habitat patches in the study site, it is inevitable that coyotes use a variety of habitats.

Coyotes clearly used Closed Spruce for hunting hares in Year 2, and they achieved a high success rate in that habitat type. However food satiation may have occurred while coyotes were hunting in dense forests, and this may have prompted the use of other habitats for activities not directly related to foraging, such as mate-seeking or territory patrol. Indeed, the higher use of Open Spruce areas in Year 2 may be due to greater availability of predator trails to be followed within that habitat, or the easier travel in habitats of lower vegetation cover. Open areas were used during Breeding Season, and snow conditions and vegetation cover are least encumbering therein; however that habitat contains little or no food, and is perhaps only used for travel between feeding patches or during mate-seeking movements.

Thus none of the factors that I examined appeared to have a strong effect on habitat use patterns of Yukon coyotes, and other factors not observed in this study may interact with the ones studied here, to influence coyote habitat selection. This is the only way to explain the complex patterns of habitat use that I documented.

Table 3.1 Distribution of coyote tracking sessions over two years in southwestern Yukon. Distances are given in kilometers.

	Year 1		Year 2	
Period	No. of Sessions	Total Distance	No. of Sessions	Total Distance
Early Winter (Nov.1-Dec.15)	-	-	28	43.7
Mid-Winter (Dec.16-Jan.31)	15	44.3	20	21.8
Breeding Season (Feb.1-Mar.4)	25	33.8	77	67.8
Late Winter (Mar.5-Mar.31)	-	-	40	54.0

Table 3.2. Mean snow depth and snow hardness (penetrometer sinking depth PSD) in 5 habitats on coyote trails snowtracked during 2 years in southwestern Yukon. Snow depth was measured during both years of study while snow hardness was recorded during Year 2 only.

	Snow Depth (cm)			Snow Hardness (cm)		
Habitat	Mean	+/- SD	(n)	Mean	+/- SD	(n)
Closed Spruce	46.4	16.1	(91)	6.6	4.1	(65)
Open Spruce	45.8	20.6	(156)	5.9	3.3	(109)
Deciduous	46.0	23.5	(33)	5.6	2.9	(20)
Shrub	48.5	23.2	(53)	5.7	2.7	(38)
Open	26.3	19.8	(33)	3.7	2.2	(26)

Table 3.3. Mean snow depth (cm) at high and low altitude sites of the study area during winter 1988-89 (Year 2).

	Low			High		
Habitat	Mean	+/- SD	(n)	Mean	+/- SD	(n)
Closed Spruce	35.1	12.3	(32)	57.6	13.0	(8)
Open Spruce	39.1	11.8	(16)	59.0	12.7	(24)
Deciduous	49.2	16.9	(8)	55.0	20.6	(8)
Shrub	49.7	13.7	(8)	58.7	10.4	(8)
Open	29.3	10.4	(8)	38.1	12.3	(8)

Table 3.4. Percent of transect crossings by coyote, lynx, red fox, wolverine, and wolf at high and low altitude levels of the study site.

	Year 1			Year 2		
Species	% Low	% High	n	% Low	% High	n
Coyote	78.4	21.6	74	64.4	35.6	104
Lynx	32.1	67.9	202	26.4	73.6	250
Red Fox	0	0	0	0	100	24
Wolverine	17.7	82.3	62	30.8	69.2	26
Wolf	62.5	37.5	8	50.0	50.0	8

Table 3.5. Rates at which coyotes chased hares in 3 habitats over two years of snowtracking in southwestern Yukon. Sample sizes are given in parentheses.

		Chases (n/km)		
Year	km	Closed Sp.	Open Sp.	Other
87	79.5	.09 (3)	.35 (10)	.17 (3)
88	187.7	.36 (16)	.25 (25)	.09 (4)

Table 3.6. Coyote success rates on snowshoe hare in relation to 3 habitat types. Sample sizes are given in parentheses.

Year	Closed Sp.	Open Sp.	Other
87	.33 (3)	.40 (10)	.33 (3)
88	.81 (16)	.40 (25)	.50 (4)

Table 3.7. Mean number of bounds taken in coyote chases of hare in 3 habitat types. Sample sizes are given in parentheses.

Chase Type	Closed Sp. Mean	+/- SD		Open Sp. Mean	+/- SD		Other Mean	+/- SD	
Kill	0.6	1.0	(14)	0.9	1.6	(14)	0.3	0.6	(3)
Attempt	3.6	1.5	(5)	4.2	2.7	(22)	5.0	2.0	(3)

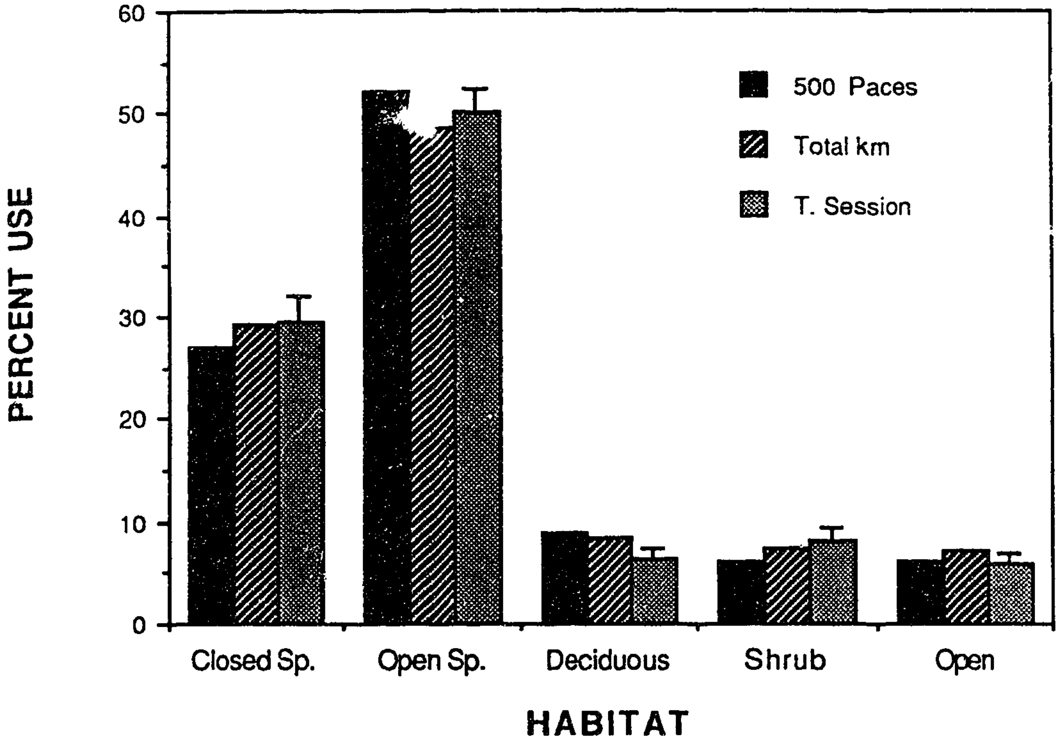

Figure 3.1 Use of habitats by coyotes snowtracked for two winters in southwestern Yukon, as determined by total km tracked, 500 randomly selected paces, and tracking session averages.

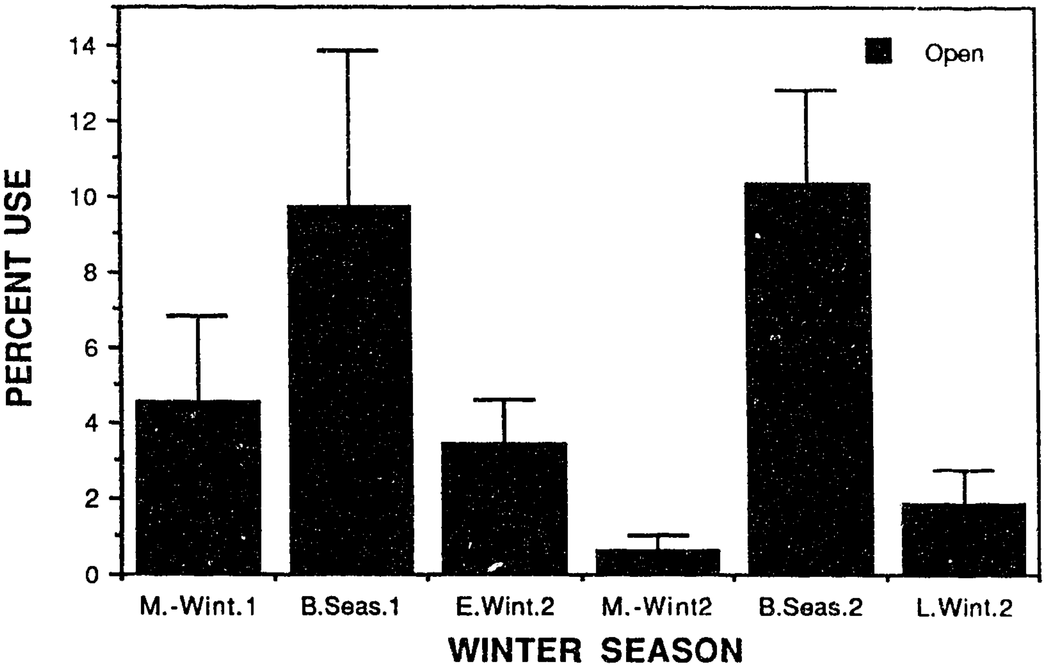

Figure 3.2 Use of open habitat over winter seasons by coyotes in southwestern Yukon. Vertical bars indicate standard errors.

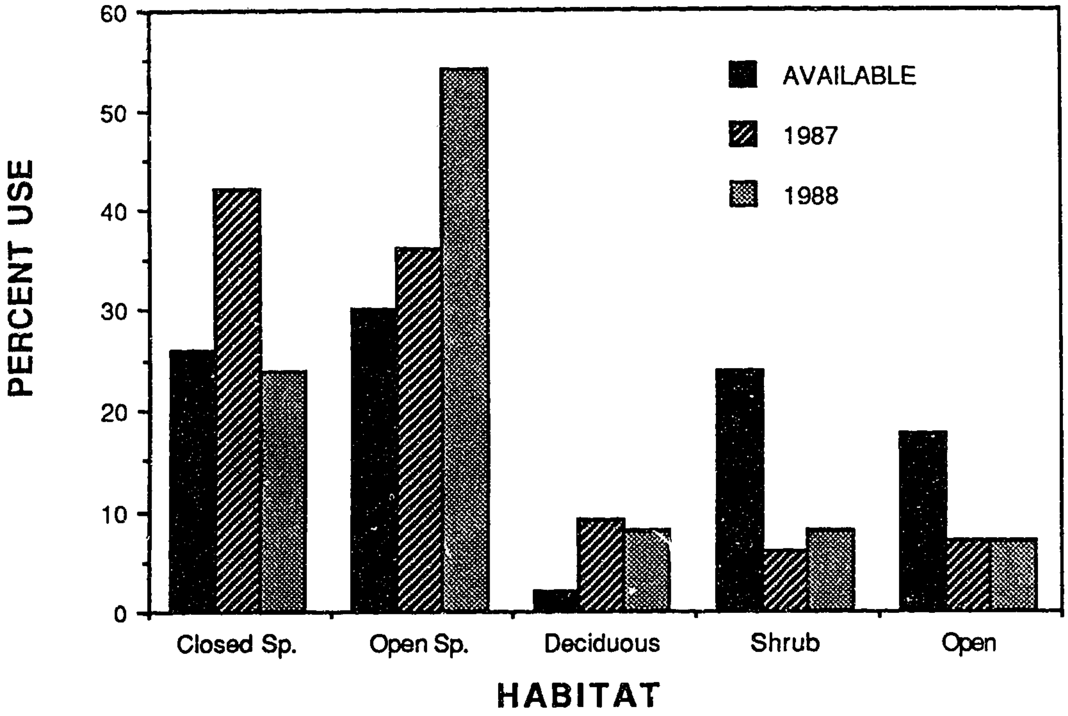

Figure 3.3. Habitat use of coyotes snowtracked over two winters in southwestern Yukon, from 500 randomly selected paces.

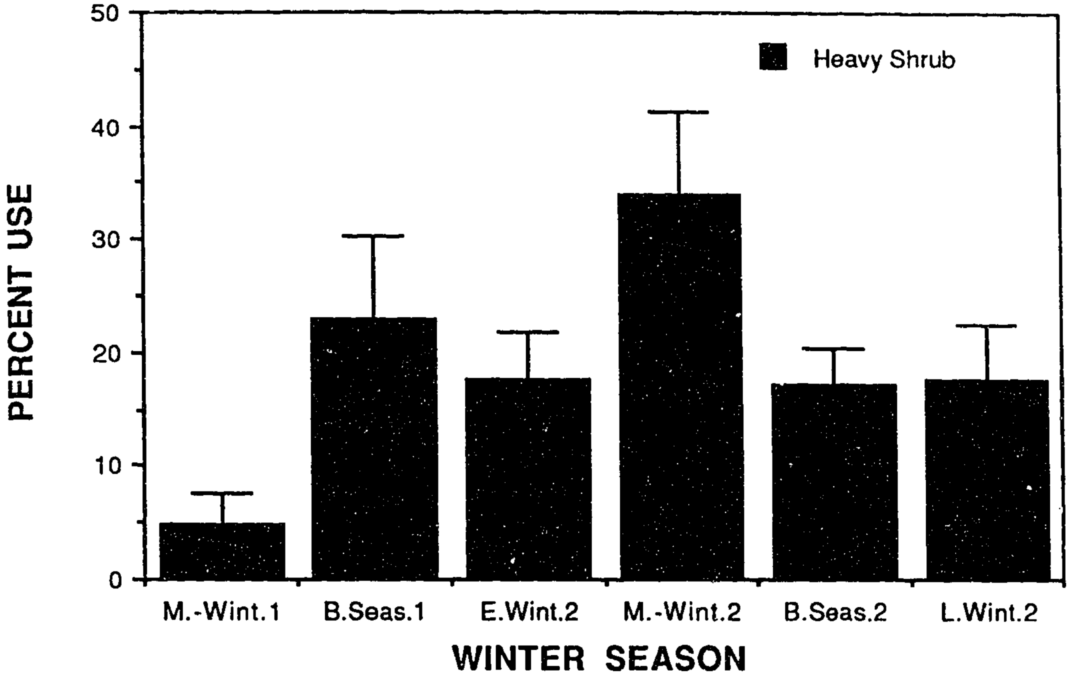

Figure 3.4. Use of heavy shrub cover by coyotes, during two winters in southwestern Yukon. Vertical bars indicate standard errors.

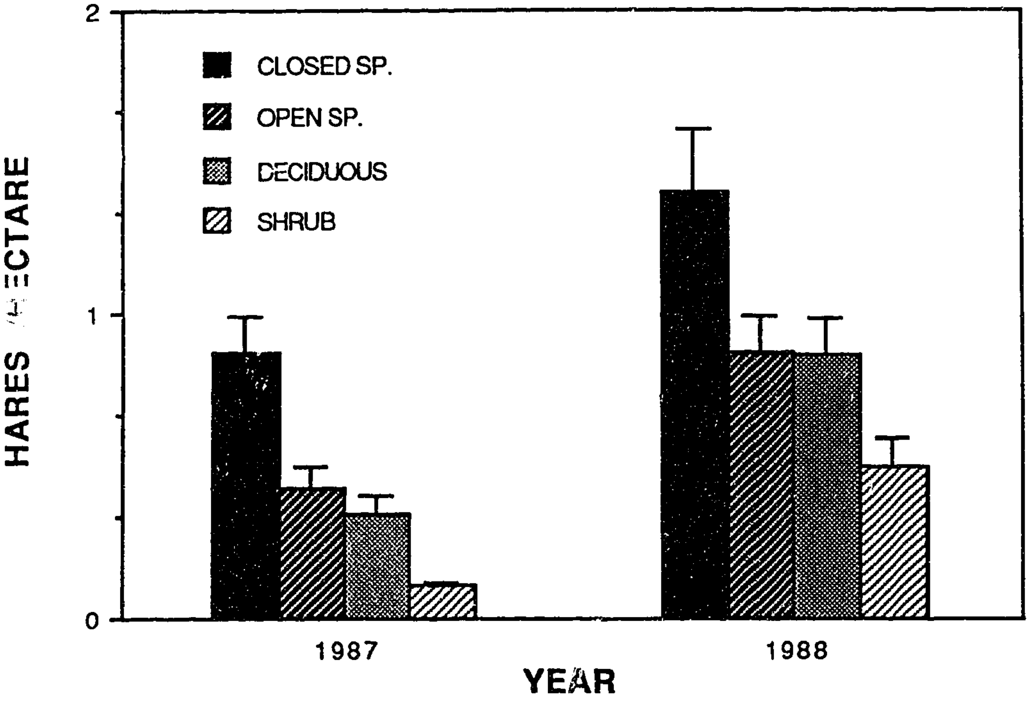

Figure 3.5. Snowshoe hare densities in four habitat types during two years in southwestern Yukon. Vertical bars indicate standard errors.

REFERENCES

Aldredge J.R., and Ratti, J.T. 1986. Comparison of some statistical techniques for analysis of resource selection. J. Wild. Manage. 50:157-165.

Bakker, R.T. 1983. The deer flees, the wolf pursues: Incongruities in predator- prey coevolution. In: Futuyama, D.J., and Slatkin M. (eds.), Coevolution. Sinauer Assoc. Inc. Sungerland, Mass. pp. 350-382.

Douglas, G.W. 1974. Mountain zone vegetation of the Alsek River region, southwestern Yukon. Can. J. Bot. 52:2505-2532.

Fuller, T.K., and Keith, L.B. 1981. Non-overlapping ranges of coyotes and wolves in northeastern Alberta. J. Mammal. 62:403-405.

Gier, H.T. 1975. Ecology and behavior of the coyote (<u>Canis latrans</u>). In: Fox, M. (ed.), The wild canids. R.E. Krieger Publ. Co. Inc., Malabar, Fl. pp. 247-262.

Halpin, M.A., and Bissonette, J.A. 1988. Influence of snow depth on prey availability and habitat use by red fox. Can. J. Zool. 66:587-592.

Harrison, D.J., Bissonette, J.A., and Sherburne, J.A. 1989. Spatial relationships between coyotes and red foxes in eastern Maine. J. Wildl. Manage. 53:181-185.

Henry, J.D. 1979. The urine marking behavior and movement patterns of red foxes during a breeding and post-breeding period. In: Muller-Schwarze, D., and Silverstein, R.M. (eds.), Chemical signals in vertebrates and aquatic animals. Symp. Chem. Signals in Vert. and Aquatic Anim. State University of New York, Syracuse. Plenum Press, N.Y. pp. 11-27.

Kleiman, D.G., and Eisenberg, J.F. 1973. Comparisons of canid and felid social systems from an evolutionary perspective. Anim. Behav. 21:637-659.

Krebs, C.J. 1989. Ecological methodology. Harper & Row, NY. 654 pp.

Krebs, C.J., Gilbert, B.S., Boutin, S., Sinclair, A.R.E., and Smith, J.N.M. 1986. Population biology of snowshoe hares. I. Demography of food-supplemented populations in the southern Yukon, 1976-84. J. Anim. Ecol. 55:963-982.

Krebs, C.J., Gilbert, B.S., Boutin, S., and Boonstra, R. 1987. Estimation of snowshoe hare population density from turd transects. Can. J. Zool. 65:565-567.

Kruuk, H. 1986. Interactions between felidae and their prey species: a review. In: Miller, S.O., and Everett, D.D. (eds.), Cats of the world: ecology, conservation and management. Nat. Wildl. Fed., Washington, D.C. pp. 353-374.

Kruuk, H., Wansink, D., and Moorhouse, A. 1990. Feeding patches and diving success of otters, Lutra lutra, in Shetland. Oikos 57:68-72.

Litvaitis, J.A. 1989. Habitat use by snowshoe hare Lepus americanus in relation to pelage color. Unpubl. man. 7 pp.

Litvaitis, J.A., and Harrison, D.J. 1989. Bobcat-coyote niche relationships during a period of coyote population increase. Can. J. Zool. 67:1180-1188.

Litvaitis, J.A., Sherburne, J.A., and Bissonette, J.A. 1985. Influence of understory characteristics on snowshoe hare habitat use and density. J. Wild. Manage. 49:866-873.

Major, J.T., and Sherburne, J.A. 1987. Interspecific relationships of coyotes, bobcats, and red foxes in western Maine. J. Wildl. Manage. 51:606-616.

Mckinlay, L.S. 1990. Scent marking and use of space by coyotes in a mixed forest region of Manitoba. M.Sc. thesis, University of Alberta, Edmonton. 114 pp.

Neu, C.W., Byers, C.R., and Peek, J.M. 1974. A technique for analysis of utilization-availability data. J.

Wildl. Manage. 38:541-545.

Nowak, R.M. 1979. North American quaternary Canis. Museum of Nat. Hist., University of Kansas, No. 6. pp. 154.

Ozoga, J.J., and Harger, E.M. 1966. Winter activities and feeding habits of northern Michigan coyotes. J.Wildl. Manage. 30:809-818.

Parker, G.R. 1981. Winter habitat use and hunting activities of lynx (Lynx canadensis) on Cape Breton Island, Nova Scotia. In: Chapman, J.A., and Pursely, D. (eds.), Proc. World. Furb. Conf., Frostburg, Md. (1980). pp. 221-248.

Pietz, P.J., and Tester, J.R. 1983. Habitat selection by snowshoe hares in north-central Minnesota. J. Wildl. Manage. 47:686-696.

Pyke, G.H. 1984. Optimal foraging theory: a critical review. Ann. Rev. Ecol. Syst. 15:523-575.

Sargent, A.B., Allen, S.H., and Hastings, J.O. 1987. Spatial relations between sympatric coyotes and red foxes in North Dakota. J. Wildl. Manage. 51:285-293.

Sokal, R.R., and Rohlf, F.J. 1980. Biometry. W.H. Freeman & co. New York, NY. pp. 859.

Stephens, D.W., and Krebs, J.R. 1986. Foraging Theory. Princeton Univ. Press. Princeton, N.J. pp. 247.

Taylor, M.E. 1989. Locomotor adaptations by carnivores. In: Gittleman, J.L (ed.), Carnivore behavior, ecology, and evolution. Cornell Univ. Press, Ithaca, N.Y. pp. 382-409.

Theberge, J.B., and Wedeles, C.H.R. 1989. Prey selection and habitat partitioning in sympatric coyote and fox populations, southwest Yukon. Can. J. Zool. 67:1285:1290.

Todd, A.W., and Keith, L.B. 1976. Responses of coyotes to winter reductions in agricultural carrion. Alta. Wildl.

Tech. Bull. No. 5. 32 pp.

Todd, A.W., Keith L.B., and Fischer, C.A. 1981. Population ecology of coyotes during a fluctuation of snowshoe hares. J. Wildl. Manage. 45:629-640.

Toweill, D.E. 1986. Resource partitioning by bobcats and coyotes in a coniferous forest. Ph.D. thesis, Oregon State University, Corvalis, Or. pp. 155.

Voigt, D.R., and Earle, B.D. 1983. Avoidance of coyotes by red fox families. J. Wildl. Manage. 53:852-857.

Voigt, D.R., and Berg, W.E. 1987. Coyote. In: Novak, M., Baker, J.A., Obbard, M.E., and Malloch, B. (eds.), Wild furbearer management and conservation in North America. Ont. Min. Nat. Res., Toronto, Ont. pp. 345-356.

Wells, M.C., and Lehner, P.N. 1978. The relative importance of the distance senses in coyote predatory behavior. Anim. Behav. 26:251-258.

Werner, E.E., and Hall, D.J. 1977. Competition and habitat shift in two sunfishes Centrarchidae. Ecology 58:869-876.

Werner, E.E., and Hall, D.J. 1979. Foraging efficiency and habitat switching in competing sunfishes. Ecology 60: 1256-264.

Werner, E.E., Gillam, J.F., Hall, D.J., and Mittlebach, G.G. 1983. An experimental test of the effects of predation risk on habitat selection in fish. Ecology 64:1540-1548.

Witmer, G.W., and deCalesta, D.S. 1986. Resource use by unexploited sympatric bobcats and coyotes in Oregon. Can. J. Zool. 64:2333-2338.

CHAPTER 4

FACTORS AFFECTING WINTER HABITAT USE BY LYNX IN SOUTHWESTERN YUKON.

INTRODUCTION

Search and acquisition of prey, by carnivores, are activities which ultimately influence survival. All felids rely on physical characteristics of the environment in their approach to prey, and though habitat selection is an important component of the relationship between predator and prey, few studies have quantified the effects of habitat, on predation and hunting success (Sunquist and Sunquist 1989).

Lynx are thought to specialize on snowshoe hare as a source of food, and good hare habitat is generally thought to be synonymous with good lynx habitat (Quinn and Parker 1987). Though lynx habitat use has been described previously (Koehler et al. 1979; Parker 1981; Parker et al. 1983; Koehler 1990), including in the Yukon (Major 1989), lynx habitat requirements are still poorly understood (Quinn and Parker 1987).

Lynx have long been present in the boreal forest of North America (Quinn and Parker 1987), and their morphology is well adapted for travel in snow (Parker et al. 1983). Though they select regions and areas of deep snow, they also facilitate their winter movements by using trails (Chapter 1); however it is not known if snow conditions affect their use of habitat.

Given the paucity of information on the factors governing habitat use in lynx, I undertook this study to examine the influence of the following factors a) habitat availability, b) snow conditions, c) presence of other predators, d) food availability, and e) prey vulnerability, on their winter habitat use. A second objective of the study was to compare habitat use patterns of lynx to those observed in a sympatric population of coyotes (_Canis latrans_), described in Chapter 3.

STUDY AREA

Lynx were studied during 2 winters in a 175 km^2 study site in the Kluane Lake area of southwestern Yukon (61°N 138°W) previously described in detail (Chapter 1). The study site was located in a broad east-west valley within the boreal forest zone (Douglas 1974), where white spruce (_Picea glauca_) was the dominant tree. A strong altitudinal gradient existed in the study site, and I worked from the base of the valley (830 m) to an altitude of 1169 m, which was near the base of the mountains. The altitude of the valley floor also differed with the central area, being up to 215 meters higher than that of either end. Altitude was inversely related to canopy cover, and though spruce cover ranged from 0 to 100%, most areas in the valley had between 25 and 75% cover. Other winter habitat types available to predators included deciduous (_Populus_ _sp_.) forests, shrub (_Salix_ _sp_. and _Betula_ _sp_.), and open areas. Snowfall was directly related to altitude in the study site, and total snow accumulation for both years of study averaged 65 cm, which was average for that region (Krebs et al. 1986). I estimated that there were at least 10 lynx in the study area during winter 1987-88 (Year 1), based on track transects and known locations of radiocollared animals. Sixteen lynx were thought to be present during winter 1988-1989 (Year 2). Other, less abundant terrestrial predators in the study site included coyote (Chapter 3), red fox (Vulpes vulpes), wolverine (Gulo gulo), and wolf (C. lupus).

METHODS

Habitat Availability

The availability of the five predominant habitat types within the study area was estimated using LANDSAT imagery. To measure the similarity of the LANDSAT system and the habitat classification system that was used while I tracked predators, I groundtruthed LANDSAT with the tracking method. The LANDSAT system was refined once, after which both methods classified habitats similarly.

Lynx Snowtracking

Lynx were snowtracked during both years for a total of 378 km. Tracking was undertaken daily after snowfall, and continued until fresh tracks could no longer be differentiated from older trails (usually 7-10 days). Frequent snowfall permitted me to track lynx between

December and March during Year 1 and between November and March during Year 2, with no inactive period longer than 8 days. Tracks were usually encountered along a network of snowmobile trails within the study area, though on occasion I trailed tracks crossing the Alaska Highway, which bisects the study area. I tried to spread tracking sessions throughout the study area, by rarely initiating track searches from the same point of departure on consecutive days, and by choosing tracks to be followed from all parts of the study site. Tracks were either backtracked or, if estimated as being older than 24 hrs, forward tracked. If the animal being tracked was disturbed, the session was immediately ended; however more commonly a track was followed until it was either lost, or light levels and/or snow conditions made it difficult to read. Distances tracked were obtained by counting steps with a hand counter and converting to kilometers (Parker 1981). The estimate was truthed on several occasions by counting the number of paces taken to traverse a known distance.

Habitat types encountered while tracking were recorded according to a 4 point classification system which estimated percent canopy cover in blocks of 50%, predominant canopy species, percent understory cover (in blocks of 25%), and predominant understory species. I recorded habitat changes on lynx trails as they were encountered, however habitat types that I estimated were used for less than 10 consecutive meters of the predator trail were not recorded.

Snow Conditions

The method used to obtain snow measurements on lynx tracks and in the study site has previously been described in detail (Chapter 1). Snow depth was measured at the beginning, at the end, and every 500 paces (approx. 600 meters) during both years of study. Snow hardness was measured in Year 2 by the sinking depth of a penetrometer (PSD), at the same locations where snow depth measurements were taken. Habitat type was noted at each site where snow measurements were taken. General snow conditions in the study area were measured at 16 sites in all habitat types along the network of snowmobile trails. At each site 4 measures of snow depth and snow hardness were taken, and averaged. The sites were visited 8 times between November and March of Year 2.

Use of Altitude Levels by Lynx and Other Predators

I documented regions of the study area used by lynx and other predators by snowmobiling along a network of trails which bisected the study area and recording all predator crossings. For analysis, the study area was divided into high and low altitude regions (Chapter 1); at each location where a predator track crossed the trail, species and location were noted. Tracks were noted along the transect for the first 4 to 6 days after snowfall, and an average of 30 km of trails were checked each day for predator tracks. Track crossings were recorded between

November and April of both years.

Prey Availability

Snowshoe hare densities within major habitats of the study site were estimated by counting all fresh (less than 1 year old) hare turds along 480 transects, during June 1987 and June 1988, and extrapolating numbers of hare turds collected to an estimate of the number of hares per hectare (see Krebs et al. 1987). Though we placed transects within the major habitat types available in the study area, no turd transects were present in completely open areas. Hares tend to avoid open habitats (Pietz and Tester 1983), and turds are rarely observed in such locations; therefore I assumed that hare density was zero in that habitat type. The number of transects placed within each other habitat type was roughly proportional to its availability in the study area.

Prey items other than hare were less important in the diet of lynx during both years of study (Chapter 2). Therefore the relative abundance of these species with respect to habitat type was not examined. Relative abundance of scavengeable food items was estimated by recording habitats in which lynx scavenged food while I tracked them. However scavenging is less common in felids than in canids (Kleiman and Eisenberg 1973), and I found that lynx that I tracked scavenged about 3 times less often per distance, than did coyotes which cohabited the same study area (Chapter 2). Therefore lynx clearly did not scavenge at all food items that were available to them, and habitat in which scavenging occurred did not necessarily correspond to availability of all scavengeable food items.

Hare Vulnerability

Hare vulnerability in a habitat was defined as the percent of lynx chases at hare within that habitat that resulted in a kill. However this definition only assessed hare vulnerability once a chase had been initiated, and may have excluded lynx encounters with hare that did not result in a chase. Lynx chases at prey were recorded as they were encountered during a snowtracking session, and at these sites I recorded species chased, number of bounds in the chase, and chase outcome (kill or attempt), while also observing standard habitat characteristics of the site.

Statistical Analyses

I used criteria outlined by Aldredge and Ratti (1986) to determine which analysis method was appropriate for most of the resource use-availability data; as the number of habitats was small (5), observations were numerous, and observations were independent (see below), the method proposed by Neu et al. (1974) was selected, though a G-test with Williams' correction (Sokal and Rohlf 1981) was used rather than a Chi-square. Probabilities less than .05 were considered significant, and proportional data were transformed prior to analysis, using the arcsin of the square root (Krebs 1989).

The way in which the snowtracking data were collected may have violated the assumption of independence which is implicit to both G-test and ANOVA. I therefore analysed habitat use data in 3 ways: a) randomly selecting 500 tracking paces for each year (out of 140833 for Year 1 (=.4%), and 173500 in Year 2 (=.3%)), and subjecting these to a G-test (this method maximized independence between observations), b) using total kilometers tracked in each habitat in a G-test (minimum independence), and c) using tracking sessions as experimental units, calculating proportional use of each habitat per session, and subjecting each habitat to a seperate ANOVA (independence between sessions but dependence within sessions). The proportional use of habitat types as determined by each analysis method is given (Figure 4.1). All values are similar, which suggests that the 3 methods are representative of the overall habitat use patterns that I observed.

Effect of Session Length

Length of lynx tracking sessions varied from .04 to 10.9 km and I was concerned that tracks of differing lengths may not produce similar interpretations when subjected to ANOVA. Therefore I divided sessions into 3 groups: less than 1 km, between 1 and 3 km, and greater than 3 km, and performed a one-way ANOVA for each of the 5 habitat types by session length groups. The analysis showed no effect on the frequency of use of any habitat types (lowest P value was in Open habitat, where F=1.90;

df=2,203; P=.152). A G-test on total kilometers tracked, also did not indicate any significant length effect (G=2.6993; df=8; P<.975). Thus tracking sessions of all lengths were treated equally.

Effects of Winter Season

Winters were divided into 4 seasons: Early Winter (Nov. 1 - Dec. 14), Mid-Winter (Dec. 15 - Jan. 31), Breeding Season (Feb. 1 - Mar. 5), and Late Winter (Mar. 6 - Mar. 31). Winter seasons in which lynx were tracked were not identical between years (Table 4.1), and this could have confounded some of my results. Therefore I examined the effect of winter season on habitat use by subjecting km tracked in each habitat to a G-test. Results indicated no differences between seasons (Year 1:G=4.6548; df=8; P<.90; Year 2:G=6.3351; df=12; P<.90). I also performed an ANOVA on habitat use during winter seasons for each year, and found that lynx use of all habitats between seasons was similar in Year 1 (lowest P value was in Deciduous, where F=1.19; df=2,54; P=.312), and Year 2 (lowest P value was in Closed Spruce, where F=2.24; df=3,145; P=086). Therefore seasonal effects on lynx movements did not appear to be great, and all winter seasons were pooled when I analysed for yearly shifts in habitat use.

RESULTS

Habitat Selection

Lynx did not use habitats according to relative availability in either year of the study (Year 1: G=34[illegible].1

(n=500); df=4; P<.001; Year 2: G=428.7 (n=500); df=1; P<.001). Strong selection for Open Spruce (cover < 50%) occurred in both years of study (Figure 4.2). Deciduous habitat was used slightly more than its availability in both years, however lynx only travelled short distances in that habitat (Year 1: 4%; Year 2: 6%). Shrub and Open areas were strongly avoided during both years.

Changes Between Years

I next analysed habitat use between years to determine if yearly effects existed in the patterns that I observed. Though a slight increase in the use of Open Spruce occurred in Year 2, at the expense of use of Closed Spruce, (Figure 4.2), a G-test did not detect a dependence of habitat selection on year (G=9.1690; df=4; n=500; P<.10). The same result was obtained for a one-way ANOVA on each habitat type (lowest P value was in Shrub habitat, where F=1.59; df=1,204; P=.209).

Use of Understory

I examined the use of areas where understory availability was high (shrub cover > 75% ground cover) by lynx, independently of canopy cover. Both tests detected a higher use of heavy shrub cover in Year 2 (G-test: G=12.376; df=1; P<.001; ANOVA: year: 7.24; df=1,199; P=.008; winter season: F=2.25; df=3,199; P=.084). Overall use of thick shrub areas was (mean +/- SD) 9.3 +/- 18.4% (n=57) in Year 1 and 23.4 +/- 31.2% (n=149) in Year 2.

Snow Conditions

There was no difference in snow depth on lynx tracks between different habitats (F=2.15; df=4,291; P=.075), altitude levels (F=1.91; df=1,291; P=.168), or years (F=1.91; df=1,291; P=.168; Table 4.2). I detected an interaction term between habitat and altitude levels, in my analysis of snow depth in the study area (at the snow sites) (ANOVA; snow: F=6.01; df=4,118; P<.001; altitude levels: F=13.49; df=1,118; P<.001; habitat by altitude level interaction: F=4.69; df=4,118; P=.002). This result suggests that snow accumulation rates differed between habitats at different altitudes, and I found that overall snow accumulation to be greater at the high altitude level of the study area (Chapter 1). Snow depth was shallower in most habitats at low altitudes, and Closed Spruce and Open habitats usually had shallower snow than other habitats (Table 4.2).

Snow hardness on lynx trails in Year 2 by habitat type and altitude level was not influenced by habitat (ANOVA: F=1.23; df=4,190; P=.299), or altitude (F=.58; df=1,190; P=.446). Similarly, snow hardness in the study site (at the snow sites) was similar between habitats (F=.13; df=4,118; P=.972; Table 4.2), and altitude levels (F=2.81; df=1,118; P=.096; Figure 1.4).

Use of Altitudes by Lynx and Other Predators

I examined the distribution of predator tracks with respect to altitude. Most lynx crossings occurred at the high altitude level of the study site during both years (G=1.799; df=1; P<.05), and tracks of red fox and wolverine were also more common at the high altitude level (Table 3.4). Coyote crossings were more abundant at the low altitude level, as were those of wolf in Year 1. Wolf crossings during both years were few, and the presence of wolves in the study site was rare and sporadic (pers. obs.). Based on these results the potential effects of red fox and/or wolverines on habitat use of lynx was greatest at the high altitude level, while the influence of coyotes on lynx habitat use was greatest at the low altitude level.

Habitat use of lynx was similar at both altitude levels. Both a G-test on km tracked in each habitat type at both levels (G=1.6253; df=4; P<.90), and a one-way ANOVA on each habitat encountered while tracking lynx at high and low levels indicated that all habitats were encountered at similar rates between levels. Lowest probability for ANOVA was in Open Spruce (F=2.18; df=1,203; P=.116). Therefore lynx use habitats in similar proportions at both altitude levels of the study site, and there seems to be little effect of the presence of other species of predators on lynx habitat use patterns that I recorded.

Hare Density

Hare turds were most abundant in Closed Spruce forest, and this difference translated into a significantly higher number of hares per hectare in this habitat type over all others (Figure 3.5). Open Spruce and Deciduous habitats were second, with roughly the same number of hares per area, while Shrub was third. Relative number of hare turds present in each habitat type was similar between Year 1 and Year 2, however a doubling in the number of hares per hectare occurred in Year 2. As a result, overall hare densities which were estimated at .39 +/- .05 hares/hectare (mean +/- SD) in Year 1, were at .77 +/- .11 hares/hectare in Year 2.

Rate of Lynx Chases of Hare

The rate at which lynx chased hares in various habitats during both years of study did not closely reflect the increase in hares in all habitats in Year 2, nor the relative number of hares present in different habitat types. Rates were similar in all habitats in Year 1, and only chase rates in Open Spruce increased with time (Table 4.3). However distribution of attempts among habitats did not differ between years (G=5.80; df=2; P<.10).

Kill-rates in different habitats did not closely reflect either the relative abundance of hares in different habitats, or the doubling in hare densities observed in Year 2. Hare kill-rate (kills/km) in Year 1 was .13 (n=7 kills) in Closed Spruce, .10 (n=10) in Open Spruce, and .06 (n=1) in Other habitats. In Year 2, rates in Closed Spruce decreased (.11; n=5), while rates in Open Spruce (.18; n=24) and Other habitats (.16; n=4) increased. The distribution of kills among the three habitat types did not change between years (G=3.441; df=2; P<.50). The percentage of hare kills that occurred in thick understory areas was 15.7% (n=53 total kills), which was between values obtained for use of dense shrub areas in Year 1 and Year 2.

Scavenging Rates

A total of 25 sites where lynx scavenged food were encountered while snowtracking. The proportion of scavenges occurring in Closed Spruce, Open Spruce, and Other habitats did not change between years (G=2.7596; df=2; P<.50). However scavenges in Closed Spruce rose from the lowest to the highest proportion, in Year 2. In Year 1, the number of scavenges encountered per kilometer trailed was 0 in Closed Spruce, .04 in Open Spruce (n=4), and .07 (n=1) in Other habitats. In Year 2 rates were highest in Closed Spruce (.13; n=6), followed by Open Spruce (.10; n=14) and Other habitats (.04; n=1). Most scavenges in both years were of snowshoe hare remains: 80.0% (n=5) in Year 1, and 95.2% (n=21) in Year 2. However scavenging rates within each habitat type were not closely related to hare densities there in Year 1, while Year 2 values are more similar to those of relative abundance of hares.

Hare Vulnerability

Lynx made most of their hare kills in Open Spruce in both years (Table 4.4). Success rates in 2 of the 3 habitats increased with time, however this was mostly attributable to a higher proportion of family groups in the

Year 2 cohort, and the higher hunting success (though not significant) of family groups (Chapter 2). If results for both years are pooled, overall success rate for lynx was 35.3% (n=34 kills) in Closed Spruce, 34.3% (n=99) in Open Spruce, and 38.5% (n=13) in Other habitats, and these differences are not significant (G=.0847; df=2; P<.50). The percentage of hare kills occurring in thick understory cover areas was 19.6% (n=51) at kills, while 13.7% (n=95) of attempts occurred in thick shrub areas. Though these differences are not significant (G=.843; df=1; P<.50), the percentage of kills in areas of thick understory cover is almost identical to the average use of high shrub areas by lynx.

The number of bounds in lynx chases was not influenced by habitat (F=.26; df=2,141; P=.767), though differences in the number of bounds at kills and attempts were detected (F=34.36; df=1,141; P<.001; Table 4.5). The average number of bounds for both years was 1.8 +/- 2.2 (n=51) at lynx kills and 6.3 +/- 4.4 (n=95) at attempts.

DISCUSSION

Habitat Selection of Lynx

Lynx did not use habitats according to their availability, but strongly selected Open Spruce forests in both years of study, and avoided Shrub and Open areas. I found that lynx spent over 85% of the distance that they were tracked in various types of coniferous forest, which is similar to results from other studies (Parker 1981;

Koehler 1990).

Snow Conditions

If habitat use of lynx was affected by snow conditions, I would have expected lynx to select habitats where either snow depth and/or snow hardness were favorable for their movements. However snow conditions appeared most favorable in Open habitats, but I found that habitat to be strongly avoided at all times, perhaps because of the lack of food therein. Lynx have a morphology that is well equipped to deal with unfavorable snow conditions (Parker et al. 1983), and though they use regions and areas where deep snow is present, they also utilize travel routes of shallow and hard snow (Chapter 1). Snow conditions on lynx tracks were found to be similar in all habitats, and in general deeper than on average in the study site. This result suggests that lynx actively selected areas within habitats where snow depths were similar (deeper than average), but this phenomenon may not have directly influenced the habitat use patterns of lynx in the Yukon. Lynx use of deep snow areas within all habitat types may be due to higher hare density, higher hare vulnerability, or avoidance of other predators (Chapter 1) in those areas.

Use of Altitude Levels by Lynx and Other Predators

A shifting of habitat use patterns as a direct result of interspecific competition has been demonstrated in fish (Werner and Hall 1977), and speculated upon in carnivores (Major and Sherburne 1987; Litvaitis and Harrison 1989;

Theberges and Wedeles 1989). There was no shift apparent in this study. If the presence of other species affected habitat use of lynx, I would have expected to observe different patterns between altitude levels. The fact that habitat use was similar between both levels suggests that neither the higher presence of coyotes at low altitudes, or of lynx and red fox at high altitudes affect habitat use by the lynx that I studied. The higher frequency of lynx trails at high altitudes suggests that lynx do not actively avoid regions of the study site where red fox and wolverine are present. Lynx may avoid regions where coyotes are present (Chapter 1) as the lack of lynx tracks at low altitudes may have been the result of lynx avoidance of coyote inhabited areas. Given the similarity in habitat use at both levels, lynx avoidance of coyotes may occur at the regional scale rather than at the habitat level. However I did not estimate habitat availability between both altitude levels, and if availability of habitats was different, it is possible that, though use was similar, selection was different between levels, and that this may have been influenced by a lower number of coyotes in one of the two regions.

Though lynx appear to avoid predator trails (Chapter 1), they do not shift habitats in different areas of interspecific competitors. However it is possible that the number of potential interspecific competitors in the study site was too low to cause lynx habitat use to shift.

Hare Density

Hares were more abundant in Closed Spruce, and relative hare numbers varied directly with cover density of the four habitat groups that were examined. Visibility in Closed Spruce is inferior to that in all other habitat types, and hares have been shown to select areas of highest cover during winter, partly by virtue of the greater concealment from predators provided by those areas (Litvaitis et al. 1985). Consequently heterogeneous distribution of hares in the study area may be at least partly related to potential predator detection in each habitat type. Hare is the primary food of lynx in southwestern Yukon (Major 1989; Chapter 2). If hare availability had a strong effect on habitat selection of lynx, I would have expected to observe selection of Closed Spruce forests. Though previous studies have suggested that good hare habitat is synonymous with good lynx habitat (Parker 1981; Koehler 1990), I did not find that lynx selected the habitat in which hares were most abundant. Rather, the best hare habitat, Closed Spruce, was used roughly according to its availability in both years, while the habitat of moderate hare density (Open Spruce) was strongly selected during both years. The higher chase rate in Open Spruce forest during Year 2 suggests that lynx were perhaps more adept at detecting, or more prone to chase hares in that habitat, despite the lower relative hare densities therein. Though hare density does not directly affect habitat selection of lynx, it should be noted that lynx avoided Shrub and Open habitats, and these were the habitats where hare densities were lowest. Therefore low hare densities would seem to influence habitat avoidance rather than habitat selection.

Other Foods

Non-hare food items obtained strictly through predation were encountered only infrequently while tracking lynx (Chapter 2), and the presence of these did not appear to strongly affect habitat use of lynx that I tracked. Similarly, though lynx consumed a variety of small mammals, the importance of these in their diet was substantially less than hare (Chapter 2), and seemed not to have greatly affected lynx habitat use patterns.

Lynx were found to scavenge less frequently than coyotes in southwestern Yukon (Chapter 2), and the importance of scavenging in their diet does not appear to be major. Though scavenging rates increased in both spruce habitats during Year 2, use of those habitats was similar in both years. It is unlikely that the availability of scavengeable food items affected lynx habitat use in this study.

Hare Vulnerability

If habitat would have had an effect on hare vulnerability, once a chase had been initiated, I would have expected to observe a difference in lynx success rates between habitats. However success rates were similar in all habitats, suggesting that hare vulnerability to lynx predation is similar, and that this should not be an important factor in determining habitat use of Yukon lynx.

Hunting Tactics

All felids commonly use either an ambush or a stalking approach in predation (Leyhausen 1956a, cited in Turner and Meister 1989; Kruuk 1986). When the latter tactic is used by felids, vegetative cover usually allows for close approach to prey before a chase is initiated (Sunquist and Sunquist 1989). The presence of vegetation cover has been shown to be inversely related to length of the chase (Elliot et al. 1977), and directly related to success rates (Schaller 1972; Van Ordsdol 1984) in ungulate predation by large felids. Habitat has also been shown to be important in predation on snowshoe hare by smaller felids; bobcats (L. rufus) have been found to seek areas of highest cover when hunting hares (McCord 1974; Litvaitis et al. 1986; Knowles 1985), and Parker et al. (1983) attributed lynx success on hares to cover abundance.

Though I found that lynx typically use a stalking method to approach hares in my study, neither understory nor overstory level affected either success rates or the number of bounds in a lynx attempt at hare. The olfactory sense is less important in felids than in many other carnivores (Ewer 1973), and vision appears to be the primary sense used during hunting (Leyhausen 1956b cited in Kleiman and Eisenberg 1973). High use of Open Spruce forests by lynx may be related to a preference for areas where habitat composition (vegetation cover) is suitable for long distance facility in spotting prey. Hares may be difficult to detect in heavier canopy types, hence the lower chase rates with respect to relative density, therein. However it should be noted that differences in terms of length of chase and success rate were similar among cover types.

Differences Between Lynx and Coyotes

Chapter 2 examined factors that affected habitat selection of coyotes in the study area. When habitat use patterns of both species are compared, it is evident that both species share certain similarities; they select spruce habitats, and avoid shrub and open areas (Figures 3.3, 4.2). I found that both species used Closed Spruce (ANOVA of species by year; F=3.96; df=1,437; P=.047) less, and high understory areas more (F=6.24; df=1,437; P=.013) in Year 2 (ANOVA on Open Spruce; F=3.67; df=1,437; P=.056). However when I analysed each species individually I did not find a significant change over time. The use of thick understory areas was similar for both species.

Differences in patterns of habitat use of each species also exist, whereby lynx used Open Spruce more (ANOVA: F[illegible].68; df=1,437; P<.001), and Open areas less than coyotes. Coyotes altered habitat use patterns between years by switching to Open Spruce at the expense of Closed Spruce in Year 2, while an apparently similar habitat shift was not significant in lynx, with habitat use being essentially the same in both years. Habitat use by lynx and coyotes became more similar in Year 2.

Habitat use by both predators was not strongly affected by the presence of other species of predators, though lynx may have avoided areas where coyotes were present. Unlike coyotes, however, lynx seemed to select areas within habitats where snow conditions were deeper than on average.

In Year 2, lynx chased hares in Open Spruce forests more regularly than coyotes, whereas coyotes chased hares more frequently in Closed Spruce. Success rates in killing hares were similar for lynx in all habitats, whereas for coyotes this rate was highest in Closed Spruce. Coyotes had a higher foot-load than either lynx or snowshoe hare, and as lynx chases consist of more bounds than do those of coyotes, presumably lynx travel speeds and behavioral adaptations to snow can compensate for this difference between morphological adaptation to snow of prey and predator. This in turn may reduce the importance of vegetation cover on the approach of hares. This would enable lynx to kill hares in a variety of habitats, and after a short chase; while coyote morphology would restrict them to hunting hares in areas where they could use concealment as a tactic to approach hares and pounce on them at close range.

Table 4.1. Distribution of lynx tracking sessions over two years in southwestern Yukon. Distances are given in kilometers.

	Year 1		Year 2	
Period	No. of Sessions	Total Distance	No. of Sessions	Total Distance
Early Winter (Nov.1-Dec.14)	-	-	32	55.4
Mid-Winter (Dec.15-Jan.31)	28	105.8	23	43.0
Breeding Season (Feb.1-Mar.5)	22	51.7	55	54.5
Late Winter (Mar.6-Mar31)	7	11.3	59	54.2

Table 4.2. Mean snow depth and snow hardness (penetrometer sinking depth PSD) in 5 habitats on lynx trails snowtracked in southwestern Yukon. Snow depths are from both years of study, while snow hardness is from winter 1988-1989 (Year 2).

	Snow Depth (cm)			Snow Hardness (cm)		
Habitat	Mean	+/- SD	(n)	Mean	+/- SD	(n)
Closed Spruce	55.8	18.8	(79)	7.3	3.1	(54)
Open Spruce	60.2	20.3	(157)	6.9	3.1	(106)
Deciduous	50.5	20.9	(37)	6.2	2.9	(24)
Shrub	55.1	26.8	(32)	5.7	2.2	(14)
Open	38.8	31.5	(6)	4.0	4.2	(2)

Table 4.3. Rates at which lynx chased hares in 3 habitat types over two years of snowtracking. Sample sizes are given in parentheses.

		Chases (n/km)		
Year	km	Closed Sp.	Open Sp.	Other
87	169.0	.38 (20)	.35 (35)	.39 (6)
88	209.2	.30 (14)	.46 (64)	.28 (7)

Table 4.4. Proportion of lynx chases of hare that resulted in a kill, in relation to 3 habitat types. Total number of chases are given in parentheses.

Year	Closed Sp.	Open Sp.	Other
87	.35 (20)	.29 (35)	.17 (6)
88	.36 (14)	.38 (64)	.57 (7)

Table 4.5. Mean number of bounds taken by lynx while chasing hares in 3 habitat types. Sample sizes are given in parentheses.

Chase Type	Closed Sp. Mean +/- SD			Open Sp. Mean +/- SD			Other Mean +/- SD		
Kill	2.3	2.0	(12)	1.8	2.3	(35)	.8	1.5	(5)
Attempt	6.7	4.0	(21)	6.0	4.5	(66)	7.8	4.6	(8)

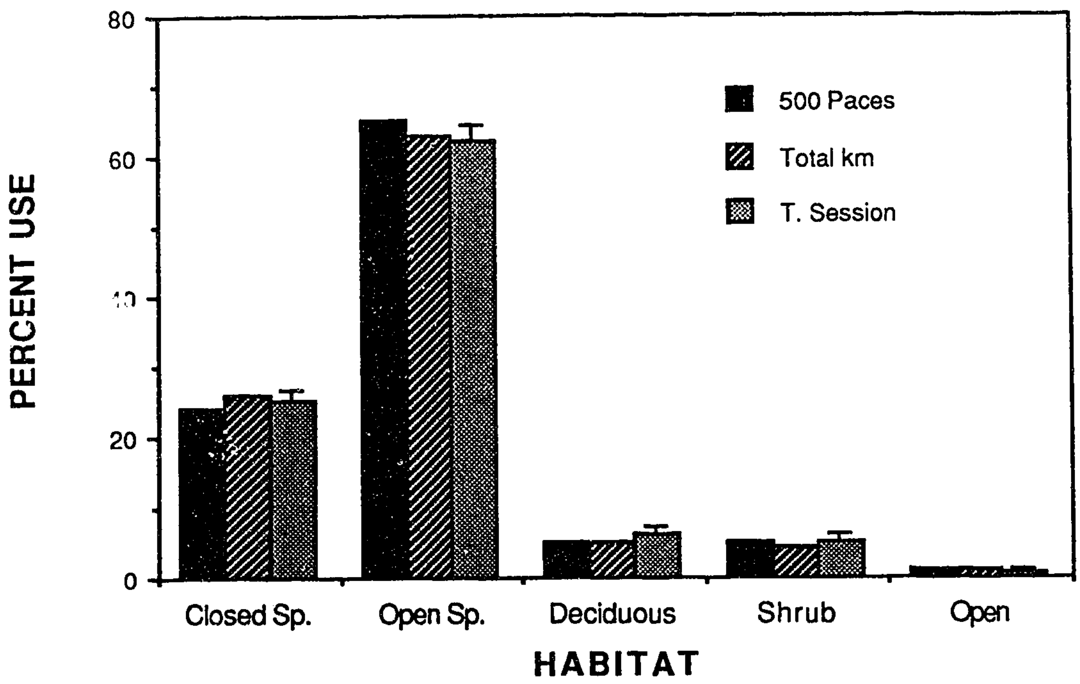

Figure 4.1 Use of habitats by lynx snowtracked for two winters in southwestern Yukon, as determined by total km tracked, 500 randomly selected paces, and tracking session averages. Vertical bars indicate standard errors.

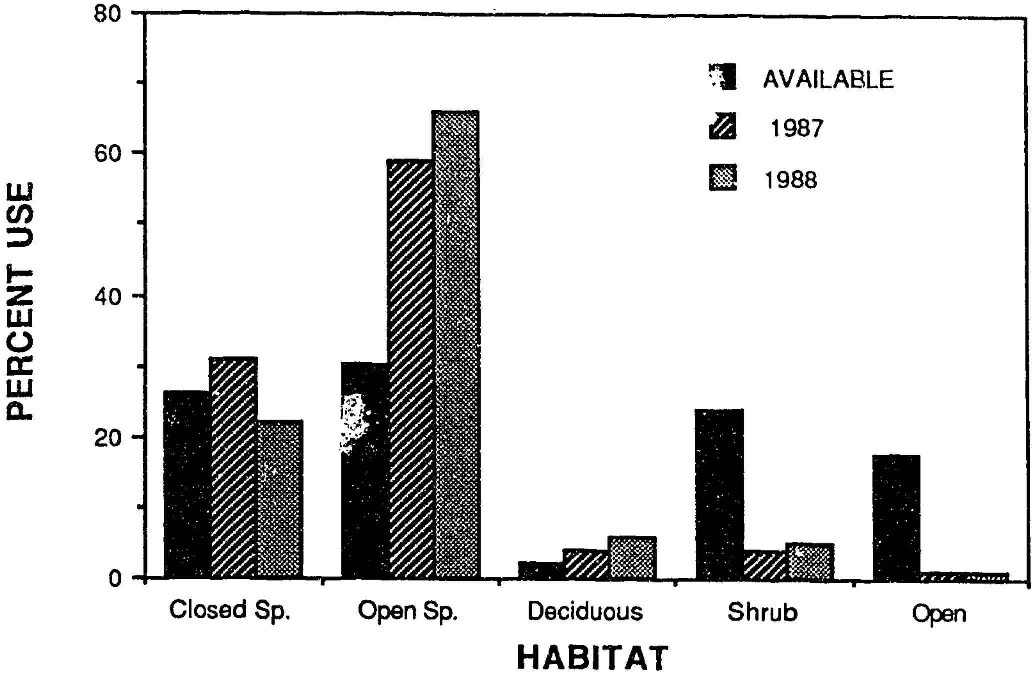

Figure 4.2. Habitat use of lynx snowtracked over two winters in southwestern Yukon, from 500 randomly selected paces.

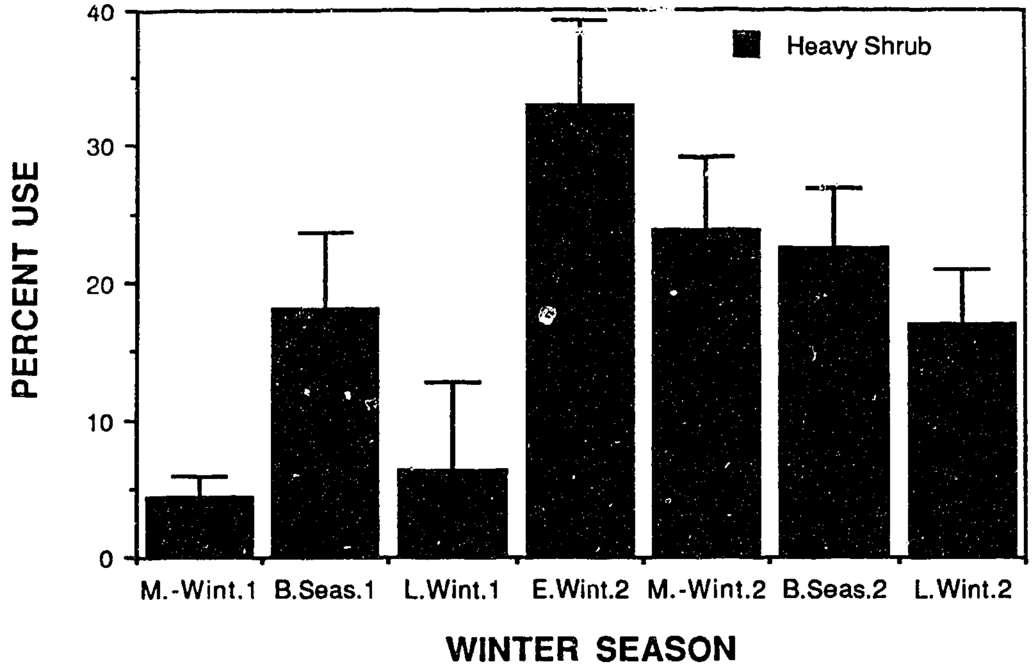

Figure 4.3. Use of heavy shrub cover by lynx during two winters in southwestern Yukon. Vertical bars indicate standard errors.

REFERENCES

Aldredge, J.R., and Ratti, J.T. 1986. Comparison of some statistical techniques for analysis of resource selection. J. Wild. Manage. 50:157-165.

Douglas, G.W. 1974. Mountain zone vegetation of the Alsek River region, southwestern Yukon. Can. J. Bot. 52:2505-2532.

Elliot, J.P., Cowan, I.M, and Holling, C.S. 1977. Prey capture in the African lion. Can J. Zool. 55:1811-1828.

Ewer, R.F. 1973. The carnivores. Cornell Univ. Press, Ithaca, N.Y. 494 pp.

Kleiman, D.G., and Eisenberg, J.F. 1973. Comparisons of canid and felid social systems from an evolutionary perspective. Anim. Behav. 21:637-659.

Knowles, P.R. 1985. Home range Size and habitat selection of bobcats, <u>Lynx</u> <u>rufus</u>, in north-central Montana. Can. Field-Nat. 99:6-12.

Koehler, G.M. 1990. Population and habitat characteristics of lynx and snowshoe hares in north-central Washington. Can. J. Zool. 68:845-851.

Koehler, G.M., Hornocker, M.G., and Hash, H.S. 1979. Lynx movements and habitat use in Montana. Can. Field-Nat. 93:441-442.

Krebs, C.J. 1989. Ecological methodology. Harper & Row, N.Y. 653 pp.

Krebs, C.J., Gilbert, B.S., Boutin, S., Sinclair, A.R.E., and Smith, J.N.M. 1986. Population biology of snowshoe hares. I. Demography of food-supplemented populations in the southern Yukon, 1976-84. J. Anim. Ecol. 55:[illegible]-982.

Krebs, C.J., Gilbert, B.S., Boutin, S., and Boonstra, R. 1987. Estimation of snowshoe hare population density from turd transects. Can. J. Zool. 65:565-567.

Kruuk, H. 1986. Interactions between felidae and their prey species: a review. In: Miller, S.O., and Everett, D.D. (eds.), Cats of the world: ecology, conservation and management. Nat. Wildl. Fed., Washington, D.C. pp. 353-374.

Leyhausen, P. 1956a. Das verhalten der katzen (Felidae). Handbuch Der Zoologie VIII:1.34.

Leyhausen, P. 1956b. Verhaltensstudien an katzen. Berlin: P. Parey-Verlag.

Litvaitis, J.A., Sherburne, J.A., and Bissonette, J.A. 1985. Influence of understory characteristics on snowshoe hare habitat use and density. J. Wild. Manage. 49:866-873.

Litvaitis, J.A., Sherburne, J.A., and Bissonette, J.A. 1986. Bobcat habitat use and home range size in relation to prey density. J. Wildl. Manage. 50:110-117.

Litvaitis, J.A., and Harrison, D.J. 1989. Bobcat-coyote niche relationships during a period of coyote population increase. Can. J. Zool. 67:1180-1188.

Major, A.R. 1989. Lynx predation ecology and habitat use in the Yukon territory, Canada. M.Sc. thesis, State University of New York, Syracuse, N.Y. pp. 75.

Major, J.T., and Sherburne, J.A. 1987. Interspecific relationships of coyotes, bobcats, and red foxes in western Maine. J. Wildl. Manage. 51:606-616.

McCord, C. M. 1974. Selection of winter habitat by bobcats (Lynx rufus) on the Quabbin Reservation, Massachusetts. J. Mammal. 55:428-437.

Neu, C.W., Byers, C.R., and Peek, J.M. 1974. A technique for analysis of utilization-availability data. J. Wildl. Manage. 38:541-545.

Parker, G.R. 1981. Winter habitat use and hunting activities of lynx (Lynx canadensis) on Cape Breton Island, Nova Scotia. In: Chapman, J.A., and Pursely, D. (eds.), Proc. World. Furb. Conf., Frostburg, Md. (1980). pp. 221-248.

Parker, G.R., Maxwell, J.W., and Morton, L.D. 1983. The ecology of the lynx (Lynx canadensis) on Cape Breton Island. Can. J. Zool. 61:770-786.

Pietz, P.J., and Tester, J.R. 1983. Habitat selection by snowshoe hares in north central Minnesota. J. Wildl. Manage. 47:686-696.

Quinn, N.W.S., and Parker, G. 1987. Lynx. In: Novak, M., Baker, J.A., Obbard, M.E., and Malloch B. (eds.), Wild furbearer management and conservation in North America. Ont. Min. Nat. Res., Toronto, Ont. pp. 683-694.

Schaller, G.B. 1972. The Serengeti lion: A study of predator- prey relations. Univ. Chicago Press, Chicago, Ill. pp. 480.

Sokal, R.R., and Rohlf, F.J. 1981. Biometry. W.H. Freeman & co. New York, NY. pp. 859.

Sunquist, M.E., and Sunquist, F.C. 1989. Ecological constraints on predation by large felids. In: Gittleman, J.L. (ed.), Carnivore behavior, ecology, and evolution. Cornell Univ. Press, Ithaca, N.Y. pp. 283-301.

Theberge, J.B., and Wedeles, C.H.R. 1989. Prey selection and habitat partitioning in sympatric coyote and red fox populations, southwest Yukon. Can. J. Zool. 67:1285:1290.

Turner, D.C., and Meister, O. 1989. Hunting behavior of the domestic cat. In: Turner, D.C., and Bateson P. (eds.), The domestic cat: the biology of its behavior. Cambridge Univ. Press, New York, N.Y. pp. 111-121.

Van Ordsol, K.G. 1984. Foraging behavior and hunting success of lions in Queen Elisabeth National Park, Uganda. African J. Ecol. 22:79-99.

Werner, E.E., and Hall, D.J. 1977. Competition and habitat shift in two competing sunfishes Centrarchidae. Ecology 58:869-876.

GENERAL DISCUSSION

In this study I examined three aspects of winter foraging in sympatric populations of lynx (*Lynx canadensis*) and coyotes (*Canis latrans*) from southwestern Yukon, in an attempt to better understand the mechanisms which affect winter survival of each species. The three aspects that I dealt with were: a) the morphological and behavioral adaptations of each species to snow, b) the diets and foraging rates of both predators during an increase in snowshoe hare (*Lepus americanus*) abundance, and c) the factors affecting habitat selection of each predator species. Lynx and coyotes are similarly-sized carnivores which cohabit areas of the boreal forest, and rely on similar foods (Quinn and Parker 1987; Voigt and Berg 1987), and I observed some similarities in their foraging behaviors. I also detected a number of important differences in their relationships to their prey, the use of snow and habitat, and in their hunting tactics.

Telfer and Kelsall (1984) predicted that behavioral adaptations to snow may be used to offset morphological disadvantages in some species, and results from my work with both predators supported their prediction. I found that lynx morphology was better adapted to snow than that of coyotes, and though both species utilized travel routes where snow was shallow and hard, coyotes also selected regions, and areas within regions, where snow was shallower than it was on lynx tracks. Conversely, the lighter foot-load of lynx enabled them to use regions of the study site where snow was deep and soft, and therefore probably inaccessible to coyotes. Foot-load of snowshoe hares was lighter than that of either predator. However, lynx and coyotes were nonetheless able to prey heavily on hares during winter. This was achieved by different hunting tactics; lynx usually ran down hares during short chases, while coyotes pounced on hares when they were in very close proximity to them. The use of these types of hunting tactics were not expected, as canids typically run down their prey over long distances, and felids usually stalk or ambush prey (Kleiman and Eisenberg 1973; Sunquist and Sunquist 1989). These different tactics may have been used as a result of the presence of snow.

Though canids are thought to be generalist feeders while felids appear to be specialists (Kruuk 1986), the importance of hares and other food items in the diet of the two species were similar. Keith et al. (1977) suggested that lynx performed a Type II functional response to a change in hare abundance, while coyotes responded with a Type III response. The major difference between responses is shown during the increase in prey density, when Type II responses show a decrease in predation rate, while Type III responses show an increase in predation rate, during an increase in prey (Taylor 1984). During an increase in hare abundance both predators responded similarly to an increase in hare numbers by increasing their kill-rates less than the magnitude of the increase in hare abundance. Therefore, for the 2 years of my study, both species appeared to respond with a Type II response.

Lynx and coyotes demonstrated similarities in their patterns of habitat use: both selected spruce forests with low cover, and avoided shrub and open habitats. However, the mechanisms governing habitat selection by each species appeared quite different. Given that coyotes are morphologically ill-equipped for dealing with deep or soft snow, they were expected to select habitats in which snow conditions were most favorable. However, coyotes avoided the areas where snow was shallowest and hardest, perhaps because of a lack of food in that habitat. Coyotes did not select closed spruce forest, which was the habitat type in which densities of snowshoe hares were highest. However, coyotes clearly used that habitat for hunting, as most kills and their highest success rate was achieved there. This phenomenon appears to be related to the use of dense spruce cover for concealment while approaching hares, reducing the chase distance and thus, the potential influence of snow on a coyote chase of hare. Canids usually use open habitats for chasing prey (Kleiman and Eisenberg 1973), therefore the strong tendency for use of dense forests by Yukon coyotes is atypical of most canids. Habitat use by coyotes changed between years, and no factor examined here could fully explain this phenomenon.

Though lynx selected areas of each habitat type where snow was deeper than average, snow conditions were similar in most habitats and snow did not appear to influence habitat selection of lynx. During the course of this study I observed signs of lynx avoidance of coyotes, though the presence of coyotes did not appear to affect habitat selection of lynx. They selected habitats similarly in areas where coyotes were abundant and in those where coyotes were rare. Most chases of hare taken by lynx occurred in low spruce cover, and though lynx preferred that habitat type for hunting, success rates were similar among all habitat types, suggesting that once an attempt had been initiated, hares were equally vulnerable to lynx predation in all habitats. Rather, lynx use of open spruce areas for hunting may be explained by an increased ability to detect hares in that habitat. Vision is the most important sense used by felids when hunting (Leyhausen 1956, cited in Kleiman and Eisenberg 1973), and high chase rates of hare within that habitat in year 2 suggest that hare detection in that habitat was higher than it was in denser spruce forests, despite higher hare densities in the latter habitat.

In summary, sympatric lynx and coyotes in the boreal forest during winters of mid to high hare densities use similar habitats, and respond similarly, to an increase in hare. However they differ in their adaptations to snow, and this in turn appears to affect their choice of foraging tactics and hunting habitats.

REFERENCES

Keith, L.B., Todd, A.W., Brand, C.J., Adamcik, R.S., and Rusch, D.H. 1977. An analysis of predation during a cyclic fluxuation of snowshoe hares. Proc. XIII Int. Cong. Game Biol. pp. 151-175.

Kleiman, D.G. and Eisenberg, J.F. 1973. Comparisons of canid and felid social systems from an evolutionary perspective. Anim. Behav. 21:637-659.

Kruuk, H. 1986. Interactions between Felidae and their prey species: a review. In: Miller, S.O., and Everett, D.D. (eds.), Cats of the world: ecology, conservation, and management. Nat. Wildl. Fed., Washington, D.C. pp. 353-374.

Leyhausen, P. 1956. Verhaltensstudien an Katzen, Berlin: P. Parley-Verlag.

Taylor, R.J. 1984. Predation. Chapman & Hall, New York N.Y. 166 pp.

Telfer, E.S., and Kelsall, J.P. 1984. Adaptation of some large North American mammals for survival in snow. Ecology 65:1828-1834.

Quinn, N.W.S., and Parker, G. 1987. Lynx. In: Novak, M., Baker, J.A., Obbard, M.E., and Malloch, B. (eds.), Wild furbearer management and conservation in North America. Ont. Min. Nat. Res. Toronto, Ont. pp. 683-694.

Sunquist, M.E., and Sunquist, F.C. 1989. Ecological constraints on predation by large felids. In: Gittleman, J.L. (ed.), Carnivore behavior, ecology, and evolution. Cornell Univ. Press, Ithaca, N.Y. pp. 283-301.

Voigt, D.R., and Berg, W.E. 1987. Coyote. In: Novak, M., Baker, J.A., Obbard, M.E., and Malloch, B. (eds.), Wild furbearer management and conservation in North America. Ont. Min. Nat. Res. Toronto, Ont. pp. 345-356.