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Behavioural responses of coyotes and lynx to the snowshoe hare cycle

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Coyotes and lynx are the two most important mammalian predators of snowshoe hares throughout much of the North American boreal forest. Populations of hares cycle in abundance, with peaks in density occurring every 8–11 years. We used snow-tracking to measure the diets, use of habitats, and hunting tactics of coyotes and lynx during a cyclic fluctuation of hare populations in the southwest Yukon. Our objective was to determine changes in foraging behaviour of the predators leading to functional responses to densities of hares.

Coyotes and lynx both preferred snowshoe hares over available alternative prey at all phases of the cycle. Lynx switched to preying on red squirrels during the cyclic low and subsequent early increase. The pattern of changes in habitat use by coyotes and lynx paralleled that of snowshoe hares, and both concentrated their hunting activity in areas of high density of hares. Coyotes used more open cover to hunt voles during years of low abundance of hares and high numbers of small mammals. Lynx increasingly used ambush beds for hunting hares and red squirrels during the cyclic decline and low. Hunting success was not higher from beds. Lynx hunted in adult groups for the first time during the cyclic decline and low.

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Populations of snowshoe hares (*Lepus americanus*) in the boreal forests of North America exhibit regular cycles in abundance, with amplitudes over two orders of magnitude, and 8–11 years between cyclic peaks (Elton and Nicholson 1942, Keith 1990). These cycles have major effects on many predators and other herbivores in the relatively simple boreal ecosystem (Finerty 1980). This paper examines the behavioural responses of coyotes (*Canis latrans*) and lynx (*Lynx canadensis*), the two most important mammalian predators of hares throughout much of their range, to the population cycle of hares.

Predators may respond to fluctuating abundance of prey with demographic (e.g., changes in reproduction or survival) and behavioural (e.g., switching prey or habitats) adjustments to prey density. Demographic responses and migratory movements relative to prey density are termed “numerical responses”, while responses leading to changes in kill rates with density of prey are “functional responses” (Solomon 1949). The total impact of predators on their prey is determined by their combined numerical and functional responses (review in Murdoch and Oaten 1975). The shapes and timing of the numerical and functional responses of

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predators to prey are therefore critical to determining the effects of predation.

Holling (1959) described three basic forms of functional responses of predators to changes in density of prey. Type-1 responses describe linearly increasing kill rates with prey density up to a threshold, above which the rate is constant. Type-2 responses describe kill rates increasing at a monotonically decreasing rate with prey density, up to an asymptote, and type-3 responses are sigmoidal in shape. Type-2 responses may be typical of specialist predators, predators with few alternative prey, or they may arise due to adaptive adjustment of duration and rate of searching to the profitability of foraging (Abrams 1990, 1992). Type-3 responses are more typical of generalist predators, and they may result from a number of mechanisms: 1) predators learning to recognize, capture, or handle prey better with increasing prey density (Holling 1959), 2) predators switching among prey types, habitats, or foraging tactics (Royama 1970, Murdoch and Oaten 1975, Akre and Johnson 1979), 3) adaptive variation in foraging rates (Holling 1966, Hassell et al. 1977, Dunbrack and Giguère 1987), and 4) changes in the behaviour of prey, or prey having a refuge below a fixed density (Murdoch and Oaten 1975, Taylor 1984).

Functional responses of predators thus can result from increasing encounter rates with prey at higher densities of prey, density-dependent changes in the behaviour of prey, or changes in the behaviour of predators. Any of these can lead to changes in the shape of the functional response, and on predator-prey dynamics.

As the density of a prey species changes, so often does its relative density to alternative prey. Predators may "switch" between prey species based on the relative abundances of the prey. "Switching" is defined as feeding on a prey species disproportionately less when its relative abundance to other prey is low, and disproportionately more when it is high (Murdoch 1969). A number of mechanisms for switching have been proposed: 1) predators may develop "search images", or learn to "see better" the prey as it becomes relatively more abundant (Tinbergen 1960, Lawrence and Allen 1983), 2) predators may switch habitat types, which leads to switches in prey (e.g., Royama 1970), or 3) predators may change foraging tactics as relative densities of prey change (e.g., Lawton et al. 1974).

There is ample evidence that switching among prey species does occur (e.g., Murdoch and Oaten 1975, Akre and Johnson 1979), but few demonstrations are from field data. Laboratory and theoretical investigations suggest that switching usually, but not always, leads to type-3 functional responses by predators (Murdoch and Oaten 1975), which can stabilize predator-prey interactions (Oaten and Murdoch 1975,

Hassell and Comins 1978, Hassell 1979, Nunney 1980).

Switching among habitat types by predators may also occur in response to changes in the relative frequency of prey, and the resulting changes in relative profitabilities of foraging in different habitats (Royama 1970, Murdoch and Oaten 1975). Concentration of predators in habitat patches with high density of prey can lead to type-3 functional responses (Murdoch and Oaten 1975). Such aggregation can be considered as a functional response or a numerical response, depending on the scale of movement of predators, but the effect on prey dynamics may be similar (Solomon 1949, Murdoch and Oaten 1975, Hanski et al. 1991, Korpimäki and Krebs 1996).

Switching foraging tactics in response to changes in the relative frequency of prey has also been documented in a number of studies (Lawton et al. 1974, Davies 1977, Akre and Johnson 1979, Formanowicz and Bradley 1987). Changing tactics may involve switches between active searching and ambush, differences in travel patterns, or changes in the size of foraging groups.

Animals vary in their foraging strategies, and some are more versatile than others in the range of prey types, habitats, and foraging tactics that they will use (review in MacNally 1995). "Generalists" are more plastic in their behaviour than "specialists", and may more readily switch among foraging strategies.

Coyotes are often considered prototypical generalists. Over their large and expanding range in North America, they are adapted to a wide variety of habitats, climates, and foods (see papers in Bekoff 1978). Lynx, in contrast, are usually considered prototypical specialists on snowshoe hares, and all studies of their food habits have shown hares to be their predominant prey (Saunders 1963a, Brand and Keith 1979, Parker et al. 1983, Ward and Krebs 1985). Coyotes usually stalk and rush prey larger than small mammals, while lynx may either stalk or ambush their prey (Saunders 1963a, b, Wells and Bekoff 1982, Murray et al. 1995).

Both coyotes and lynx showed clear functional responses to changing densities of snowshoe hares in the Yukon (O'Donoghue et al. 1998). The main objective of this paper is to investigate and contrast the behavioural responses of these predators that were associated with their functional responses. Specifically, we will look at evidence for prey-switching, changes in habitat use, and changes in foraging tactics, including hunting technique, use of trails, and group hunting.

Study area

This study was conducted in the southwest Yukon Territory, Canada (60°57'N, 138°12'W), in a broad

glacial valley approximately 350 km² in area. The study area was bounded to the north and south by alpine tundra, to the west by Kluane Lake, and to the east by Kloo Lake and the Jarvis River. Elevation ranges from approximately 830 m to 1170 m. The dominant vegetation of the area is white spruce forest (*Picea glauca*) with scattered aspen stands (*Populus tremuloides*), and a dense but patchy understorey of willow (mostly *Salix glauca* and *S. alaxensis*), bog birch (*Betula glandulosa*), and soapberry (*Shepherdia canadensis*) (Douglas 1974). The climate is cold continental, with mean January temperatures of -18°C , and about 65 cm average snow accumulation. Snow cover is usually continuous from October through May.

Methods

This study was conducted as a part of the Kluane Boreal Forest Ecosystem Project, an experimental study of the vertebrate food web in the northern forests (Krebs et al. 1995). Field work was started in 1986, and continued through the winter of 1994–95. With the exception of some scat collection, live-trapping and radio telemetry, field work was conducted during the winter months, from October to April.

Estimation of prey and predator densities

We estimated densities of snowshoe hares, red squirrels (*Tamiasciurus hudsonicus*), and small mammals (mostly *Clethrionomys rutilus*, *Microtus oeconomus*, and *M. pennsylvanicus*) by live-trapping (Boutin et al. 1995). Snowshoe hares were trapped on 1–3 60-ha grids each March and October–November; population estimates were made using the jackknife estimator in program CAPTURE (White et al. 1982). Populations of hares were also monitored on two experimental grids with supplemental food, using the same methods (Krebs et al. 1995). Red squirrels were trapped on 1–3 8-ha grids each May and August; population estimates were made using the estimators recommended by the model selection procedure of program CAPTURE. *Clethrionomys* were trapped on two 2.8-ha grids, and *Microtus* on two 1.5-ha grids each May and August; population estimates were made based on the minimum number of animals alive (MNA; Krebs 1966). The means of “autumn” and “spring” estimates of density of prey species were used for calculating availabilities during winter.

We estimated the densities of coyotes and lynx from a combination of monitoring radio-collared animals, locations of tracks, and recording howling by coyotes (described in O’Donoghue et al. 1997).

Snow-tracking of coyotes and lynx

We followed the tracks of coyotes and lynx each winter from 1987–88 through 1994–95, beginning as soon as there was enough snow, in October or November, and finishing at the end of March. Nineteen different observers snow-tracked predators during the 8 winters of study. This was the main method that we used for determining species and frequencies of kills and attempted kills, frequencies of beds, use of habitats, and use of trails.

Fresh tracks were selected along snowmobile trails and roads in our study area on any days that weather and snow conditions permitted. We spread our tracking effort as evenly as possible over the study area, between coyotes and lynx, and among different group sizes of predators. Once a track was selected, we usually followed it backwards (relative to the animal’s direction of travel) until it was lost due to poor snow conditions or confusion with the tracks of other animals. We then tried to follow it forwards as far as possible, to have segments of maximum length – this sometimes required several days of following the same tracks.

We counted the distance tracked on hand-held tally counters (numbers of paces were later converted to metres, using observer-specific conversion factors), and recorded events along the tracks on micro-cassette recorders. We recorded the prey species and characteristics of chases and feeding for all kills and attempted kills. All beds were classified as crouches (or hunting beds), “short” beds (where the predator had laid down but did not stay long enough to melt the snow), or resting beds. We kept a continuous record of the habitat through which the animal was travelling. We characterized the overstorey by cover (subjectively classed as <5%, 5–25%, 25–50%, 50–75%, or 75–100%), dominant species (white spruce, trembling aspen, or balsam poplar), and age (immature or mature). We also recorded when the animals we were following were travelling on trails made by other predators, hares, snowmobiles, or snowshoes. At high densities of hares, it became very difficult to keep track of every time a predator followed or left trails of hares, so we changed our protocol to recording whether the coyote or lynx was on or off a hare trail at each 100th step. For subsequent analyses, we converted all trail-use data to “on” or “off” at 100-m intervals.

We analysed tracking data using the MGLH (Multivariate General Linear Hypothesis) procedure in SYSTAT (Wilkinson 1990) and Wilcoxon paired-sample tests, and considered $P < 0.05$ the criterion for rejecting null hypotheses. Availabilities and proportions of diet by biomass were calculated by multiplying numbers of prey by 1500 g for hares, 250 g for red squirrels, and 20 g for small mammals.

Analysis of prey switching by coyotes and lynx

We used a graphical analysis similar to that suggested by Murdoch (1969) to investigate evidence for prey switching by coyotes and lynx. Analysis of switching is typically carried out by comparing the percent of a given prey species in the diet of a predator, relative to its availability in the environment (Murdoch 1969). The null hypothesis of no preference and no switching predicts that use and availability should be equal (i.e., when plotted, the points should fall on a straight line) at all relative availabilities of the prey. Predators may have "innate preferences" for certain prey species though, in which case the null hypothesis for no switching predicts that, when percent use is plotted against percent availability, the points should all lie on a curve (convex for preferred prey, concave for those not preferred) determined by the degree of preference (Murdoch 1969). Alternatively, if points lie below the null-model curve at low relative availabilities (indicating disproportionately low use), and above the curve at high availability (indicating disproportionately high use), this is taken as evidence of prey switching.

Most analyses of switching have been carried out in the laboratory or experimentally controlled situations, using similar-sized prey (review in Murdoch and Oaten 1975). Relative availability and use have been determined, in these cases, by relative frequencies of the prey. In our field study though, the main available prey – hares, red squirrels, and small mammals – were of very different body sizes. Considering their relative frequencies as equivalent to the relative amounts of food available to predators was clearly inappropriate. A further difficulty is presented by the fact that abundance and availability were almost certainly not equivalent in the field – red squirrels have refuges from predation in trees and under frozen ground, and small mammals have subnivean refuges.

Our analysis of switching was designed to take these potential biases into account. We calculated preference indices for hares, squirrels and small mammals for each predator in each winter using Manly's alpha (Manly et al. 1972), with the proportions of prey available and in diets expressed as biomass rather than frequencies. Manly's alpha measures the probability that an individual prey item is selected from a prey class when all prey species are equally available (Krebs 1989). We took the means of preference indices for the eight winters of this study as the overall preference index for each prey group. The ratio of the preference index for a given species to those of the other prey was then used as the "proportionality constant" to calculate null-model curves to test for switching (equation 2 in Murdoch 1969). While this analysis is not strictly equivalent to that proposed by Murdoch (1969), it nonetheless provides a similar graphical method of comparing relative use of prey to relative availabilities, to test for prey switching.

Analysis of habitat use by coyotes and lynx

We collected data on habitat use by coyotes and lynx continuously along their trails. However, it is obvious that the habitat we measured at each step cannot be considered an independent sample, since it is likely to be the same as that at an adjacent step simply by virtue of being in the same habitat patch. Before analysing these data, therefore, we had to first determine the appropriate interval along trails at which our observations of habitat were independent.

We used data from parallel linear transects run through the study area at 2-km intervals, along which habitat was classified in the same manner as when snow-tracking. From these data, we calculated the set of "patch lengths" for each overstorey type. We then used a bootstrapping procedure in which each set of patch lengths was randomly sampled 5000 times, and for each random sample, we calculated the 95% quantile (patch length longer than all but 5% of measured patch lengths). We took the median of these for each overstorey type – these ranged from 79 m to 188 m for different habitat types. We therefore chose to consider our measurements of habitat each 200 m along our trail to be independent samples in subsequent analyses.

We considered the distribution of hare trails, recorded as present or absent at each 100th step along the trails of predators, as an indication of their selection of habitat.

A second potential bias with our habitat data became apparent in early analyses. Over the course of our study, 22 different observers snow-tracked predators. Preliminary analyses of the data indicated that there were differences among observers in their subjective classification of overstorey cover. We therefore conducted separate analyses of habitat use, using *t*-tests to compare between years and between species, for each observer. We then combined the statistical results of the tests from different observers to evaluate overall statistical significance using "meta-analyses" (Arnqvist and Wooster 1995); specifically, we used the method of adding *Z*'s (Rosenthal 1978).

Track counts of coyotes and lynx around experimental grids

We conducted counts of the tracks of coyotes and lynx around the perimeters of control and food-addition grids (36 ha), established by the Kluane Project, in order to determine if predators were concentrating their activities in the pockets of high hare density created by the food addition. Beginning in the winter of 1988–89, we counted all tracks of predators crossing a transect around each of two food-addition grids and 1–2 control grids, 1–5 d after fresh snowfalls. We compared track counts between control and food-addition grids

using ANOVAs with log-transformed data, controlling for number of days after snowfall. In these analyses, we used number of tracks per day per grid as the sample unit. These data points were not strictly independent, since some animals certainly used the experimental grids on more than one day. However, grids were sampled, on average, only 12 times per winter (only once after each snowstorm), and the sizes of the grids represented less than 5% of the home range of any of our coyotes and lynx. Given the wide-ranging movements of the predators in their home ranges, we considered each sample day as an independent opportunity for any predator to hunt or not hunt on a given grid.

Variance among individual predators

Although we closely monitored the abundance of coyotes and lynx in our study area (O'Donoghue et al. 1997), we were unable to distinguish the tracks of individuals, and therefore, could not calculate the true (i.e., inter-individual) variances of our measures of diet and foraging behaviour. We were most concerned with the pattern of year-to-year changes in foraging by predators, as the composition of the prey community changed. We examined the consistency of these observed patterns by analysing our data separately in three different regions (west, central, and east thirds) of our study area. Coyotes and lynx are territorial, and different individuals concentrated their activities in distinct parts of the study area. Some individual predators certainly overlapped our regional boundaries though, so variation among regions only indexed true variances.

Results

Prey and predator populations

Populations of snowshoe hares peaked between 1988 and 1990 at approximately 2/ha (Fig. 1; see also Boutin et al. 1995). There were locally abundant pockets of hares through the autumn of 1991 (Boutin et al. 1995), and populations declined to very low numbers by the end of winter 1992–93. Densities of hares started to increase again in 1994. Depending on whether autumn or late winter estimates of hare numbers are used, the cyclic amplitude was 26–44-fold (Boutin et al. 1995).

Population trends of other potential prey species varied. Numbers of red squirrels stayed relatively stable, with a slight increase during the last two winters of the study (Fig. 1). Populations of small mammals fluctuated with a 10–50-fold amplitude, with the highest numbers occurring from 1991 through 1993 (Fig. 1). There were few other alternative prey species. Arctic ground squirrels hibernate, and were therefore not available to predators during the winter. Spruce grouse,

ruffed grouse, and ptarmigan were present (Boutin et al. 1995), but were seldom utilized by predators (2% of all kills from 1987 to 1995; O'Donoghue et al. 1998).

Snowshoe hares were by far the most abundant potential food source during winter for predators from 1987–88 through 1991–92, comprising 63–81% of the total biomass of the main prey species. Red squirrels were the second largest food source during these years. During the last three winters of the study (1992–93 through 1994–95), however, once hare numbers had crashed, red squirrels comprised 58–72% of the total biomass. Small mammals represented less than 10% of the total biomass of prey in all winters except 1992–93 (14%).

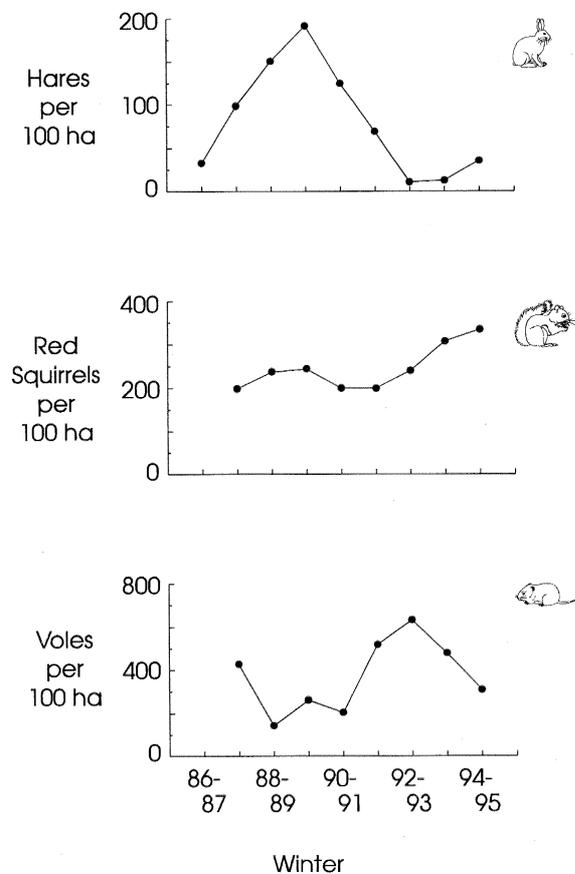


Fig. 1. Estimated densities of snowshoe hares (means of autumn and late winter estimates from live-trapping on 1–3 60-ha grids), red squirrels (means of late summer and spring estimates from live-trapping on 2–3 8-ha grids), and small mammals (means of late summer and spring estimates from live-trapping on two 2.8-ha grids for *Clethrionomys rutilus*, and on two 1.5-ha grids for *Microtus oeconomus* and *M. pennsylvanicus*) from 1986 to 1995 in the southwest Yukon. The mean coefficients of variation were 34% and 44% for autumn and late winter estimates of hares, 45% and 28% for late summer and spring estimates of red squirrels, and 48% and 79% for late summer and spring estimates of small mammals, respectively (Boutin et al. 1995).

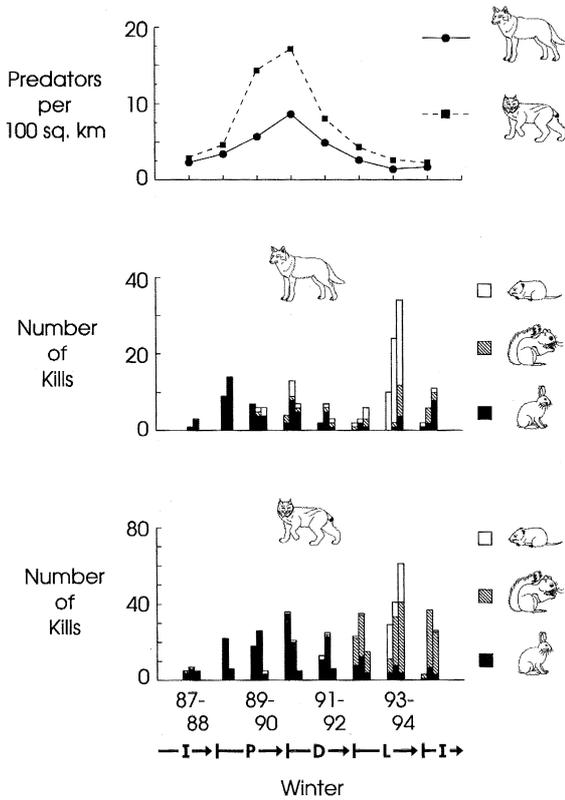


Fig. 2. Densities of coyotes and lynx (estimated from monitoring radio-collared animals, snow-tracking and coyote howling; O'Donoghue et al. 1997), and spatial distribution of kills (of snowshoe hares, red squirrels, and voles) in a 350-km² study area in the southwest Yukon during winter from 1987–88 through 1994–95. The three bars presented for each winter represent kills located while snow-tracking in the western, central, and eastern thirds of the study area, and, as it was not possible to distinguish among individuals, they are presented to illustrate the consistency among different animals in dietary shifts during the hare cycle. The phases of the hare cycle (I = increase, P = peak, D = decline, L = low) are shown by the horizontal bar below the bottom x-axis.

Numbers of coyotes and lynx varied 6-fold (from 5 to 30) and 7.5-fold (from 8 to 60), respectively, from 1987–88 through 1994–95, with peaks in abundance occurring in 1990–91, one year after the peak of the hare cycle (Fig. 2; O'Donoghue et al. 1997).

Prey switching by coyotes and lynx

Coyotes

We followed the tracks of coyotes for 1897 km during the eight winters from 1987–88 through 1994–95 (mean per winter, 237 ± 100 (S.D.) km). We found 189 kills by coyotes, 47.1% of which were hares, 13.2% red squirrels, and 37.6% small mammals (Fig. 2; see also O'Donoghue et al. 1998). Coyotes killed mostly hares from 1987–88 through 1991–92, plus some red squirrels

and small mammals from 1989–90 through 1991–92. Small mammals comprised most kills in 1992–93 and, especially, in 1993–94, while hares and red squirrels were killed more in 1994–95. These patterns were consistent among regions of the study area, although sample sizes were quite small in some winters (Fig. 2). In terms of biomass, the diets of coyotes were comprised largely of hares in all winters (Fig. 3). Small mammals made up a maximum of 9.5% in 1993–94, a winter of high vole density, and red squirrels made up maximum of 19.9% in 1994–95.

Coyotes showed a strong preference for hares throughout the eight winters of this study ($\alpha = 0.88 \pm 0.11$ (S.D.), range 0.73–1.00). The null model for switching is therefore a convex curve for hares, and concave curves for red squirrels and small mammals (Fig. 3). Based on these data, there is no evidence that

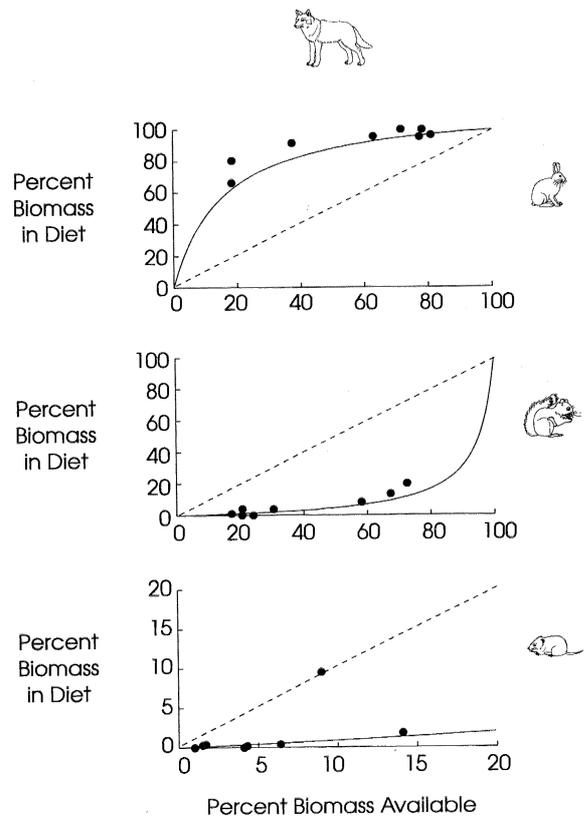


Fig. 3. Graphical tests for prey switching by coyotes preying on snowshoe hares, red squirrels, and small mammals from 1987–88 through 1994–95. The dashed line in each graph represents the null hypothesis of no preference and no switching. The solid curve is the null hypothesis of no switching, taking into account the “innate” dietary preferences of coyotes (calculated from equation 2 in Murdoch 1969). Proportions of prey in the diets of coyotes are based on the observed kills from snow-tracking. Evidence of switching is inferred when data points lie below the null-model curve at relatively low prey availability, and above it at high availability.

coyotes switched among prey species (i.e., no consistent pattern of data points below the null-model curves at low relative availabilities, and above at high availabilities), as their relative abundances changed.

Lynx

We followed the tracks of lynx for 2232 km during the eight winters from 1987–88 through 1994–95 (mean per winter, 279 ± 85 (S.D.) km). We found 502 kills by lynx, 50.2% of which were hares, 34.7% red squirrels, and 11.0% small mammals (Fig. 2; see also O'Donoghue et al. 1998). Lynx killed mostly hares from 1987–88 through 1991–92, plus some red squirrels in 1987–88. Red squirrels comprised most kills from 1992–93 through 1994–95, with some small mammals in 1993–94. These patterns were consistent in the separate regions of the study area (Fig. 2). In terms of biomass, the diets of lynx were comprised largely of hares from 1987–88 through 1991–92, but red squirrels became increasingly important from 1992–93 through 1994–95 (20.4–43.9%; Fig. 4). Small mammals made up a negligible proportion of the diet in all winters.

Lynx also showed a strong preference for hares throughout the eight winters of this study ($\alpha = 0.90 \pm 0.12$ (S.D.), range 0.65–1.00). Preference was very high from 1987–88 through 1992–93 (range 0.92–1.00), but declined to 0.79 in 1993–94 and 0.65 in 1994–95. The null model for switching is therefore a convex curve for hares, and concave curves for red squirrels and small mammals (Fig. 4). Based on these data, there is some evidence that lynx switched from hares to red squirrels during the last three winters of this study (1992–93 through 1994–95). Preference for small mammals was very low in all years.

Use of habitat by coyotes, lynx and hares

Coyotes showed a general pattern of using progressively more dense cover from the peak year of hare abundance (1989–90) into the early cyclic decline (Fig. 5). They used the most dense cover in 1991–92, the second year of decline in hare abundance, and then more open habitat in each of the next two winters (1992–93 and 1993–94). There was an increase in the density of cover used again in 1994–95.

Lynx showed a pattern of habitat use similar to that of coyotes – they used progressively more dense cover from 1988–89 (late increase phase of the cycle) to the early cyclic decline (Fig. 5). They used the most dense cover in 1991–92, the second year of decline in hare abundance, and then showed a general trend towards using more open habitat during the last three winters of the study (1992–93 through 1994–95).

The pattern of habitat use by coyotes and lynx described above roughly paralleled that of hares from 1988–89 (late increase of cycle) through 1992–93 (late

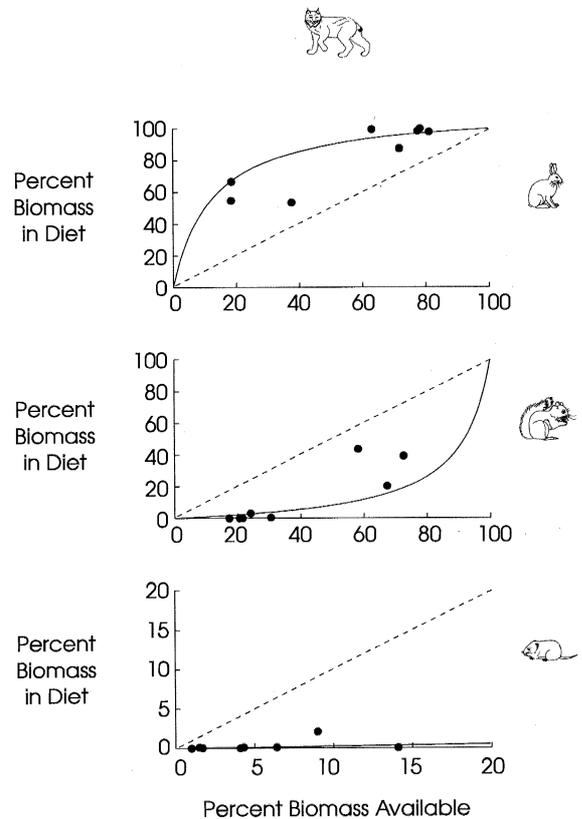


Fig. 4. Graphical tests for prey switching by lynx preying on snowshoe hares, red squirrels, and small mammals from 1987–88 through 1994–95. The dashed line in each graph represents the null hypothesis of no preference and no switching. The solid curve is the null hypothesis of no switching, taking into account the “innate” dietary preferences of lynx (calculated from equation 2 in Murdoch 1969). Proportions of prey in the diets of lynx are based on the observed kills from snow-tracking. Evidence of switching is inferred when data points lie below the null-model curve at relatively low prey availability, and above it at high availability.

decline; Fig. 5). Hares used progressively more dense cover to a maximum in 1991–92, and then more open cover the next winter. Hares were consistently in more dense habitat than either coyotes or lynx (Fig. 6).

In summary, these data show that coyotes and lynx did change their patterns of habitat use over the course of the cycle in numbers of hares, and that these changes roughly paralleled changes in habitat use by hares. Coyotes generally used more open habitat than lynx, particularly during the cyclic decline (Fig. 6).

Additional evidence that predators concentrated their activity in habitats with high numbers of hares comes from our track counts around experimental hare grids. Food-addition grids had roughly three times the density of hares as controls during the peak and decline in the hare cycle (Krebs et al. 1995). Coyotes consistently used food-addition grids more intensively than controls from

1990–91 through 1993–94 (ANOVA, effect of treatment, $F = 19.46$, d.f. = 1,150, $P = 0.000$; Fig. 7; too few data were gathered in 1988–89 and 1989–90 for meaningful analyses), and lynx used them more from 1990–91 through 1992–93 (ANOVA, $F = 4.52$, d.f. = 1,150, $P = 0.035$; Fig. 7).

Foraging behaviour by coyotes and lynx

Hunting tactics

While lynx used both ambush and stalking to hunt prey, coyotes seldom made hunting beds (Fig. 8). There was a large increase in the frequency of hunting beds by lynx during the decline in hare abundance (1990–91 through 1992–93), and they continued to use them frequently in 1993–94 and 1994–95. This pattern was

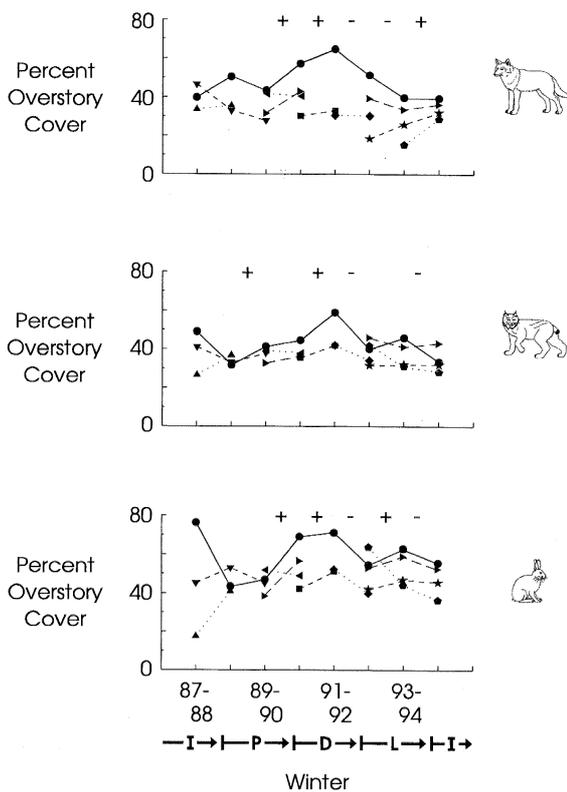


Fig. 5. Use of habitat (by overstorey density) by coyotes, lynx, and snowshoe hares in the southwest Yukon, from snow-tracking data, 1987–88 through 1994–95. Each symbol represents a different observer who tracked in two consecutive winters. Differences in use of habitat between consecutive years were tested for each observer individually, and the results of these tests were combined in meta-analyses to analyse overall trends between the two years. “+” signs indicate overall statistically significant increases in the density of cover used between years, and “-” signs indicate significant decreases. The phases of the hare cycle (I = increase, P = peak, D = decline, L = low) are shown by the horizontal bar below the bottom x-axis.

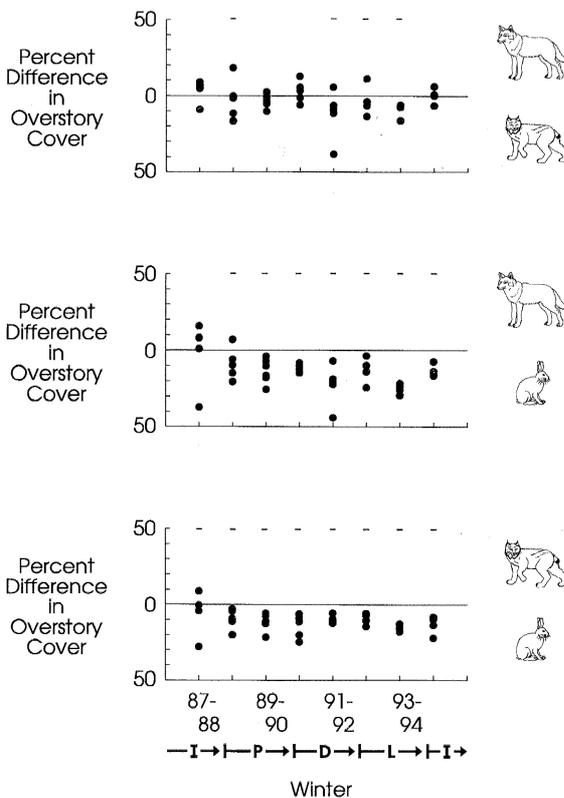


Fig. 6. Differences in use of habitat (by overstorey density) by coyotes, lynx, and snowshoe hares in the southwest Yukon, from snow-tracking data, 1987–88 through 1994–95. Each data point represents a different observer – data points above the line at 0% indicate the species on top in each graph used denser cover; those below the line show use of denser cover by the species on bottom. Differences in use of habitat between species were tested for each observer individually, and the results of these tests were combined in meta-analyses to analyse overall trends between the two species. “-” signs indicate overall statistically significant use of less dense cover by the species on top of each graph. The phases of the hare cycle (I = increase, P = peak, D = decline, L = low) are shown by the horizontal bar below the bottom x-axis.

consistent in all regions of the study area. Coyotes made few crouches during any winters.

Lynx initiated progressively more chases of hares from hunting beds during the decline and low years of the hare cycle in all parts of the study area (1990–91 through 1993–94; Fig. 9). (This is based on the criterion of chases actually starting from beds, and does not include cases where lynx may have seen hares from beds, but stalked them before initiating a chase.) From 1992–93 through 1994–95, 20–30% of all chases of red squirrels by lynx were made from beds (Fig. 9); sample sizes are too low before this time period for meaningful analyses. Hunting success of lynx chasing hares was approximately the same whether they were chased directly from hunting beds or not (Fig. 10), while success was generally lower from beds for lynx chasing squirrels (Fig. 10).

During winters when voles were abundant, coyotes hunted them with a "mousing" foraging tactic, mostly in open habitat (Wells and Bekoff 1982). Coyotes searched in grassy areas for subnivean prey; when located, coyotes pounced and tried to pin them with their forepaws. Frequency of mousing was very low (0.00–0.05 attempts per 10 km trail) during winters of high and declining abundance of hares (1988–89 through 1991–92; except for 1991–92, these also corresponded with winters of low densities of voles (Fig. 1)). During winters of higher vole and lower hare abundance, coyotes hunted voles more actively (0.70–1.91 attempts per 10 km trail in 1987–88, 1992–93, and 1994–95), and in 1993–94, they spent a great deal of effort "mousing" (13.98 attempts per 10 km trail).

Use of trails

Coyotes spent more time than did lynx on the trails of other predators (Wilcoxon paired-sample test, $P = 0.008$) and human-made trails (Wilcoxon paired-sample test, $P = 0.008$; Fig. 11). Both lynx and coyotes spent more time on hare trails during the peak and early decline phases of the cycle (Fig. 11). Lynx used hare trails more than did coyotes during periods of low numbers of hares, but there was no statistical difference between the two predators over the course of the study (Wilcoxon paired-sample test, $P = 0.945$).

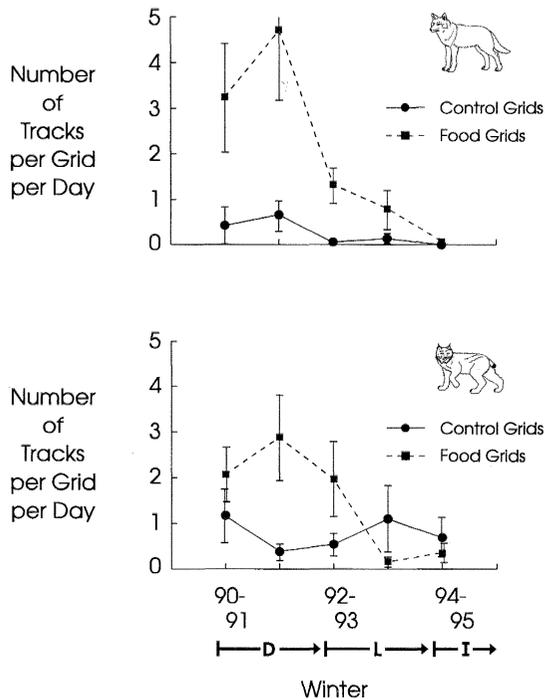


Fig. 7. Use of food-addition (high density of hares) and control grids by coyotes and lynx (tracks per day \pm S.E.) at Kluane in winter from 1990–91 through 1994–95. The phases of the hare cycle (D = decline, L = low, I = increase) are shown by the horizontal bar below the bottom x-axis.

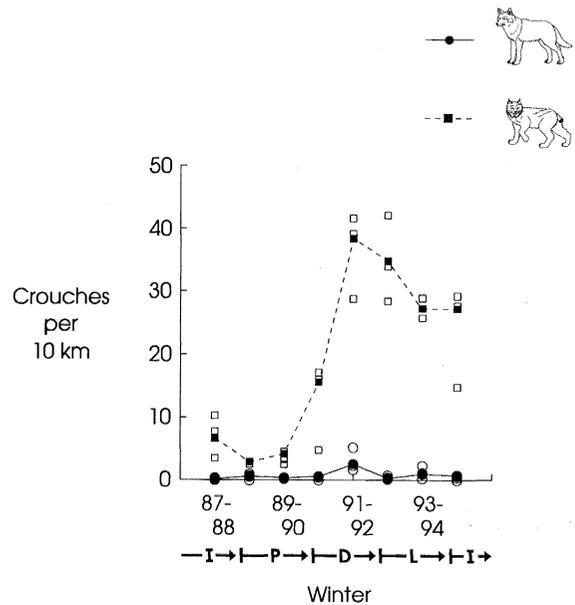


Fig. 8. Frequency of crouches (hunting beds) along trails of coyotes and lynx in the southwest Yukon, from 1987–88 through 1994–95. Filled symbols indicate overall frequencies, while unfilled symbols are frequencies of crouches in the western, central, and eastern thirds of the study area (presented here as indices of variance). The phases of the hare cycle (I = increase, P = peak, D = decline, L = low) are shown by the horizontal bar below the x-axis.

Group hunting

Both coyotes and lynx sometimes travelled in and hunted in groups. To investigate whether group hunting conferred advantages of higher food intake to predators, we calculated kill rates of hares by coyotes and lynx in different group sizes (we limited our analyses to group sizes which we tracked for more than 10 km in a given winter), as in O'Donoghue et al. (1998). We adjusted these by group size to calculate average per-individual kill rates.

Coyotes hunted in groups of 1–3; groups larger than 2 were tracked only in 1990–91 and 1991–92. We were unable to determine the ages of animals in these groups. The relationship between group size and per-individual kill rates was variable (Fig. 12). Larger groups generally killed more hares, but this usually translated into fewer hares per individual, although this was not statistically significant (ANOVA, $F = 11.31$, d.f. = 1, 2, $P = 0.078$).

Lynx hunted in groups of 1–5. All of these were family groups (females with kittens, distinguished by clear differences in the sizes of their tracks) up to the winter of 1991–92. In the winters from 1991–92 through 1993–94, however, we observed few family groups (none after 1991–92), but rather several groups of adults hunting together for the first time. As with coyotes, larger groups of lynx generally killed hares more frequently, but per-individual kill rates were lower

from 1987–88 through 1991–92 (Fig. 12). In 1992–93 and 1993–94, there was a suggestion that larger adult groups may have benefited individuals in them with equal or higher kill rates, but sample sizes were small. The overall relationship between group size and individual kill rates was statistically insignificant (ANOVA, $F = 0.82$, $d.f. = 1,6$, $P = 0.401$).

Discussion

Coyotes and lynx showed strong preferences for snowshoe hares throughout the cycle. Our data suggest that lynx switched from preying on hares to red squirrels during the winters of low and early increasing densities of hares. Habitat use by both predators roughly paralleled that of hares, and both concentrated their hunting efforts in areas of high hare density. As numbers of hares declined, lynx increasingly used hunting beds for ambushing prey. Coyotes and lynx frequently travelled along the trails of hares while hunting, and coyotes, in

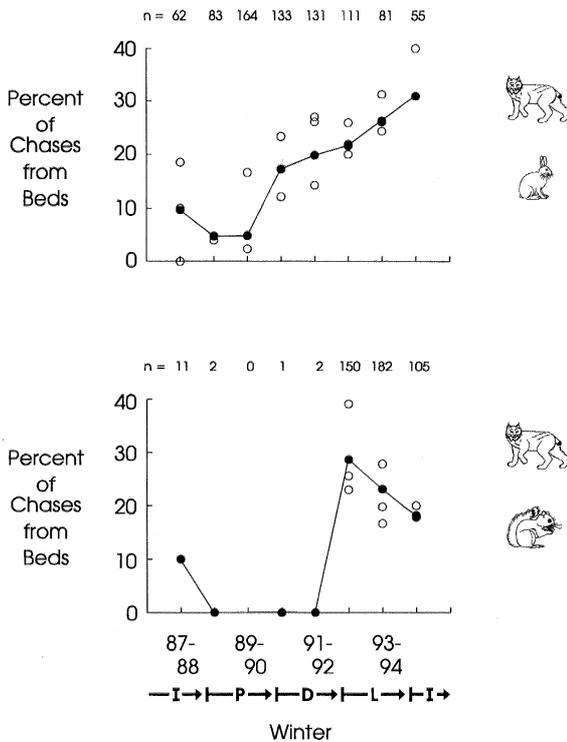


Fig. 9. Percentages of chases of hares and red squirrels by lynx that were initiated from hunting beds in the southwest Yukon, during winter, 1987–88 through 1994–95. Sample sizes (number of chases) are given above graphs. Note very low sample sizes for chases of squirrels before 1992–93. Filled symbols indicate overall percentages, while unfilled symbols are these values in the western, central, and eastern thirds of the study area (presented here as indices of variance). The phases of the hare cycle (I = increase, P = peak, D = decline, L = low) are shown by the horizontal bar below the bottom x-axis.

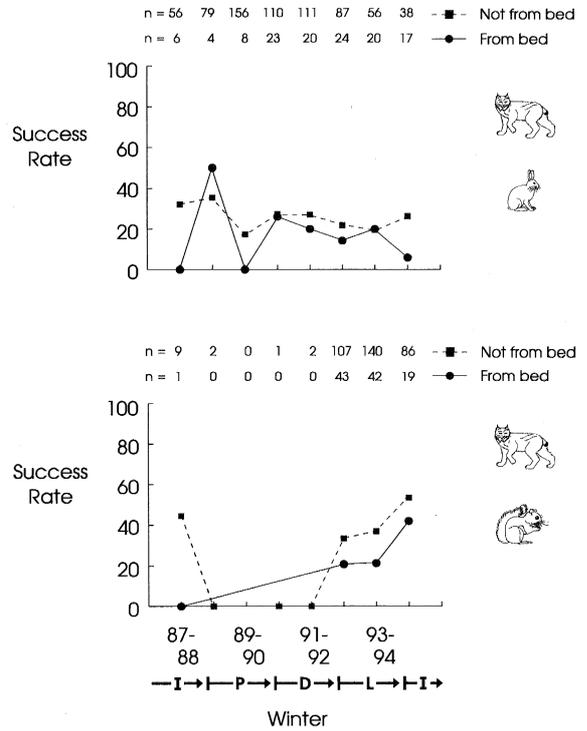


Fig. 10. Hunting success rates (% of all chases that were successful) of lynx chasing hares and red squirrels from hunting beds, compared to success rates not initiated from beds, from 1987–88 through 1994–95. Sample sizes (number of chases) are given above the bars. Note very low sample sizes for chases of squirrels before 1992–93. The phases of the hare cycle (I = increase, P = peak, D = decline, L = low) are shown by the horizontal bar below the bottom x-axis.

particular, often used trails made by other predators and humans. We observed lynx hunting in adult groups during the late decline phase of the cycle, and these groups had higher kill rates in one winter.

Prey switching by coyotes and lynx

“Switching”, as defined by Murdoch (1969), strictly refers to disproportionately low and high use of prey at low and high relative availabilities, respectively, where availabilities are determined by the relative abundances of prey. In this paper, we have used relative biomasses rather than abundances because of the large differences in body sizes of available prey. Our data show a clear increase in the relative use of red squirrels by lynx when squirrels represented more than about 55% of the available biomass of prey (1992–93 through 1994–95); virtually no squirrels were killed when they represented 30% or less of the biomass (1987–88 through 1991–92; Fig. 4). We would argue that this represents a definite “switch” in prey by lynx to red squirrels during periods of low densities of hares. Hares remained the preferred

prey throughout the cycle, but more hunting effort was devoted to pursuing squirrels during these winters.

How robust is our evidence of prey switching by lynx? We were unable to measure the variance among individual predators in percent use of prey, and our measures of prey availability were subject to both sampling error and potential violations of the assumption that relative abundances of prey could be equated with relative availabilities. Given these limitations, we will first examine potential biases in our analysis.

Our conclusions about prey switching are robust to several assumptions that we made. We used the means of autumn and spring prey density estimates as our measures of prey availability, but the pattern of use vs availability in predator diets (Figs 3 and 4) was the same if we used either autumn or spring densities instead of their mean. Likewise, analysing these data using lower availability of squirrels and voles, due to their use of arboreal and subnivean refuges (the

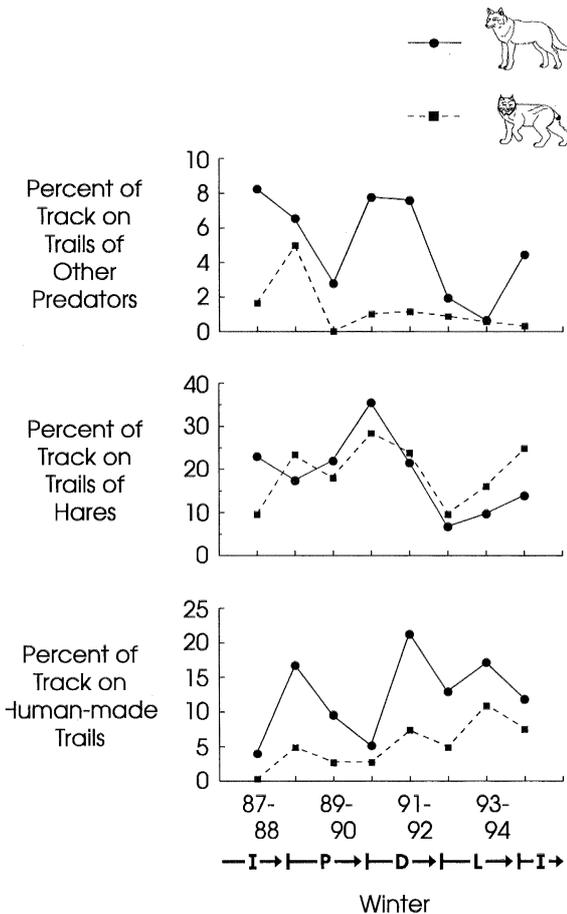


Fig. 11. Percentages of trails of lynx and coyotes on trails made by other predators, snowshoe hares, and humans, in the southwest Yukon during winter, 1987–88 through 1994–95. The phases of the hare cycle (I = increase, P = peak, D = decline, L = low) are shown by the horizontal bar below the bottom x-axis.

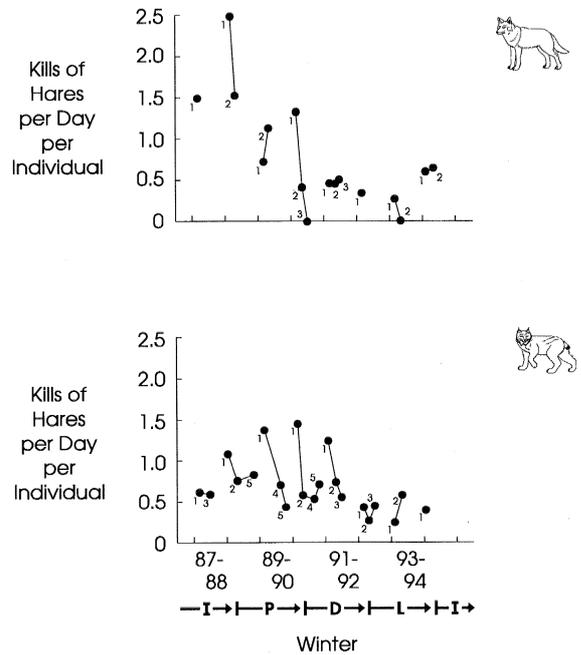


Fig. 12. Average kill rates per individual relative to group size of coyotes and lynx in the southwest Yukon during winter, 1987–88 through 1994–95. Numbers next to the data points indicate group sizes; data points within the same winter are connected by lines. The phases of the hare cycle (I = increase, P = peak, D = decline, L = low) are shown by the horizontal bar below the bottom x-axis.

availability of which varied little among years of this study), did not change our interpretation of prey switching. Different prey species are unlikely to be equally available to predators in any field situation, but the home ranges of coyotes and lynx were extremely large relative to those of their prey, and predators had access to all prey species during their typical wide-ranging daily foraging.

Our graphical analysis of prey switching considered use-availability data relative to a null curve, which we calculated based on overall observed prey preferences of predators, using Manly's alphas. We estimated the proportionality constant (c = ratio, by biomass, in this case, at which squirrels would be eaten if presented in equal abundances with other prey; Murdoch 1969) as 0.09 for squirrels for the lynx null model (Fig. 4). Our interpretation of switching would remain the same though if c was as high as approximately 0.20 (a 5-to-1 selection for other prey – hares, in our study – as opposed to an 11-to-1 selection). The interpretation becomes less clear at very low values of c , since the null curve is then near 0 at low availabilities of squirrels.

In summary, we have strong evidence that the proportion of red squirrels in the diets of lynx increased greatly during the final three years of this study (years of low abundance of hares), that this increased use of squirrels was consistent in all parts of our study area

(suggesting low variance among individuals), and that this change was accompanied by a clear shift in foraging tactics. Our analysis suggests that this shift in use of prey represents prey switching sensu Murdoch (1969), and that this conclusion is robust to violations of the assumptions we have made. We caution though that we cannot generalize our conclusions beyond our study area and period. Our analysis is based on data from one study area over one cyclic fluctuation. However, evidence for prey switching from large-scale, long-term field studies is extremely rare, and replicates will only accumulate over periods of decades.

Prey switching by the "specialist" lynx, rather than the "generalist" coyote was the opposite of what we expected. Coyotes fed heavily on hares during all winters of this study. However, coyotes likely had few other options in our study area (O'Donoghue et al. 1998). While numbers of small mammals were high during some winters, their availability was limited by snow cover. Coyotes spent a large amount of time hunting voles during only one winter, 1993–94. Red squirrels can escape predation by coyotes by climbing trees, and they often spend long periods in their arboreal nests during cold periods (Stuart-Smith and Boutin 1995). The slower hunting speed and ambush beds of lynx seem better suited to hunting squirrels, and lynx were observed to successfully pursue squirrels into trees on several occasions, an option not open to coyotes. "Facultative specialists" (Glasser 1982) may better describe both coyotes and lynx in the boreal forest.

Prey switching is not expected when predators have strong preferences for specific prey, and when there is little variation among individuals in their choice of prey (Murdoch 1969, Murdoch and Oaten 1975). Our data suggest that both predators preferred hares over other prey. We do not know though, whether the shift in diets of lynx towards red squirrels from 1992–93 through 1994–95 was due to all individuals hunting more squirrels, or certain individuals specializing on them. We found that lynx killed mostly squirrels all across our study area from 1992–93 through 1994–95 (Fig. 2), which suggests that prey switching was not just a localized phenomenon. However, we would need to conduct intensive analyses of predation by known individuals to distinguish between these alternatives. Individual preferences for prey, probably learned, have been noted in many felids (Kruuk 1986).

Prey switching may, in some cases, lead to type-3 functional responses (Murdoch and Oaten 1975). However, hares were at very low densities before lynx actively pursued squirrels in large numbers. Our data on kill rates of hares by lynx suggest that the switch back from squirrels to hares may occur at higher densities of hares during the increase phase of the cycle than during the decrease phase (O'Donoghue et al. 1997a). We suggest then that lynx may not be as plastic as coyotes in modifying their foraging behaviour in response to changing relative availabilities of prey.

Use of habitat by coyotes and lynx

Patterns of habitat use by coyotes and lynx changed over the course of the hare cycle, and they were similar to those of hares (Fig. 5). Increasing use of more dense cover by hares during population declines has been noted in a number of studies (e.g., Wolff 1980, Hik 1995). Very dense cover may act as a refuge for hares during population lows (Wolff 1980, Akçakaya 1992). Coyotes and lynx used less dense cover than hares at all phases of the cycle (Fig. 6), and several researchers have concluded that the predators were ineffective at hunting hares in very dense habitats (e.g., Major 1989). During the increase and peak phases of the hare cycle in this study, the hunting success of lynx was about the same in all habitat types, while coyotes were more successful in closed cover (Murray et al. 1994, 1995).

Coyotes and lynx both concentrated their activities in more closed forest types, and in areas with higher densities of hares (Figs 5 and 7). This is consistent with other studies of habitat use by these species in the boreal forest (Brand et al. 1976, Ward and Krebs 1985, Staples 1995, Poole et al. 1996). Coyotes used more open cover during periods of low abundance of hares, which, in 1992–93 and 1993–94, corresponded with winters in which they were often "mousing" in meadows. Lynx used denser habitats than coyotes during these years (Fig. 6), while they hunted red squirrels and hares.

We have no evidence that habitat selection by coyotes and lynx was affected by intraspecific or interspecific competition. Both species used the most dense habitats, where higher numbers of hares were found, during periods of peak abundance of predators, which is the opposite pattern expected if interference among predators was pushing them to suboptimal habitats.

Hunting tactics of coyotes and lynx

Greater use of ambush, as opposed to active searching, is characteristic of felids, whereas most canids typically run down their prey (Eisenberg 1986, Kruuk 1986). The use of hunting beds by lynx has been noted in many studies (Saunders 1963a, b, Haglund 1966, Nellis and Keith 1968, Parker 1981, Murray et al. 1995), but the percent of kills from beds has ranged from 12% (Nellis and Keith 1968) to 61% (Saunders 1963a, b). The density of hares and range of alternative prey available undoubtedly affect the frequency of use of hunting beds. The large increase in use of hunting beds by lynx, during the cyclic decline and low in our study (Fig. 8), suggests an adaptive change in hunting tactics. In Alberta, Brand et al. (1976) suggested that relatively short daily travel distances by lynx at cyclic lows may have been due to increased use of hunting beds.

Hunting success of lynx was not greater from beds when they were preying on hares or squirrels (Fig. 10). As discussed previously though, we used a conservative estimate of the number of kills from beds. Using the criterion that all kills within 30 m of hunting beds were considered ambushes, Murray et al. (1995) found that chases of hares from beds were more successful (46%) than those not initiated from beds (27%) during the cyclic increase and peak at Kluane. Even with comparable or lower hunting success (once chases are initiated) though, hunting from beds may be more energy-efficient during periods of low prey abundance, and may be better suited for hunting alternative prey such as squirrels.

Coyotes made a major shift in hunting tactics during the second winter of the cyclic low in abundance of hares (1993–94), when the frequency of “mousing” greatly increased along their trails. They shifted back to hunting hares in more closed cover the following winter though.

Use of trails by coyotes and lynx can help them conserve energy while travelling, and, when following trails of hares, can increase encounter rates with prey. Coyotes have a relatively high foot-load, and deep snow inhibits their movements and hunting success (Wells and Bekoff 1982, Murray and Boutin 1991). Both predators may follow hare trails as a hunting technique (Brand et al. 1976, Keith et al. 1977). Our data showing higher use of hare trails by both predators during periods of increasing hare abundance are consistent with the suggestion of Keith et al. (1977) that this may contribute to increasing kill rates by coyotes (leading to a type-3 functional response), but they may simply be a reflection of increased abundance of trails to follow as well.

While certainly not conclusive, our data suggest that foraging success of adult groups of lynx was higher than that of single animals in 1993–94 (Fig. 12). Family groups of lynx are typical of the species during winter, and, since kittens are apparently less skilled at hunting than adults (Saunders 1963a), per-individual kill rates are lower. Families do hunt as a unit though, with young animals usually flanking the female through good hunting habitat (Saunders 1963a, Haglund 1966, Parker 1981). We have found only one other reference to groups of adult lynx hunting together (Barash 1971). We did not know the relationships among the animals in adult groups, although we suspected one group included an adult female and her grown daughter. Increased foraging success has been suggested as one of the benefits of group-living by carnivores (review in Gittleman 1989), and while it is certainly not typical of lynx, it may be temporarily beneficial to them during periods of low prey abundance.

Coyotes often hunt in pairs or family groups, particularly when hunting larger prey (Bowen 1981, Messier and Barrette 1982). Possible cooperative hunting of

hares by coyotes, in which one animal runs through good patches of cover while the other circles the perimeter, has been reported by Ozoga and Harger (1966), and observed in this study as well. Increased foraging efficiency with group size has not been generally noted for coyotes though (Messier and Barrette 1982, Bekoff and Wells 1986).

Conclusions

We found clear behavioural responses by coyotes and lynx to the snowshoe hare cycle. Coyotes preferred hares to other prey at all densities, and changes in their use of habitat followed those of hares. They concentrated their hunting activities in areas of high hare numbers. During years of low abundance of hares, and high vole numbers, coyotes used more open cover while “mousing”. Coyotes frequently used trails of other predators, humans, and, particularly during cyclic highs, hares for travel and hunting.

Lynx also preferred hares to other prey at all densities, but switched to preying on red squirrels during the cyclic low and subsequent early increase in hare abundance. Habitat use by lynx followed the same general pattern as that of hares, and lynx concentrated their activities in areas of high hare numbers. During the cyclic decline and low, lynx increasingly used ambush beds, from which they hunted both hares and squirrels. Hunting success was not higher from beds, but hunting by ambush may have been more energetically efficient during periods of low prey abundance. We observed groups of 2–3 adult lynx hunting together during the decline and low phases of the cycle, and limited data suggest that they had increased foraging success in one year.

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