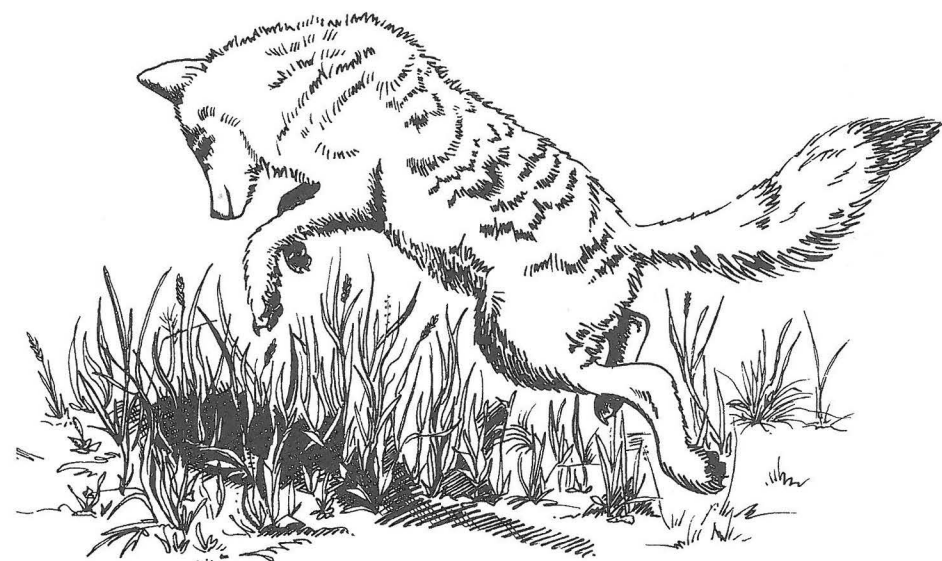

Coyotes and Lynx

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Coyotes and lynx are the two most important mammalian predators of snowshoe hares throughout much of the hare's geographic range. Between them, these two predators killed approximately 60% of all depredated radio-collared hares at Kluane from 1986 through 1996 (Krebs et al. 1995), and predation accounted for at least 78% of all mortalities during this same period.

The strong association of lynx numbers with those of snowshoe hares is well documented (Elton and Nicholson 1942, Moran 1953, Finerty 1980, Schaffer 1984, Royama 1992). The abundance of lynx typically follows the 10-year cyclic fluctuations of hares, and lynx-hare cycles have often been presented in ecology texts as classic predator-prey interactions. The geographic ranges of lynx and hares overlap almost exactly (Banfield 1974, figure 2.7), and all published studies of the food habits of lynx have found snowshoe hares to be the main dietary component (e.g., Saunders 1963a, Van Zyll de Jong 1966, Brand and Keith 1979, Parker et al. 1983). Morphologically, lynx are well adapted to hunting hares in the deep, powdery snows of the boreal forest because of their long legs and large snowshoe-like paws (Murray and Boutin 1991).

Whereas lynx may be considered prototypical specialists on hares, coyotes are generally viewed as opportunistic generalists (Bond 1939, Fichter et al. 1955, Van Vuren and Thompson 1982, but see MacCracken and Hansen 1987, Boutin and Cluff 1989), consuming prey items in the same relative proportions as are available. Indeed, across their large and expanding range in North America (figure 2.7), coyotes show a wide variety of feeding habits, habitat preferences, and social groupings (see Bekoff 1978). Coyotes are relatively recent colonizers of the boreal forest (Moore and Parker 1992); historical records suggest they arrived in the Yukon Territory between 1910 and 1920 (M. Jacquot and J. Joe, from unpublished transcripts of interviews by G. Lotenberg for Parks Canada). Unlike lynx, coyotes have fairly small paws, which restrict their ease of travel over soft snow (Murray and Boutin 1991).

There have been few studies of coyotes in the boreal forest, and only those in Alberta (Nellis and Keith 1968, 1976, Nellis et al. 1972, Brand et al. 1976, Keith et al. 1977, Brand and Keith 1979, Todd et al. 1981, Todd and Keith 1983) and the Yukon (Murray and Boutin 1991, Murray et al. 1994, 1995, O'Donoghue et al. 1995, 1997, 1998a,b) have addressed the relative roles of coyotes and lynx as predators of snowshoe hares and alternative prey. In the Alberta study, approximately one-third of the study area was agricultural land, and this area was used extensively by coyotes when hares were scarce. These Yukon studies therefore represent the first comparison of the dynamics and foraging behavior of coyotes and lynx in the contiguous northern forests.

Based on the generalist-specialist contrast between coyotes and lynx, we predicted that the two predators would respond dissimilarly to cyclic fluctuations of hares and, as a result, could affect populations of hares and other prey species differently as well. The direct effects of predation on prey populations are determined by the combined numerical (changes in rates of reproduction, survival, immigration, and emigration) and functional (changes in kill rates) responses of the predators to varying densities of prey (Solomon 1949). In Alberta, coyotes and lynx responded to a cyclic fluctuation in numbers of hares with similar four- to sixfold numerical responses; the highest numbers of coyotes occurred at the peak of the hare cycle, while abundance of lynx lagged 1 year behind (Keith et al.

1977). Coyotes, however, maintained densities roughly double those of lynx at all phases of the cycle (Brand et al. 1976, Keith et al. 1977, Todd et al. 1981). The calculated functional response of coyotes to changing densities of hares in Alberta was sigmoidal (type 3; Holling 1959b), whereas that of lynx was convex curvilinear (type 2) (Keith et al. 1977), which appears to support the generalist-specialist contrast between coyotes and lynx.

The estimated numerical and functional responses of coyotes, lynx, and avian predators during the cycle in abundance of hares in Alberta led Keith et al. (1977) to conclude that predation rates were not sufficient to account for the slowing of growth and eventual cyclic decline in hare populations. Rather, they considered the hare cycle to be primarily generated by an interaction between hares and their winter food supply (Keith and Windberg 1978, Keith et al. 1984, Keith 1990), with delayed density-dependent predation acting to increase mortality rates of hares once population growth had halted due to food shortage, thus deepening and hastening the cyclic declines. This view of the role of predation in generating population cycles corresponded with the conventional wisdom summarized by Finerty (1980). In addition to affecting cyclic amplitudes and the rapidity of population declines, predators could also act to increase the length of population cycles, due to the lag effect of predators persisting into periods of low prey populations, and possibly synchronize cycles over large geographic areas, due to the large-scale movements of northern predators (Finerty 1980).

The empirical results of the Kluane experiments presented in this book (see also Krebs et al. 1986, 1995, Sinclair et al. 1988, Smith et al. 1988) and the conclusions from recent models (Trostel et al. 1987, Akçakaya 1992, Royama 1992, Stenseth 1995) suggest that predation may play a larger role in generating cyclic fluctuations in numbers of snowshoe hares than previously thought. Likewise, researchers in Fennoscandia have suggested that differences in the degree and nature of predation can explain the geographic pattern of cyclicity in abundance of voles in that region. More diverse prey communities in the south support higher numbers of generalist predators, which can regulate vole numbers by strong functional responses (Erlinge 1987, Erlinge et al. 1983, 1984, 1988), while the resident specialists (weasels) of the north respond numerically, which results in a time lag and cyclic fluctuations (Henttonen et al. 1987, Hanski et al. 1991, Korpimäki et al. 1991, Korpimäki 1993, Lindström and Hörnfeldt 1994). This pattern is in agreement with the different theoretical effects of generalist and specialist predators on the stability of predator-prey interactions (Murdoch and Oaten 1975, Hassell and May 1986, Crawley 1992).

The aim of the research on predators that was conducted as a part of the Kluane Project was to examine in detail the changes in densities, demographics, predation rates, and behavior of the most important species during a cyclic fluctuation of hares. These studies would then complement the smaller-scale experimental manipulations of prey densities in elucidating the roles of different predators in the boreal food web (Boutin 1995). In particular, the main objectives of the studies of coyotes and lynx were to

1. Determine and contrast the numerical responses of coyotes and lynx during a cyclic fluctuation in numbers of snowshoe hares and the demographic mechanisms behind them,
2. Determine and contrast the functional responses of coyotes and lynx to changes in densities of hares,

3. Examine changes in foraging behavior (e.g., prey switching, changes in foraging tactics) of coyotes and lynx that contribute to their functional responses, and
4. Estimate the total effects of predation by coyotes and lynx on populations of snowshoe hares and the main alternative prey.

13.1 Methods

We used snow tracking (following and counting tracks) of coyotes and lynx during winter and radio telemetry as our main field methods during these studies. With the exception of some limited collection of scats, live trapping, and radio monitoring, field work was conducted during the winter months, from October to April.

13.1.1 Population Monitoring

Densities of large, mobile predators are notoriously difficult to estimate. We combined data from the movements of radio-collared coyotes and lynx with those from our snow tracking to make annual early-winter estimates of numbers of predators in our study area (O'Donoghue et al. 1997).

From 1986 through 1996, we live trapped and radio collared 21 individual coyotes (CD-ROM frame 35) and 56 lynx (CD-ROM frame 34) (techniques similar to Poole et al. 1993, Mowat et al. 1994). Most of the radio collars were equipped with mercury activity switches (Telonics, Mesa, Arizona), which allowed us to monitor the activity patterns of collared animals in addition to gathering data on their movements, home ranges, and survival rates (CD-ROM frame 41). We attempted to obtain at least one precise location per week for each collared coyote and lynx to calculate the boundaries of their home ranges; from 1990 through 1992, lynx were monitored more frequently, as a part of a study of their social organization (U. Breitenmoser, unpublished data). We plotted telemetry locations using LOCATE II (Nams 1990) and calculated home ranges as 95% minimum convex polygons (Mohr 1947) using CALHOME (Kie et al. 1994).

We counted the tracks of coyotes and lynx each winter (October through April) along a 25-km transect that traversed our study area, on days after fresh snowfalls while tracks were distinguishable (CD-ROM frame 43). These counts gave us indices of the numbers of predators present each winter and also information on the locations of animals that we did not radio collar (O'Donoghue et al. 1997). From 1986–1987 through 1996–1997, we counted tracks along 12,194 km of transect.

We also followed the tracks of coyotes (2134 km) and lynx (2500 km) during winter from 1987–1988 through 1996–1997 to gather data on foraging behavior (described below). Tracking began each season as soon as there was enough snow, usually in late October, and finished at the end of March. We selected fresh tracks crossing roads and trails on any days when weather and snow conditions were suitable. We attempted to distribute our tracking over the entire study area, throughout the winter, and among all group sizes of predators. During a tracking session, tracks were followed first backward (relative to the animal's direction of travel) as far as possible, and then forward from the starting point, to attain segments of trail of maximum length. The routes taken by predators we tracked provided us with additional information on the presence and locations of uncollared coyotes and lynx.

We estimated the total populations of coyotes and lynx in our study area by plotting the home ranges of radio-collared animals, and filling in missing animals based on our data from the track transects, snow tracking, and, in the case of coyotes, records of howling (O'Donoghue et al. 1997). We were not in the field enough during the first and last winters of this study (1986–1987 and 1996–1997) to estimate populations of predators accurately. We estimated survival and dispersal rates from our radio monitoring (Pollock et al. 1989) and calculated indices of recruitment by examining the distribution of group sizes of coyotes and lynx along the track transect (O'Donoghue et al. 1997).

13.1.2 Foraging Behavior

We gathered most of our detailed data on the foraging behavior of coyotes and lynx by snow tracking. Trackers, on snowshoes for most of the winter, followed the trails of predators and made a continuous record of the animals' hunting behavior, use of habitat and trails, and notable activities. Data were recorded on microcassettes in the field, and all events along the trails were noted at the tracker's step number, which was kept track of with a tally counter (steps were later converted to meters, using observer-specific conversion factors). Over the course of the study, 22 different observers collected data, of which 19 were full-time trackers.

We recorded all instances of kills and attempted kills by predators along trails. At each kill site, the prey species, the length of the chase, the percentage and parts of the carcass consumed, and any observations about feeding or caching behavior were noted. For attempted kills, we recorded the prey species and the length of the chase. Details of all scavenging by coyotes and lynx were also collected. We estimated the amount of food the predator had consumed when possible (from impressions in the snow), noted whether the prey had been previously cached, and looked for any evidence of the initial cause of death of the prey. We collected all scats along trails for later dietary analyses.

Data on the travel patterns of coyotes and lynx were also recorded. We classified all beds used by predators as "crouches" (or ambush beds), "short beds" (those in which the animal lay down, but did not stay long enough to melt the snow), or "resting beds." Instances of running, circling, or other hunting activities were noted. We recorded the amount of time that the trails we followed were on top of trails of other predators, moose, hares, snowmobiles, and snowshoes. (At high densities of hares, it became nearly impossible to record all instances of travel on hare trails, so we switched to noting whether predators were on or off of hare trails at 100-step intervals. For analyses, all records of travel on hare trails were converted to these 100-step measures; O'Donoghue et al. 1998a.)

We kept a continuous record of habitat used by coyotes and lynx by estimating the percent canopy cover (as <5%, 5–25%, 25–50%, 50–75%, or 75–100%) and dominant species and age (mature or immature) of the trees in the overstory. We also measured the sinking depth of the predator in the snow and snow depths and hardness on the trail and 1 m off the trail at 500-step (1987–1988 and 1988–1989) or 600-step (after 1988–1989) intervals (Murray and Boutin 1991). In 1996–1997, the last winter of tracking, we gathered data only on kills, attempted kills, scavenging, and beds used by predators, and discontinued our collection of data on habitat use, snow characteristics, and use of trails.

Our data on habitat use were collected continuously by many different observers, each of whom subjectively estimated canopy cover; these characteristics necessitated addi-

tional steps in the analyses of these data. We calculated the interval length (200 m) at which measurements of habitat should be independent based on patch sizes in our study area by using a bootstrapping technique with a set of patch lengths from transects run to classify habitat types (O'Donoghue et al. 1998a). We then sampled at 200-m intervals from each tracker's records separately to calculate frequencies of habitat types and mean overstory cover used by coyotes and lynx. Statistical analyses comparing habitat use between years and species were conducted separately by observer, and the results were combined using meta-analyses (Rosenthal 1978, Arnqvist and Wooster 1995) to control for observer-specific biases (O'Donoghue et al. 1998a).

The scats collected while tracking and during other field work were frozen and stored for later analysis. We subsampled scats by month and location in the study area each winter to maximize the temporal and spatial distributions of our samples. We identified the hairs in 10–30 random subsamples of each scat and summarized the data as relative frequency of occurrence by prey species (O'Donoghue et al. 1998b). Although prey species with small body sizes are often overrepresented in diets inferred by scat analyses (Floyd et al. 1978, O'Gara 1986), relative frequency of occurrence of prey in scats of coyotes was approximately equal to the percent biomass ingested in one study (Johnson and Hansen 1979). We also identified the species for any recognizable teeth and bone fragments found in scats.

In addition to snow tracking, we used several other field methods to supplement our data on foraging behavior of coyotes and lynx. While tracking, we made frequent observations of predators, particularly coyotes, scavenging prey from caches, but we were seldom able to tell how the prey had initially died, which predator had made the cache, or when the initial kill had been made. We were able to gather data on the frequency and timing of caching by predators by examining the patterns of caching of depredated, radio-collared hares. Beginning in 1992–1993, we monitored use of these caches by leaving all caches located while snow tracking or retrieving mortalities of radio-collared hares undisturbed, except for the attachment of a radio monitor (O'Donoghue et al. 1998b). A beacon radio was hung in a nearby tree at each cache site, and a second "cache collar" was hidden under the snow nearby with a steel wire running from its battery to the cache. When a cached carcass was disturbed, the battery from the cache collar became dislodged, and we could then return to the site and collect data on the return time, amount of carcass eaten, and details of cache use by predators.

Finally, to investigate the degree of use of prey hot spots by predators during the hare cycle, we made use of the experimental grids of the Kluane Project. Starting in 1988–1989, we counted tracks of predators around two food addition grids (which had roughly three times the density of hares as on control grids; Krebs et al. 1995; chapter 8) and one or two control grids after fresh snowfalls during the winter, when weather conditions were suitable. These counts were summarized as tracks per day for subsequent analyses (O'Donoghue et al. 1998a).

13.1.3 Functional Responses

The kill rates of coyotes and lynx from our snow-tracking data were expressed as kills/distance of trail, but this was not a useful measure for calculating the functional responses or total impacts of predation by the two predators on densities of prey. We needed to con-

vert our kill rates to kills/day for this purpose. Our annual tracking records consisted of measured distances that the predators were traveling and a variable number of events during which animals were inactive (beds) or stationary (kills, scavenging). To calculate the amount of time represented by our tracking records, we estimated the time spent by predators at each of the above activities.

We calculated travel rates of coyotes and lynx by opportunistically conducting time trials with our radio-collared animals from 1989–1990 through 1994–1995 (O'Donoghue et al. 1998b). When a collared animal was in an accessible location, we obtained an accurate location by walking toward the animal and making a visual observation or finding a recently left bed. If we were successful in obtaining this location without disturbing the animal, we then monitored the animal's activity until we could obtain a second location, usually one to several hours later, after which we followed and measured the trail in between these two points. We calculated travel rates from successful time trials by dividing the distance traveled by the time interval minus any inactive periods (CD-ROM frame 42). Breitenmoser et al. (1992) used this same technique to verify the use of monitoring via intensive radio telemetry for measuring movement rates of lynx.

We estimated the total amount of inactive time spent by coyotes and lynx (on beds) by monitoring the activity patterns of radio-collared animals. From 1990–1991 through 1995–1996, we used a Lotek SRX-400 programmable receiver with a data logger (Lotek, Newmarket, Ontario) to record pulse rate and signal strength every 30 sec (based on three signal pulses each reading) for selected collared predators (O'Donoghue et al. 1998b). From these records, we used a discriminant function, developed by simultaneously monitoring the activity of predators "by ear" (with observers judging periods of activity and inactivity based on the characteristics of the radio signal) and with the programmable receiver to calculate the percent time spent inactive each winter. Based on comparisons with activity patterns inferred from manual monitoring of predators, this remote technique allowed accurate calculation of inactive periods (O'Donoghue et al. 1998b).

With the calculation of travel rates and percentages of inactive time for coyotes and lynx, we could then convert our kill rates of hares to kills/day. We calculated the amount of active predator time represented by our track records each winter for coyotes and lynx separately by dividing the total track distances by the measured travel rates and adding standard times for each occurrence of a kill or scavenging event (O'Donoghue et al. 1998b). The total number of "coyote-days" and "lynx-days" were estimated by dividing the active times by the percent of time active during each winter to account for time spent on beds.

We plotted kills/day per coyote and lynx against the autumn, spring, and mean densities of hares each winter to calculate their functional responses (O'Donoghue et al. 1998b). We fitted linear and type-2 (Holling's disc equation; Holling 1959a) curves to our estimated kill rates for graphical description. Given that we estimated kill rates in only 10 winters, with no replication at given densities of hares, we had little statistical power to distinguish among shapes of the functional response curves (Trexler et al. 1988; Marshal and Boutin 1999) and did not attempt to do so.

Switching by predators among prey types, as the relative frequencies of prey species change, is one mechanism that may affect the shape and magnitude of a predator's functional response. *Switching* is defined as feeding on a prey species disproportionately less when its relative abundance to other prey species is low and disproportionately more when

it is high (Murdoch 1969). We used a graphical analysis similar to that of Murdoch (1969) to analyze our data on prey use versus availability, using relative biomass of prey instead of relative frequencies due to large differences in body sizes of the main prey species at Kluane (O'Donoghue et al. 1998a). We first calculated null curves for coyotes and lynx preying on hares, red squirrels, and small mammals (to represent the predators' innate prey preferences: convex curves for preferred prey and concave for avoided; Murdoch 1969), using the ratios of mean Manly's alphas calculated each winter (Manly et al. 1972; these measure the probability that an individual prey item would be selected when all prey classes are equally available; Krebs 1999) as proportionality constants (Murdoch 1969, equation 2). When percent use of prey classes (in this case, hares, red squirrels, and small mammals) in predator diets are plotted against percent availability of the same prey, a pattern of points below the null curve at low relative availability (<50%) and above it at high availability suggests that switching occurred.

13.2 Numerical Responses

13.2.1 Density

Populations of both coyotes and lynx fluctuated widely during this study, following the 26- to 44-fold cyclical change in numbers of snowshoe hares (chapter 8; Boutin et al. 1995). Densities of coyotes varied sixfold, with peak numbers (approximately 9/100 km²) occurring in 1990–1991, a year after the cyclic high of hare populations (figure 13.1; O'Donoghue et al. 1997). This was followed by a rapid decline in densities of coyotes to a low of 1.4/100 km² in 1993–1994. Likewise, densities of lynx varied about 7.5-fold, and peak densities (17/100 km²) in 1990–1991 declined to a low of 2.3/100 km² in 1994–1995 (figure 13.1; O'Donoghue et al. 1997). The populations of both predators declined at similar rates: in 1992–1993, the second winter of declining predator numbers, coyote density was 30% ($r = -.60$ from 1990–1991 to 1992–1993) and lynx density 25% ($r = -.69$) of their respective peak densities. Our estimates of numbers of predators in our study area were highly correlated (coyotes: $r_s = .88$; lynx: $r_s = .95$) with the abundance of tracks along the 25-km transect (O'Donoghue et al. 1997).

When we plotted our estimates of densities of coyotes and lynx against densities of hares (means of autumn and late winter estimates), the numerical responses showed a counterclockwise pattern typical of delayed density-dependent responses (figure 13.2; O'Donoghue et al. 1997).

Coyotes in Alberta underwent a similar three- to sixfold fluctuation in abundance, but their numbers followed the cycle in numbers of hares with no lag (Keith et al. 1977, Todd et al. 1981). Densities of coyotes in that study were much higher than at Kluane, ranging from 8 to 44/100 km², and they declined at a slower rate from their peak; after 2 years of decline, densities were still 78% of peak numbers. Lynx in the Alberta study also varied three- to fourfold during the same cycle, their numbers peaking at 10/100 km² 1 year after the cyclic peak in numbers of hares (Brand et al. 1976, Keith et al. 1977). Other studies of lynx in northern Canada have found higher amplitude cycles of lynx: 10- to 17-fold in south-central Yukon (peak density 50/100 km²; Slough and Mowat 1996), and 10-fold

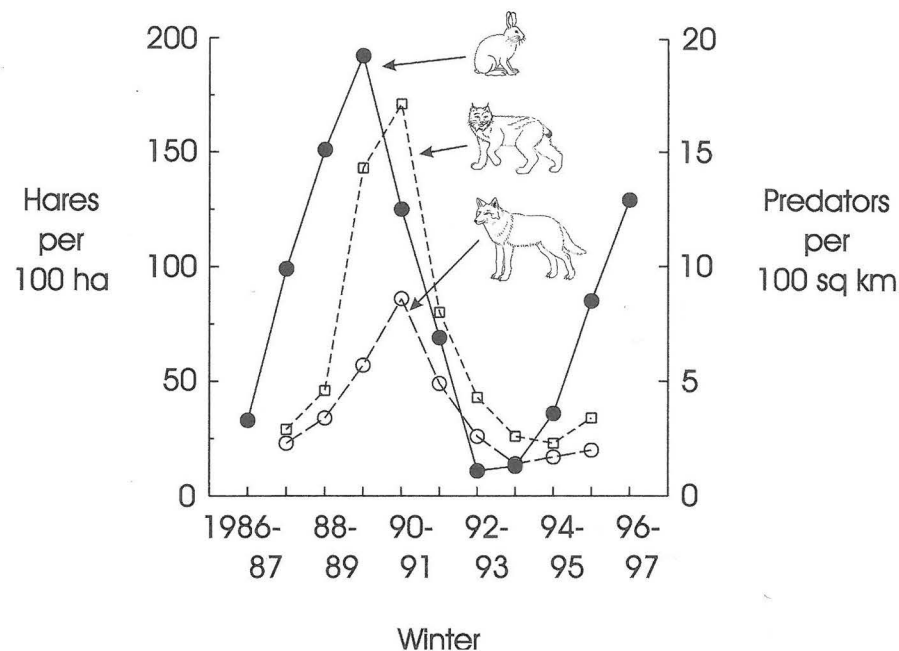


Figure 13.1 Estimated densities of snowshoe hares (means of autumn and late winter estimates) from 1986–1987 through 1996–1997, and coyotes and lynx during winter from 1987–1988 through 1995–1996 in the Kluane Project study area.

in the Northwest Territories (peak 30/100 km²; Poole 1994), both with high densities 1 year after the highest densities of hares.

Numerical responses of predators may be associated with changes in survival, migration, and reproduction. We examined our data to determine which mechanisms were most important in causing the changes in densities that we observed.

13.2.2 Adult Survival

Survival of our radio-collared lynx varied considerably among phases of the hare cycle. Overwinter survival rates were relatively high (30-week Kaplan-Meier survival rate, 0.67–1.00) from the late cyclic increase (1987–1988) to the second year of declining hare numbers (figure 13.3; O'Donoghue et al. 1997). All of the lynx we had radio-collared at the beginning of 1992–1993 (the first year of the cyclic low; $n = 9$) either died or dispersed. The low survival calculated in 1993–1994 is largely due to starting that year with only two collared lynx, one of which died; three of the four lynx subsequently collared during the winter survived (O'Donoghue et al. 1997). Lynx that survived into the subsequent cyclic increase all survived to the end of the study.

The main causes of mortality of collared lynx during the study were human caused (fur trapping), except in the cyclic low (1992–1993 and 1993–1994), when predation and star-

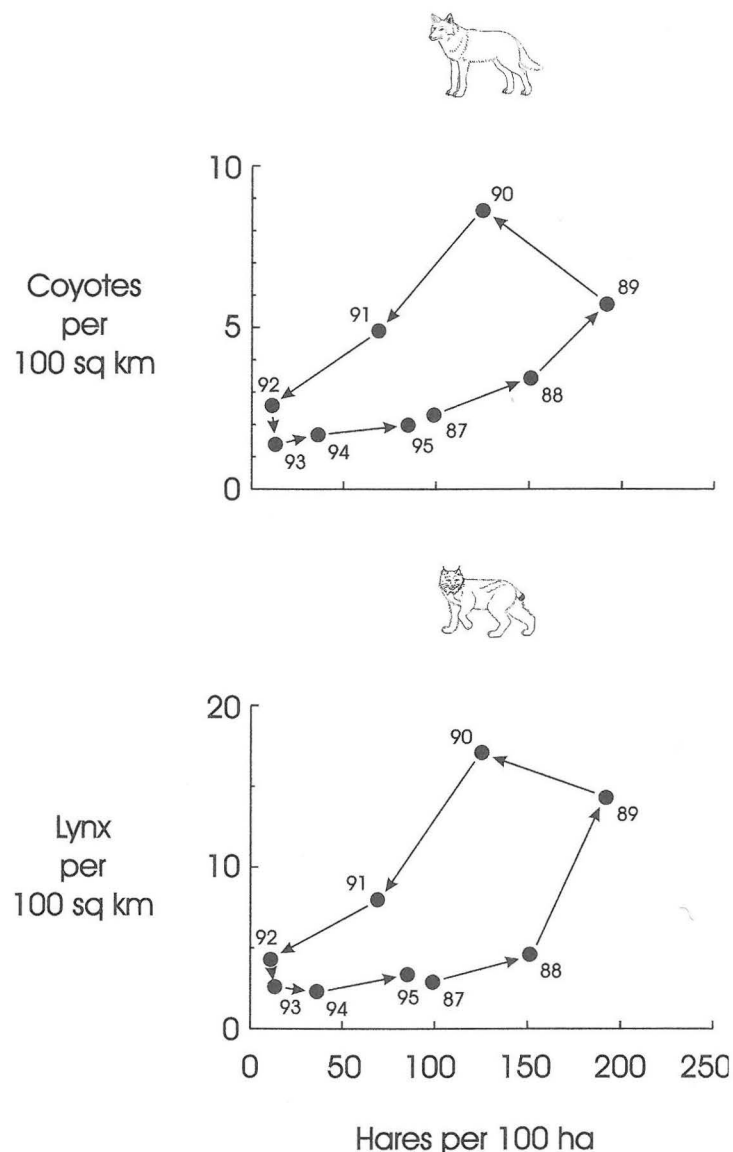


Figure 13.2 Numerical responses of coyotes and lynx to the cyclic fluctuation in densities of snowshoe hares at Kluane from 1987–1978 through 1995–1996. Densities of coyotes ($r_s = 1.00$) and lynx ($r_s = .98$) were highly correlated with densities of hares during the previous winter. Numbers next to the data points indicate years (e.g., 87 = winter of 1987–1988).

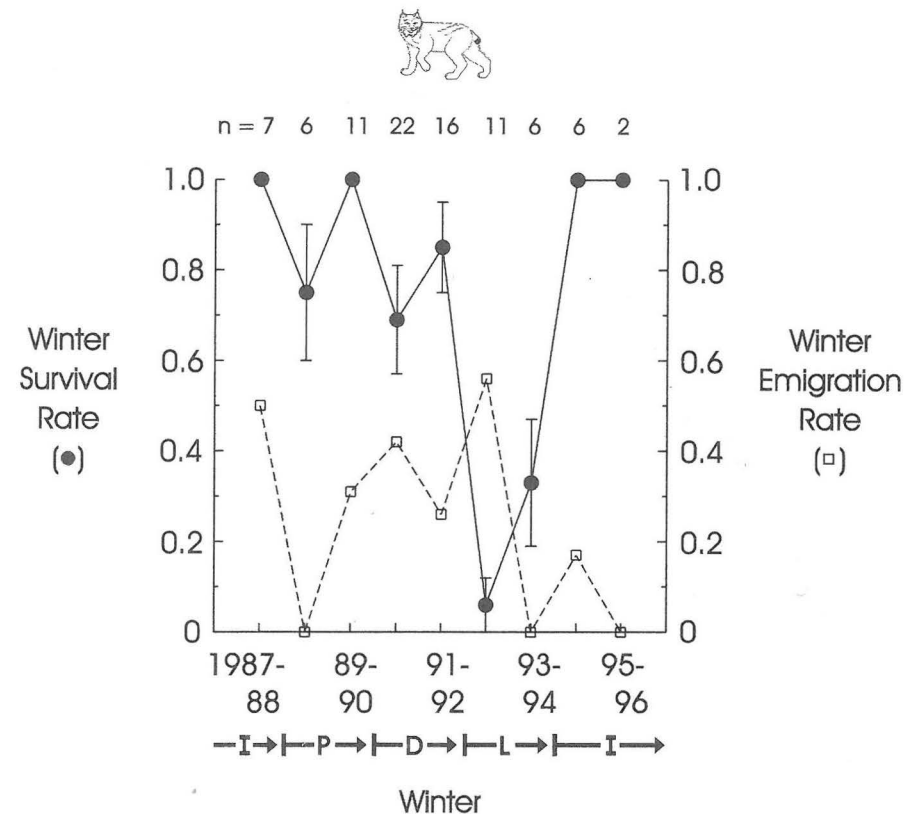


Figure 13.3 Kaplan-Meier survival (\pm SE) and emigration rates of lynx during winter (October through April) from 1987–1988 through 1995–1996 at Kluane. The number of radio-collared lynx monitored each winter is given at the top of the figure. The phases of the hare cycle (I = increase, P = peak, D = decline, L = low) are shown by the horizontal bar below the x-axis.

vation were more important (O'Donoghue et al. 1995, 1997). We confirmed three cases of predation on lynx by a wolf, a wolverine, and another lynx, and we also suspected predation by wolverines on two other lynx. Two lynx starved to death; we do not know if the depredated lynx would have survived, and suspect at least some were in poor condition.

Due to low sample sizes, we can say little about the survival rates of coyotes during our study. Of the 21 collared coyotes, 5 died, and 4 of these deaths were caused by humans. Most other animals emigrated from our study area, and we do not know if they survived.

Low survival of lynx following cyclic declines in densities of hares was noted in the two other northern studies of lynx as well. In the Northwest Territories, survival rates were high (0.90) during the peak and early decline phases, but decreased to 0.25 and 0.37 in the subsequent two winters (Poole 1994). Likewise, survival rates of lynx declined from near 0.90 at the cyclic peak to 0.40 in the second winter of declining abundance of hares in the

south-central Yukon (Slough and Mowat 1996). Natural causes (starvation and predation) were the principal reasons for mortalities in both of these lightly-trapped study areas.

13.2.3 Emigration

Emigration was the main cause of loss of radio-collared coyotes from our study area. Thirteen of the 21 collared coyotes (62%) traveled beyond the range of our radio monitoring; this included 4 of 5 pups and 9 of 16 adults (O'Donoghue et al. 1997). We documented the distances moved by two coyotes that were trapped 23 and 40 km from their initial capture sites.

Radio-collared lynx emigrated from our study area during most winters, and rates were highest in 1987–1988 and from the peak to the early low phases of the hare cycle (figure 13.3; O'Donoghue et al. 1997). The calculated rate in 1992–1993 is inflated by the emigration of one of two surviving radio-collared lynx after most others had died. Over the whole study, 17 of 39 adults (44%) and 7 of 12 juveniles (58%) left our study area. We recovered the collars of 10 radio-collared lynx that had emigrated, mostly from fur trappers, and these were collected from 23 to 830 km from their capture sites. Five of six animals that moved long distances (>200 km) from their initial locations left our study area in 1991–1992; most of those leaving their home ranges later in the cyclic decline or low died within our study area (O'Donoghue et al. 1995, 1997).

High emigration rates of lynx during cyclic declines and lows have also been reported in the previous population cycle on our study area (Ward and Krebs 1985), in south-central Yukon (Slough and Mowat 1996), and in the Northwest Territories (Poole 1997). Lynx in all three of these other studies moved long distances (up to 1100 km) from their initial locations. Survival of dispersers was poor during the first winter of the cyclic low in the Northwest Territories (Poole 1997), and Ward and Krebs (1985) also noted that no animals made long-distance migrations once densities of hares had declined below 1/ha.

13.2.4 Recruitment

Although we did not directly measure reproductive output or juvenile survival of coyotes and lynx in our study area, we examined our observations from track counts for changes in the frequency and magnitude of group sizes. Family groups of lynx are easily recognized from tracks by the smaller foot-size of kittens, but this is not possible with coyotes, so we considered all groups of more than two coyotes to be family groups.

Both predators traveled in larger groups during periods with higher densities of hares. We observed family groups of coyotes only in the four winters from 1988–1989 through 1991–1992, and again in the last two winters of the study (figure 13.4). During the three winters of lowest abundance of hares (1992–1993 through 1994–1995), no groups larger than two were noted. Group sizes were largest in 1990–1991 and 1991–1992 (O'Donoghue et al. 1997).

Evidence of recruitment by lynx also followed the same trend. Few family groups were seen after the winter of 1990–1991, and none was seen in 1993–1994 and 1994–1995 (figure 13.4; no lynx kittens were noted in 1986–1987 either, but we cannot calculate percent family groups, as individual groups were not recorded separately). Family groups were largest from 1988–1989 through 1990–1991 (O'Donoghue et al. 1997).

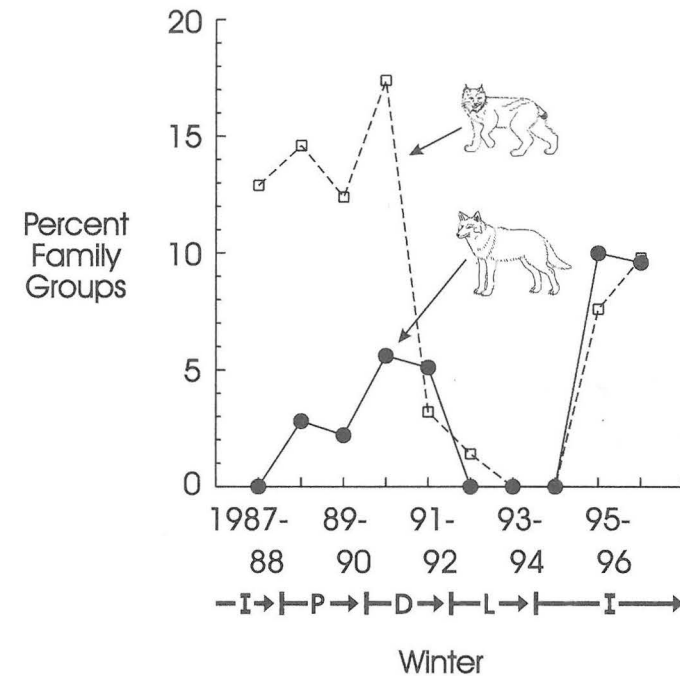


Figure 13.4 Percentages of observations of coyote and lynx tracks along a 25-km transect composed of family groups (groups of coyotes with more than two animals or groups of lynx with kittens) during winter from 1987–1988 through 1996–1997 at Kluane. The phases of the hare cycle (I = increase, P = peak, D = decline, L = low) are shown by the horizontal bar below the x-axis.

Large declines or cessation of reproduction by coyotes and lynx during cyclic declines of their main prey have been noted in many other studies. In Alberta, adult ovulation rates, pregnancy rates and litter sizes, and breeding by yearling female coyotes all declined as hare densities reached their cyclic low (Todd et al. 1981, Todd and Keith 1983). Reproductive output of coyotes in Utah was also reduced during a cyclic decline of black-tailed jackrabbits (*Lepus californicus*) (Clark 1972). Likewise, studies of lynx in south-central Yukon (Mowat et al. 1996, Slough and Mowat 1996), the Northwest Territories (Poole 1994), Alberta (Nellis et al. 1972, Brand et al. 1976, Brand and Keith 1979), Alaska (O'Connor 1986), and Nova Scotia (Parker et al. 1983) have all shown that recruitment by lynx virtually ceases during periods of low abundance of snowshoe hares. Based on examination of carcasses, several studies have suggested that postpartum mortality of kittens may be the largest factor contributing to the drop in recruitment (Brand and Keith 1979, Parker et al. 1983).

13.3 Social Organization

Our primary objectives in radio collaring coyotes and lynx were to determine their main areas of activity, measure their travel rates, determine their survival and emigration

rates, and monitor their activity patterns. Except for a more detailed study of spatial relationships among lynx from 1990 through 1992, we did not monitor predators frequently enough, or with sufficient precision, to draw robust conclusions about the social organization of coyotes and lynx in our study area. We briefly discuss the limited data we gathered here, as they relate to those from other more comprehensive studies.

13.3.1 Home Ranges

We monitored few coyotes often enough to estimate the sizes or spatial arrangement of their home ranges. The annual home ranges of five coyotes (two adult males and three adult females) averaged 24.7 ± 10.6 (SD) km^2 in years of high densities of hares (1988–1989 and 1990–1991), while those of two adult males were 75.4 ± 2.9 km^2 at the cyclic low (1993–1994), suggesting that the sizes of home ranges may have increased with lower prey abundance. We did not monitor any individual animals over the course of the cyclic decline, though, so we do not have data on the persistence of family territories.

Our data on the home ranges of lynx in our study area are more complete after 1989. In 1990–1991, the home ranges of adult males averaged 24.3 ± 9.3 km^2 ($n = 7$), while those of females were 16.7 ± 13.7 km^2 ($n = 4$). There was a general trend of increasing sizes of home ranges during the cyclic decline, and, by 1994–1995, the ranges of males and females averaged 39.5 ± 11.4 km^2 ($n = 2$) and 45.2 ± 3.4 km^2 ($n = 2$), respectively. The same trend was true for individual lynx that persisted in the study area between 1990–1991 and 1992–1993. The sizes of home ranges of males were larger than those of females in all years of this study except 1994–1995, but these differences were not statistically significant (Mann-Whitney U -tests; $p > .12$) in any year.

The degree of intrasexual spatial overlap and fidelity to home ranges by lynx changed considerably as densities of hares declined. In 1990–1991, adult lynx maintained essentially intrasexually exclusive territories (mean percent overlap = 7% among adult males and 11% among adult females with >20 radio locations; calculated as in Poole 1995), with the exception of two, probably younger, adult males, which had home ranges almost completely within those of other males. In the next two winters, this territoriality apparently broke down. Established residents made longer forays outside and shifted the boundaries of their home ranges, and new adult males were captured with ranges that broadly overlapped those of other conspecifics (mean percent overlap = 75% and 28% for males and females, respectively). During 1992–1993, all previously collared residents died or emigrated, and new lynx captured in the subsequent two winters established home ranges that were again intrasexually exclusive.

These observations about the spatial organization of lynx are consistent with those made in other studies. Several lynx became nomadic, but persisted on our study area during the previous cycle in the early 1980s, once densities of hares had declined below 0.5/ha (Ward and Krebs 1985). In the Northwest Territories, the home ranges of adult male and female lynx averaged 36.3 km^2 and 20.8 km^2 , respectively, at the cyclic peak, and these ranges increased to 44.0 km^2 and 62.5 km^2 2 years later when populations of hares had crashed (Poole 1994). The ranges of males and females were mostly intrasexually exclusive and stable in the Northwest Territories study, but this spatial organization broke down during the winter 2 years after the cyclic peak in abundance of hares, and all residents either died or dispersed (Poole 1995). The sizes of lynx home ranges also increased

>5-fold for males and >10-fold for females in the south-central Yukon study after the cyclic decline, but unlike our data and those of Poole (1994, 1995), most animals persisting into the cyclic low were known to have been born in the study area (Slough and Mowat 1996).

13.3.2 Social Groups

Both coyotes and lynx sometimes traveled in groups at Kluane. Coyotes were observed in groups of two to five, but groups larger than three animals were only noted in 1990–1991 and 1991–1992. These larger groups were likely composed of related animals, but we could not confirm this. The typical social organization of coyotes consists of exclusive family territories, with a mated pair and a variable number of their offspring that may delay or forgo dispersal, especially when food is abundant or dispersal opportunities limited (Andelt 1985, Bekoff and Wells 1986).

We observed lynx in groups of up to seven animals. Up until 1991–1992, all of the groups of lynx that we observed traveling together were composed of an adult (presumably, the mother) and one to six kittens. Lynx kittens typically remain with their mother for most of their first winter (Poole 1995, Mowat et al. 1996), and they hunt together as a group (Parker 1981). We noted lynx in adult groups of two or three animals for the first time in 1991–1992, the second winter of declining abundance of hares. These groups persisted throughout the winter and accounted for 51% of all group observations ($n = 81$) in 1991–1992, 90% in 1992–1993 ($n = 19$), and all groups in 1993–1994 ($n = 7$) and 1994–1995 ($n = 1$) on our track transects. We could not confirm the relationships among animals in groups, but we suspected one group consisted of an adult female and her grown female offspring. We have found only one other reference to adult groups of lynx (Barash 1971), although Poole (1995) also noted that the radio locations of two male–female pairs suggested positive attraction during the early part of the first winter of the cyclic low. We discuss evidence that hunting in adult groups increased the foraging efficiency of lynx below.

13.4 Foraging Behavior

13.4.1 Diets

We calculated the winter diets of coyotes and lynx from the kills we found along their trails and from analyses of their scats. During summer, we collected scats opportunistically and by searching along gravel roads; we found few scats of lynx during the summers.

We found 208 kills by coyotes during the 10 winters of tracking; 48% of these were snowshoe hares, 14% were red squirrels, and 36% were small mammals (mostly *Clethrionomys rutilus*, *Microtus pennsylvanicus*, and *M. oeconomus*). All of the kills were of hares during 1987–1988 and 1988–1989 (late cyclic increase to peak), followed by a period of increased use of small mammals and squirrels from 1989–1990 through 1991–1992 (cyclic peak to decline; figure 13.5). Coyotes killed mostly small mammals in 1992–1993 and 1993–1994, winters of low abundance of hares and high numbers of small mam-

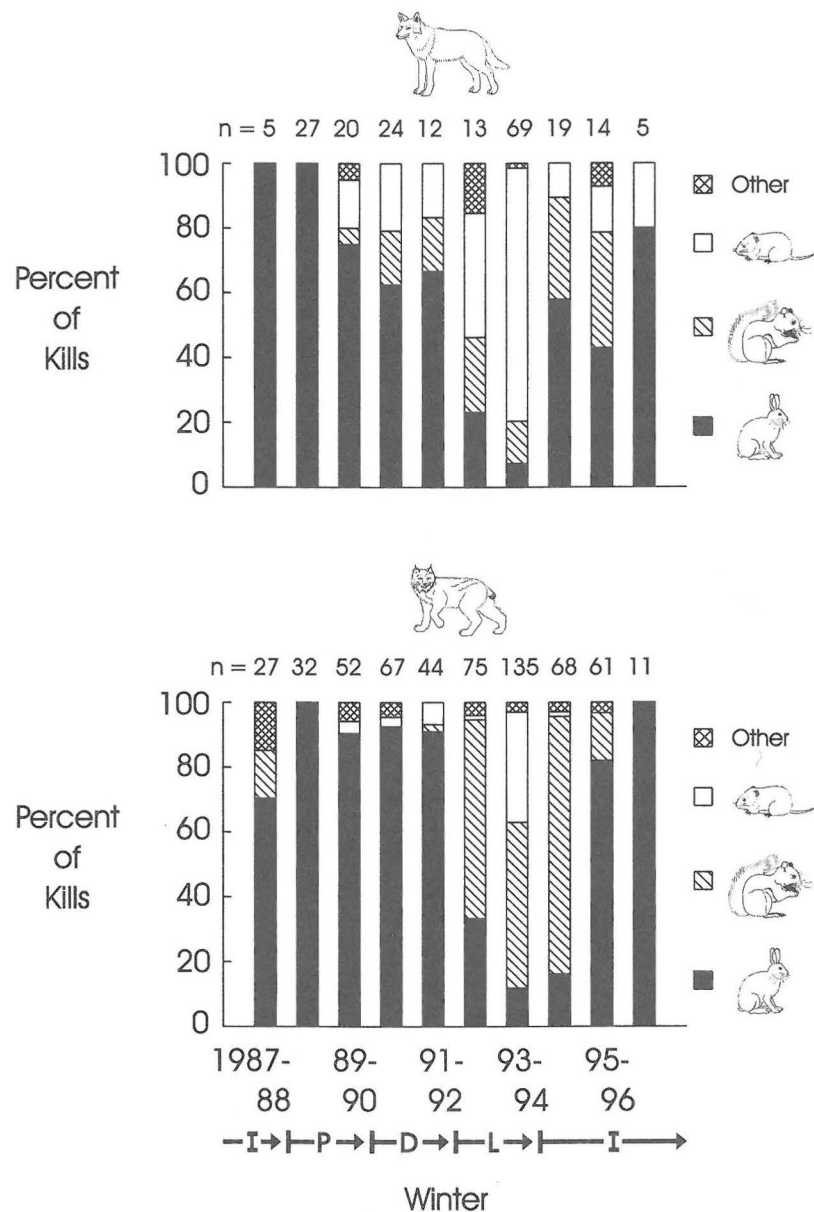


Figure 13.5 Kills by coyotes and lynx located along their tracks during winter from 1987–1988 through 1996–1997, at Kluane. Sample sizes are given above bars. “Other” kills for coyotes were 1 grouse, 2 flying squirrels, and 1 unknown prey, and for lynx were 14 grouse, 2 muskrats, 2 flying squirrels, 1 short-tailed weasel, 1 red fox, and 1 unknown prey. The phases of the hare cycle (I = increase, P = peak, D = decline, L = low) are shown by the horizontal bar below the x-axis.

mals. As densities of hares began increasing again from 1994–1995 to 1996–1997 and those of small mammals dropped, coyotes shifted their hunting to hares, with red squirrels more frequent as alternative prey in the first two of those winters (figure 13.5).

In terms of prey biomass, coyotes consumed >90% hares in all winters, based on our snow tracking, except in 1992–1993, 1993–1994, and 1995–1996, when red squirrels represented 12–20% of the biomass (figure 13.6). Small mammals represented <2% of biomass consumed in all years but 1993–1994. However, kills of small mammals are underrepresented from our tracking data because we often could not confirm whether an attempt at killing a vole had been successful. Scat analyses suggested a dietary pattern similar to that from our snow tracking, except that small mammals represented a larger proportion of the estimated biomass consumed (18–42% in winters of 1987–1988 through 1988–1989 and 1992–1993 through 1993–1994, based on their relative frequencies of occurrence), during periods of higher densities of small mammals (O’Donoghue et al. 1998b). Despite the fact that forested habitats were much more abundant in our study area than meadows (which were only about 7% of the area), coyotes killed many more *Microtus* ($n = 64$ identified jawbones in scats), which are mostly found in meadows, than *Clethrionomys* ($n = 9$). Hares made up the remaining bulk of scats in all winters; the relative frequency of occurrence of red squirrels was greater than 10% only in 1994–1995 (13%).

We collected an adequate number of coyote scats in summer only in 1988 ($n = 35$) and from 1990 through 1992 ($n = 22$ –49). Analyses of these scats suggested that summer diets were more varied than winter diets, due to the availability of ground squirrels, which made up an estimated 15–21% of biomass consumed in all summers except 1990 (0%). Hares (33–73%; highest in 1990 and 1991) and small mammals (8–25%) made up the remaining bulk of the summer diets.

We located 572 kills by lynx during snow tracking, of which 55% were of hares, 32% of red squirrels, and 10% of small mammals. Lynx killed mostly hares in winters when hares were at densities >0.5/ha (1987–1988 through 1991–1992, 1995–1996 and 1996–1997), but more red squirrels than hares during the cyclic low (1992–1993 and 1993–1994) and early increase (1994–1995) winters (figure 13.5). Substantial numbers of small mammals were killed only in 1993–1994.

When considered in terms of biomass consumed, hares made up >90% of the diets of lynx, based on our snow tracking, in all winters except 1992–1993 through 1994–1995, when red squirrels made up an increasing proportion of prey (20–44%; figure 13.6). Analyses of winter scats suggested the same patterns, except that, as with coyotes, small mammals made up a larger proportion (23–26%) of scats in the winters of 1987–1988 and 1988–1989 (cyclic late increase to peak) and 1993–1994 (cyclic low) than indicated from our tracking (O’Donoghue et al. 1998b). Of identified small mammals in scats, more *Clethrionomys* ($n = 14$) were present than *Microtus* ($n = 11$), which may reflect the avoidance of open habitats by lynx (Murray et al. 1994). The relative frequency of occurrence of red squirrels ranged from 25% to 37% in scats from 1992–1993 through 1994–1995.

We gathered enough summer scats of lynx only in 1990 ($n = 13$) and 1991 ($n = 43$). As with coyotes, the diversity of summer diets was greater than in preceding winters due to the addition of ground squirrels (8–25% relative frequency of occurrence). The rest of the scats were composed mostly of hares (67–85%).

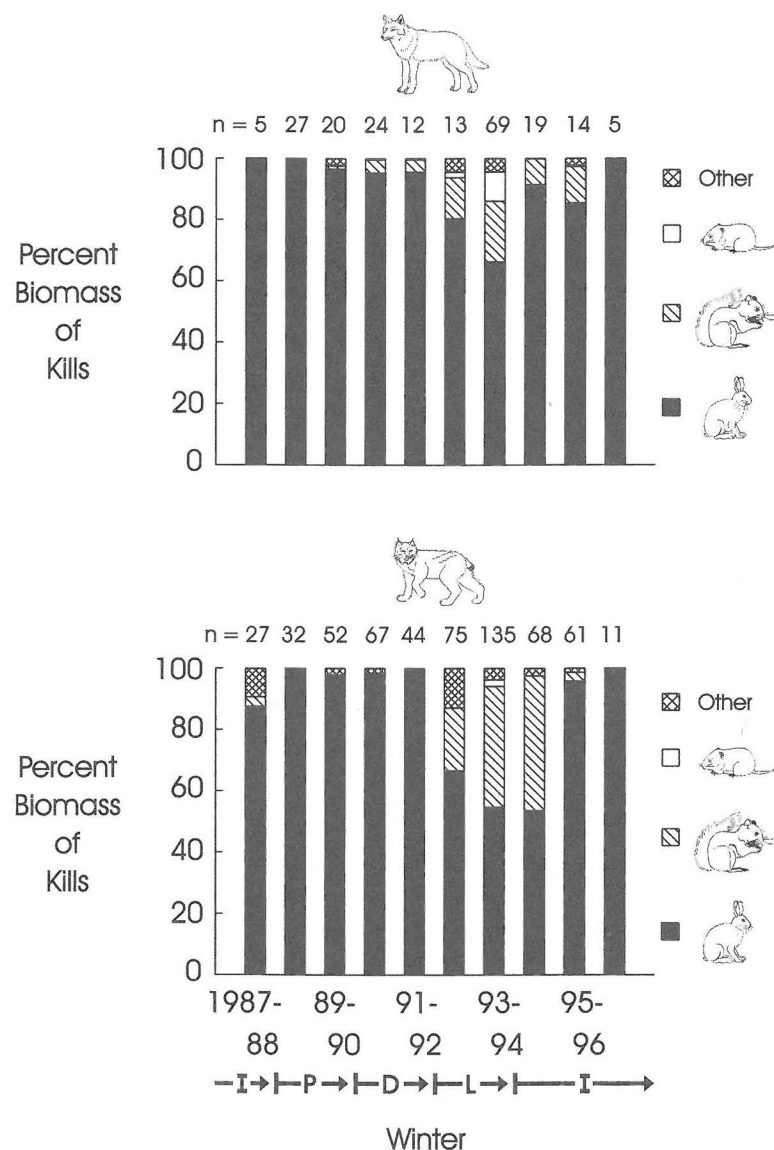


Figure 13.6 Percent biomass of kills by coyotes and lynx located along their tracks during winter from 1987–1988 through 1996–1997 at Kluane. Sample sizes (number of kills) are given above bars. The phases of the hare cycle (I = increase, P = peak, D = decline, L = low) are shown by the horizontal bar below the x-axis.

The dietary patterns that we observed for coyotes and lynx were consistent in all parts of our study area (O'Donoghue et al. 1998a). Therefore, although we were not able to distinguish among individual predators from our snow tracking, we suggest that the shifts in diets that we observed were due to most animals changing their patterns of hunting, rather than just a smaller proportion specializing in alternative prey during periods of low abundance of hares.

Changes in the diets of coyotes as numbers of snowshoe hares fluctuated were also observed in Keith's studies in Alberta. Based on analyses of scats and stomach contents, hares made up 67–77% of the estimated consumption of coyotes at the cyclic peak, but only 0–23% once densities of hares had declined (Nellis and Keith 1976, Todd et al. 1981, Todd and Keith 1983). Livestock carrion was the most important alternative food source in these studies.

Diets of lynx in Alberta were composed mostly of hares (97–100% at the cyclic peak, 65–81% during periods of low abundance of hares) at all phases of the hare cycle (Nellis et al. 1972, Brand et al. 1976, Brand and Keith 1979). Grouse and small mammals were the most important alternative prey in these studies. We are aware of only two other studies that have recorded squirrels as being more than a minor dietary component of lynx (24% of food items in scats in Washington; Koehler 1990; 28% of food items in Alaska; Staples 1995); both studies were conducted where densities of hares were low.

13.4.2 Scavenging Behavior

Signs of scavenging were much more frequent along the trails of coyotes than along those of lynx (figure 13.7; O'Donoghue et al. 1998b). Both predators also uncovered caches (40% of all opportunities to scavenge for coyotes, 25% for lynx) and encountered old kills (60% for coyotes, and 75% for lynx) most frequently during winters of highest densities of hares.

Data from monitoring the survival of radio-collared hares showed that coyotes cached the entire carcasses of 37.8% (82 of 217) of all kills they made from 1986 through 1996, and lynx cached the whole carcasses of only 0.5% (1 of 211) of their kills of hares (O'Donoghue et al. 1998b). This suggested that many of the caches dug up by coyotes were initially made by them as well. Observations of coyotes making side trips off of otherwise straight trails, sometimes for >0.5 km, to dig up caches also suggested that individual animals fed on their own caches. Caches made by coyotes were typically dug down through the snow to or into the ground, often at the bases of trees or shrubs. Cached carcasses were often pushed laterally under undisturbed snow, leaving little sign of food storage at the sites. Lynx, on the other hand, usually covered carcasses at the surface of the snow by pulling snow over them. While snow tracking, we recorded 17 observations of coyotes uncovering caches made by lynx, compared to 92 records of coyotes digging up typical coyote-made caches.

From 1992–1993 through 1994–1995, we monitored 30 caches made by coyotes (27 hares, 1 red squirrel, 1 flying squirrel, and 1 portion of a wolf-killed moose leg), and 7 caches made by lynx (all hares) that we had located while snow tracking and retrieving mortalities of radio-collared hares (O'Donoghue et al. 1998b). Coyotes cached mostly whole carcasses of hares (24 of 27 carcasses were entire; mean percent of carcass present

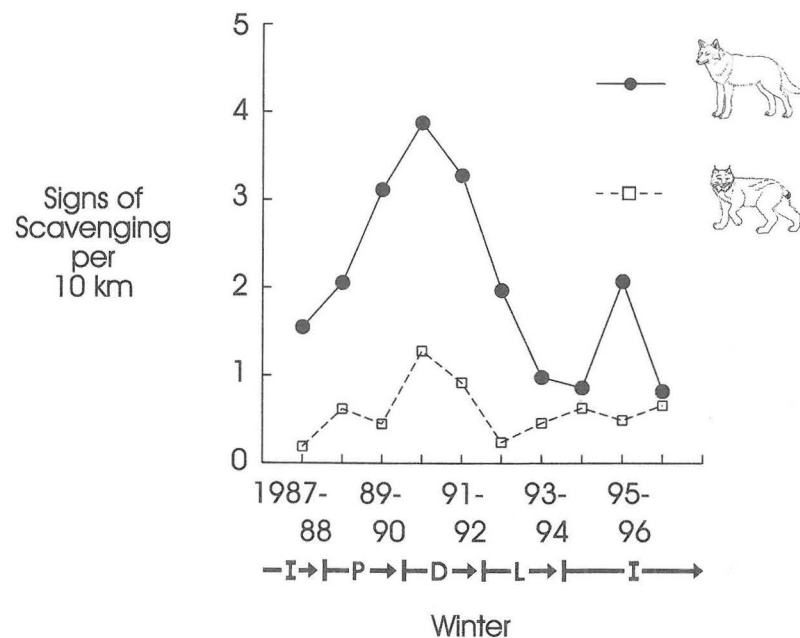


Figure 13.7 Frequency of scavenging (visiting old kills and caches) along the trails of coyotes and lynx during winter from 1987–1988 through 1996–1997 at Kluane. The phases of the hare cycle (I = increase, P = peak, D = decline, L = low) are shown by the horizontal bar below the x-axis.

= 99%, 95% CI = 97–100%), whereas lynx usually cached only portions (1 of 7 whole; mean = 61%, 95% CI = 33–86%). Most caches made by coyotes were also made early in winter (85% of the caches we monitored were made in October and November), whereas those of lynx were more evenly spread through the winter (43% in October and November). This reflects the relative temporal distributions of kills by coyotes and lynx. Of radio-collared hares killed by coyotes from 1986 through 1996 ($n = 146$, excluding hares killed on study grids with fencing or cut snowmobile trails), 77% of them were killed in October or November, compared to only 23% of hares killed by lynx ($n = 132$) in those months (figure 13.8).

Coyotes returned to 14 of the 27 (52%) caches of hares that we monitored and ate an estimated average of 74% (95% CI = 37–98%) of each carcass. They returned to caches an average of 56 ± 35 (SD) days (range 9–140 days) after making their kills. No caches made by coyotes were eaten by lynx, 2 were scavenged by red squirrels, and 11 were not used. We had evidence in two cases that coyotes approached these monitored caches but did not retrieve them, possibly because of our disturbance to the sites, so our use rates may be negatively biased.

Lynx retrieved six of their seven (86%) caches of hares and consumed an average of 99.5% (95% CI = 96–100%) of the portions cached. They returned to caches after an av-

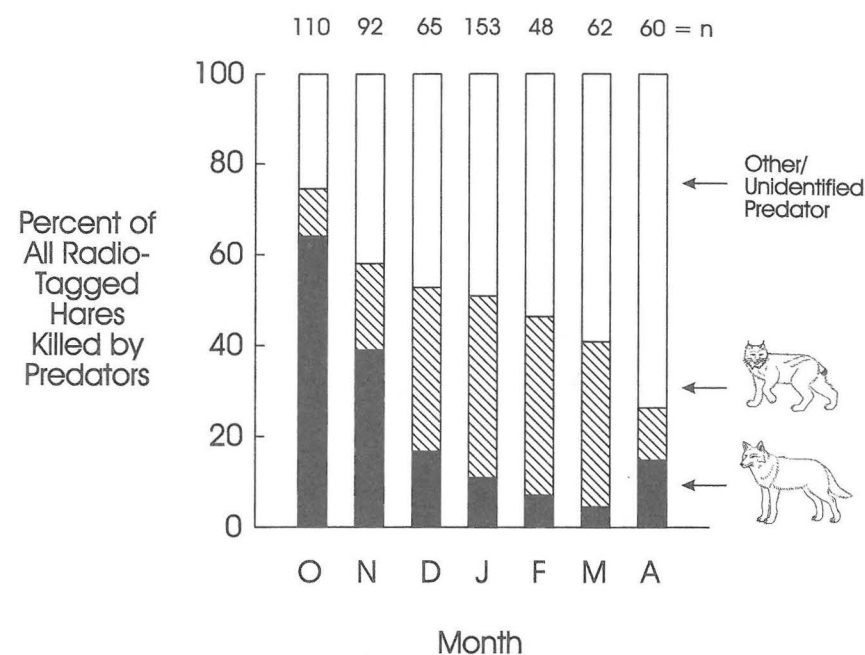


Figure 13.8 Percentages of depredated radio-collared hares killed by coyotes and lynx in each winter month from 1986 through 1995 at Kluane. Sample sizes (total number of mortalities) are given above bars. “Other” predators include red foxes, wolves, wolverines, avian predators, and cases in which the predator could not be identified.

erage of 0.9 ± 0.5 days (range 0–2 days). No lynx caches were eaten by coyotes, and one was not used. These results suggest that most of the scavenging at caches that we observed while snow tracking was likely of caches made by the predator being followed. Caching and use of caches by lynx has been noted in other studies (Nellis and Keith 1968, Parker 1981), but it does not appear to be a frequent behavior compared to consumption of freshly killed prey (Parker 1981).

13.4.3 Hunting Tactics

Coyotes usually pounced on hares from close range, with little sign of stalking, or flushed them out while walking or running through dense cover (Murray et al. 1995, O'Donoghue et al. 1998a). Coyotes seldom, if ever, used ambush beds to hunt hares (figure 13.9). During winters when coyotes actively hunted voles, they used a “mousing” hunting tactic in which they moved slowly, mostly through meadow areas, pausing frequently and leaping into the air to pin voles with their front paws. The frequency of mousing was low during winters of high and declining abundance of hares (0.00–0.05 attempts per 10 km trail in the winters of 1988–1989 through 1991–1992, 1995–1996, and 1996–1997; in all but 1991–1992, densities of voles were low during these winters). The fre-

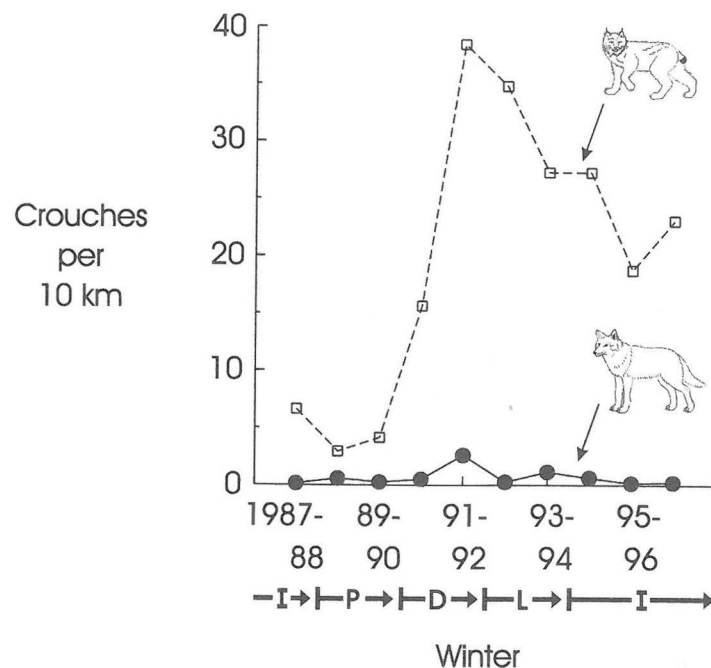


Figure 13.9 Frequency of crouches, or “ambush beds,” along the trails of coyotes and lynx during winter from 1987–1988 through 1996–1997 at Kluane. The phases of the hare cycle (I = increase, P = peak, D = decline, L = low) are shown by the horizontal bar below the x-axis.

quency of mousing was higher in winters with densities of hares $<0.5/\text{ha}$ and greater vole abundance (0.70–1.91 attempts/10 km in 1987–1988, 1992–1993, and 1994–1995), and very high in 1993–1994 (13.98 attempts/10 km).

Lynx hunted hares either by stalking them or ambushing them from crouches or ambush beds (Murray et al. 1995, O’Donoghue et al. 1998a). As densities of hares declined from the cyclic peak (1989–1990) to the low (1992–1993), the frequency of ambush beds increased more than ninefold along the trails of lynx (figure 13.9). Lynx also initiated progressively more chases of hares from hunting beds during the cyclic decline and low years (1990–1991 through 1993–1994), although hunting success from beds was about the same as that from stalks for hares, and slightly lower for red squirrels (O’Donoghue et al. 1998a). Use of beds declined after 1992–1993, but they were still frequently used until 1996–1997 (figure 13.9). This pattern was consistent in all parts of the study area, so the shift to greater use of an ambush hunting tactic during the cyclic decline was apparently widespread among individual lynx (O’Donoghue et al. 1998a).

Frequent use of ambush beds by lynx has been noted in other studies of lynx (Saunders 1963a,b, Haglund 1966), but in some studies, lynx seldom ambushed hares (Nellis and Keith 1968, Parker 1981). In Alberta, Brand et al. (1976) speculated that apparently lower daily movement rates during periods of low abundance of hares may have been related to increased use of beds, although this was not quantified.

13.4.4 Group Hunting

We observed evidence of group hunting by both coyotes and lynx. When hunting together, pairs or groups of coyotes typically traveled parallel to one another or spread out laterally relative to their direction of travel. Hares flushed by one animal were sometimes killed by another. We also observed coyotes running through dense cover, apparently with no prey initially sighted (based on distances run before hares were encountered) and killing hares flushed out. Ozoga and Harger (1966) described similar group hunting by coyotes in which one animal would run through a dense thicket and another would travel around its perimeter and chase hares flushed out.

Families of lynx hunted together in a similar manner. Although lynx seldom ran while not chasing prey, families generally spread out while moving through suitable hare habitat, and hares flushed out by one animal were often killed by another. This pattern of family hunting, with the mother typically flanked by kittens, was also described by Parker (1981).

We examined our tracking data to see if group hunting conferred advantages of higher food intake to predators. We calculated kill rates of hares by groups of coyotes and lynx (for all group sizes that we followed for >10 km in a given winter), and adjusted these to individual kill rates. There was a variable relationship between group size and individual kill rates for coyotes and no distinct trend of higher or lower food intake (O’Donoghue et al. 1998a). Larger groups of lynx killed more hares, but individual kill rates were lower with increasing group size from 1987–1988 through 1991–1992. In 1992–1993 and 1993–1994, when virtually all of the groups we tracked were adult groups, individuals in groups had similar or higher intake rates (O’Donoghue et al. 1998a). Our sample sizes are small in these years, but the limited data we gathered suggest that group hunting may confer some advantages in foraging success to lynx during periods of food scarcity.

13.4.5 Use of Trails

Coyotes traveled on top of the trails of other predators and those made by snowmobiles and snowshoes more often than did lynx at all phases of the hare cycle (figure 13.10; Murray and Boutin 1991, O’Donoghue et al. 1998a). Snow was harder on the trails of coyotes relative to those of lynx, and this likely eased their travel (Murray and Boutin 1991). Both predators often traveled along the trails of hares, especially when densities of hares were high, but there was no difference in the frequency of use between the two (figure 13.10). Keith et al. (1977) speculated that increased use of hare trails by coyotes at the cyclic peak led to higher kill rates.

13.4.6 Habitat Use

Coyotes and lynx showed a general trend of using habitats with progressively denser overstory cover (the densest habitats in our study area were dominated by young white spruce) from the winter of peak abundance of hares (1989–1990) through 1991–1992, the second winter of the cyclic decline (figure 13.11). After 1991–1992, there was an overall decline in density of cover until 1993–1994 (the cyclic low). This trend paralleled that of habitat use by snowshoe hares, which also selected progressively more dense cover as their numbers declined (Hik 1995, O’Donoghue et al. 1998a). Hares were consistently

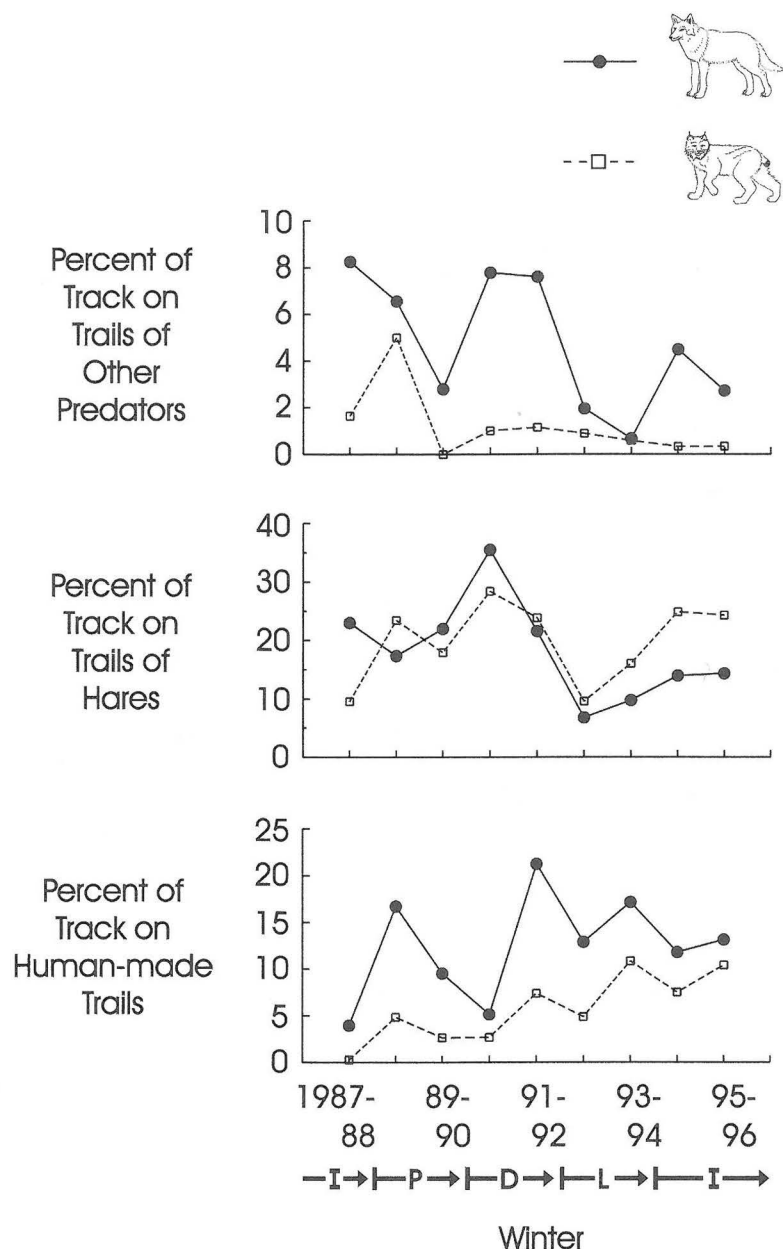


Figure 13.10 Percentages of trails of coyotes and lynx that were on the trails of other predators, snowshoe hares, and human-made (by snowmobile or snowshoes) trails during winter from 1987–1988 through 1995–1996 at Kluane. Coyotes used trails of other predators (Wilcoxon paired-sample test, $p = .004$) and humans ($p = .004$) more than did lynx; there was no difference between predators in the use of hare trails ($p = .660$). The phases of the hare cycle (I = increase, P = peak, D = decline, L = low) are shown by the horizontal bar below the x-axis.

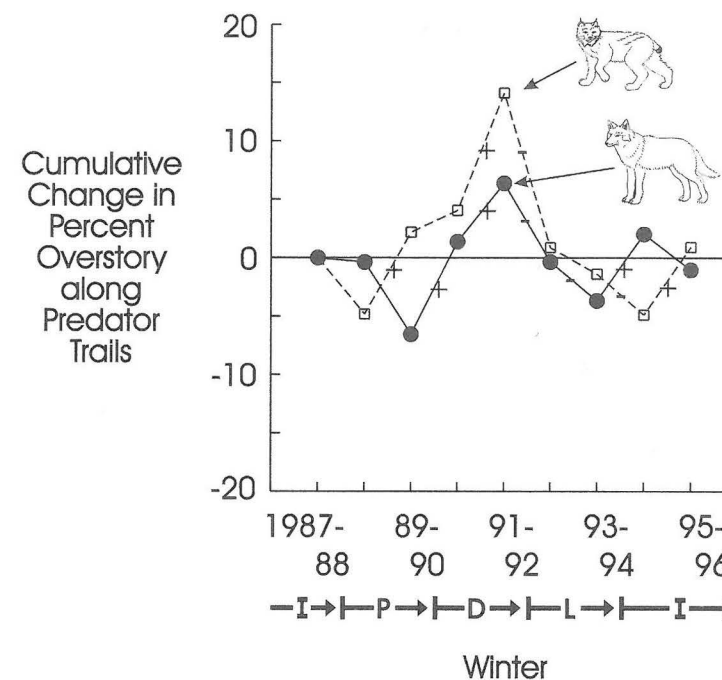


Figure 13.11 Cumulative changes between winters (starting at 0% in 1987–1988) in percent overstory cover along the trails of coyotes and lynx during winter from 1987–1988 through 1995–1996 at Kluane. The + and – signs indicate statistically significant ($p < .05$) increases and decreases, respectively, in overstory cover between two years. The phases of the hare cycle (I = increase, P = peak, D = decline, L = low) are shown by the horizontal bar below the x-axis.

found in denser habitat than either predator at all phases of the cycle. Coyotes avoided open cover less than lynx, especially during winters at the cyclic low, when coyotes often hunted *Microtus* in meadow habitats (Murray et al. 1994, O'Donoghue et al. 1998a). During winters of high abundance of hares (1987–1988 through 1990–1991), hunting success of coyotes chasing hares was highest in dense habitats, whereas lynx were equally successful in all habitat types (Murray et al. 1994, 1995). Selection of dense and early successional coniferous habitats by lynx is well documented in other areas as well (Parker 1981, Koehler and Aubry 1994, Poole et al. 1996), but no changes in habitat selection by lynx were noted during a cyclic decline in the Northwest Territories (Poole et al. 1996).

At a larger spatial scale, coyotes may select topographical areas with shallower snow; they used areas of our study area at lower elevation more than they did the central plateau, which had deeper, softer snow (Murray and Boutin 1991). In Alberta, Todd et al. (1981) speculated that habitat selection by coyotes was less affected by snow depths at the cyclic peak due to trampling of snow by hares.

Both coyotes and lynx used the experimental food-addition grids, with higher densities of hares, more than the control grids during the cyclic decline (O'Donoghue et al. 1998a). This is further evidence that the predators concentrated their hunting activity in

areas of locally high abundance of hares during this period, as was found for lynx during the previous cycle (Ward and Krebs 1985).

13.5 Functional Responses

Coyotes and lynx both showed strong functional responses to the cyclic changes in densities of hares. Estimated kill rates of coyotes varied approximately ninefold over the observed range of hare densities (figure 13.12). Linear and type-2 response curves fit the

observed data equally well, so there was little evidence of satiation at higher densities of hares (which is expected theoretically, but seldom observed from field data; Boutin 1995). When calculated separately, using autumn densities of hares and kills by coyotes from October through December, the functional response was nearly linear, whereas the observed kill rates from January through March, plotted against late-winter densities of hares, showed a clear asymptote at about 1.65 kills/day (O'Donoghue et al. 1998b).

We observed peak kill rates of 2.3 hares per day per coyote in 1988–1989, one year before the peak in numbers of hares. With the exception of 1995–1996, kill rates were higher during winters of cyclic increase (1987–1988, 1988–1989, 1994–1995, and 1996–1997) than at comparable densities of hares during the peak, decline, and low phases of the cycle (figure 13.12).

Kill rates of hares by lynx varied four- to fivefold during the cyclic fluctuation of hares (figure 13.12). There was better evidence of an asymptotic kill rate over the range of observed hare densities for lynx than for coyotes, and the fit of the type-2 curve was slightly better than that of a linear functional response. Early-winter and late-winter functional responses were similar in shape, and, as with coyotes, the peak kill rates were higher at the beginning of the winter (asymptote = 1.8 hares/day) than at the end (1.0 hares/day) (O'Donoghue et al. 1998b).

During the first increase and decline in numbers of hares (1987–1988 through 1993–1994), kill rates by lynx were lower during cyclic increase years (1987–1988 and 1988–1989) than at comparable densities of hares during the decline (O'Donoghue et al. 1998b). The highest kill rate observed during this period was 1.2 kills/day, in 1990–1991, the year after the cyclic peak of hares. This pattern appeared to repeat itself with the low kill rates observed in 1994–1995, as densities of hares began to increase but lynx continued to hunt red squirrels. However, the kill rates estimated in 1995–1996 (1.35 kills/day) and 1996–1997 (1.58 kills/day) were the highest observed during the 10 winters of study, so it is questionable whether we would again observe even higher kill rates than these during the next cyclic decline.

The maximum kill rates of hares by coyotes and lynx that we observed were higher than those reported in the literature, and higher than estimates of the energetic requirements of these predators (coyotes: 0.9 hares/day, Litvaitis and Mautz 1980; lynx: 0.4 hares/day, Nellis et al. 1972). In Alberta, maximum daily kill rates were estimated to be 0.7 and 0.8 per day for coyotes and lynx, respectively (Brand et al. 1976, Keith et al. 1977). However, the functional responses in the Alberta study were estimated assuming that coyotes killed only as many hares as they required energetically (no surplus killing or wastage) and assuming that the distance between two resting beds of lynx represented 1 day of activity. Both of these assumptions are questionable. Surplus killing is relatively common among predators (Kruuk 1972), and use of two to three resting beds per day by lynx has been documented (Haglund 1966, Parker 1981, this study).

13.5.1 Components of Functional Responses

Functional responses by predators to changing densities of prey can result from changes in a number of attributes of the foraging behavior of the predator or from characteristics of the prey. Holling (1959a, 1966) considered that the basic components of functional responses are rate of successful search (determined by the reactive distance of

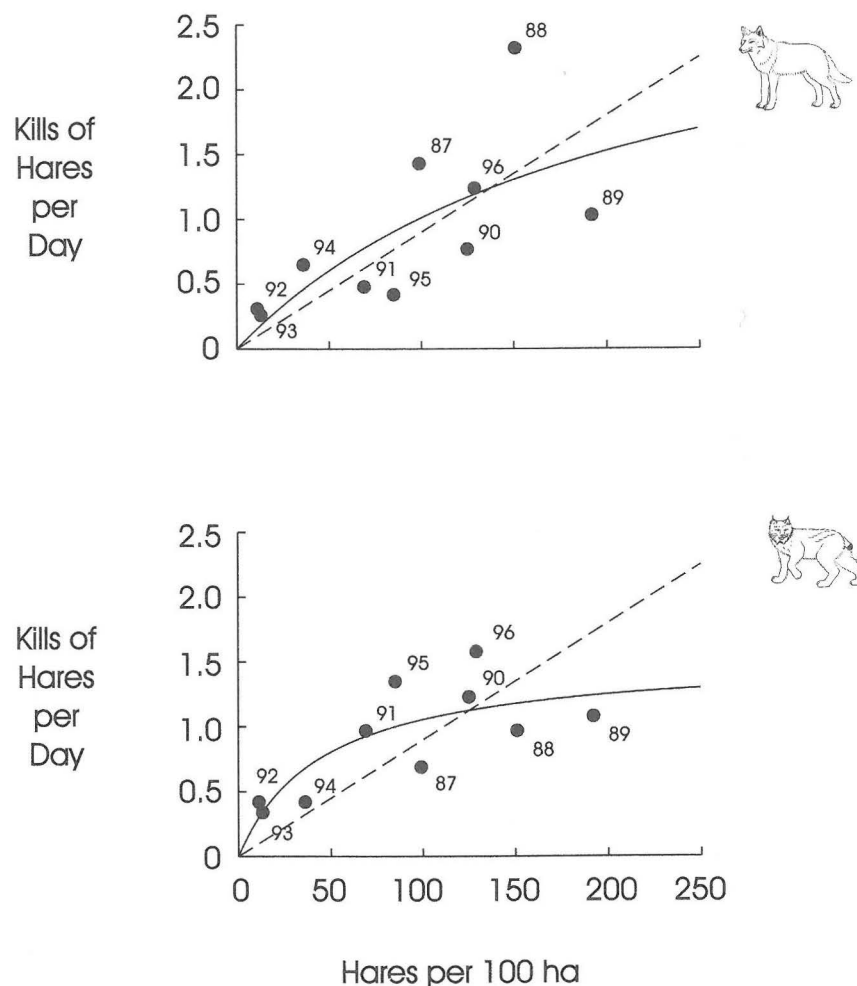


Figure 13.12 Functional responses of coyotes and lynx (kills per predator per day) to changing densities of snowshoe hares (means of autumn and late winter estimates of hare densities) during winter from 1987–1988 (labeled “87” on graphs) through 1996–1997 at Kluane. Type-2 (Holling’s disk equation; Holling 1959b; coyote, $r^2 = .83$; lynx, $r^2 = .94$) and linear curves (coyote, $r^2 = .82$; lynx, $r^2 = .86$) are fitted to the estimated kill rates.

the predator to its prey, the relative speeds of movement by predators and their prey, and the rate of successful capture by predators), foraging time by predators, and handling time (the amount of time needed to capture, consume, and digest a prey item). Although these parameters were considered constants in Holling's original equations, they may vary with changing prey densities (Abrams 1990). We examined our tracking data for evidence of changes in these components to clarify mechanisms of the functional responses.

Reactive Distances of Predators The only index of the reactive distances of predators that we measured was the length of chases of hares by coyotes and lynx. Because hares usually fled before they were captured, chase lengths were invariably longer than the true reactive distances. Lengths of chases of hares by coyotes and lynx varied significantly over the hare cycle (coyotes: ranges of annual means for successful chases = 0.4–25.0 m, unsuccessful = 3.9–21.8 m; lynx: successful 1.8–19.3 m, unsuccessful 6.3–23.0 m), and were longest from 1992–1993 through 1994–1995, when densities of hares were lowest (O'Donoghue et al. 1998b).

Travel Rates of Predators We successfully completed 7 time trials for coyotes and 16 for lynx to estimate their travel rates. The mean travel rates were 2.49 ± 0.39 (SD) km/h (range 1.77–3.06 km/h) and 1.09 ± 0.21 km/h (range 0.75–1.46 km/h) for coyotes and lynx, respectively (O'Donoghue et al. 1998b). Six of seven measures of travel rates for coyotes were made during winters of high densities of hares, so we could not examine these data for changes in travel rates. In winters with relatively high abundance of hares (1989–1990 through 1991–1992), lynx traveled at 1.02 ± 0.23 km/h ($n = 9$), while at the cyclic low (1992–1993 and 1993–1994), the comparable rate was 1.13 ± 0.16 km/h ($t = 1.63$, $df = 14$, $p = .13$), so we have no evidence of changing movement rates in response to prey density.

Hunting Success Hunting success of coyotes chasing hares was relatively constant from 1989–1990 through 1993–1994, but considerably higher in the cyclic increase years of 1988–1989 and 1994–1995 through 1996–1997 (figure 13.13). The overall success rate was 38.1%. Coyotes chased a substantial number of squirrels only from 1992–1993 through 1995–1996, and their success rate during these winters was 36.5%.

The annual success rates of lynx chasing hares were less variable from 1987–1988 through 1994–1995 than those of coyotes, but we observed high success in 1995–1996 and 1996–1997 (figure 13.13). The overall success rate was 31.7%. During the three winters of lowest hare abundance (1992–1993 through 1994–1995) hunting success of lynx chasing hares was lowest, while there was a steady increase in their success at capturing red squirrels (figure 13.13).

The rates of hunting success that we observed were higher than published rates for coyotes chasing hares (6–10%; Ozoga and Harger 1966; Berg and Chesness 1978), but within the range of those reported for lynx (19–57%; Saunders 1963a, Haglund 1966, Brand et al. 1976, Parker 1981, Major 1989). Hunting success of lynx was not related to the density of hares in Alberta (Brand et al. 1976).

Foraging Time We monitored the activity of radio-collared coyotes and lynx for 1342 and 4257 h, respectively, from 1990–1991 through 1994–1995 (O'Donoghue et al.

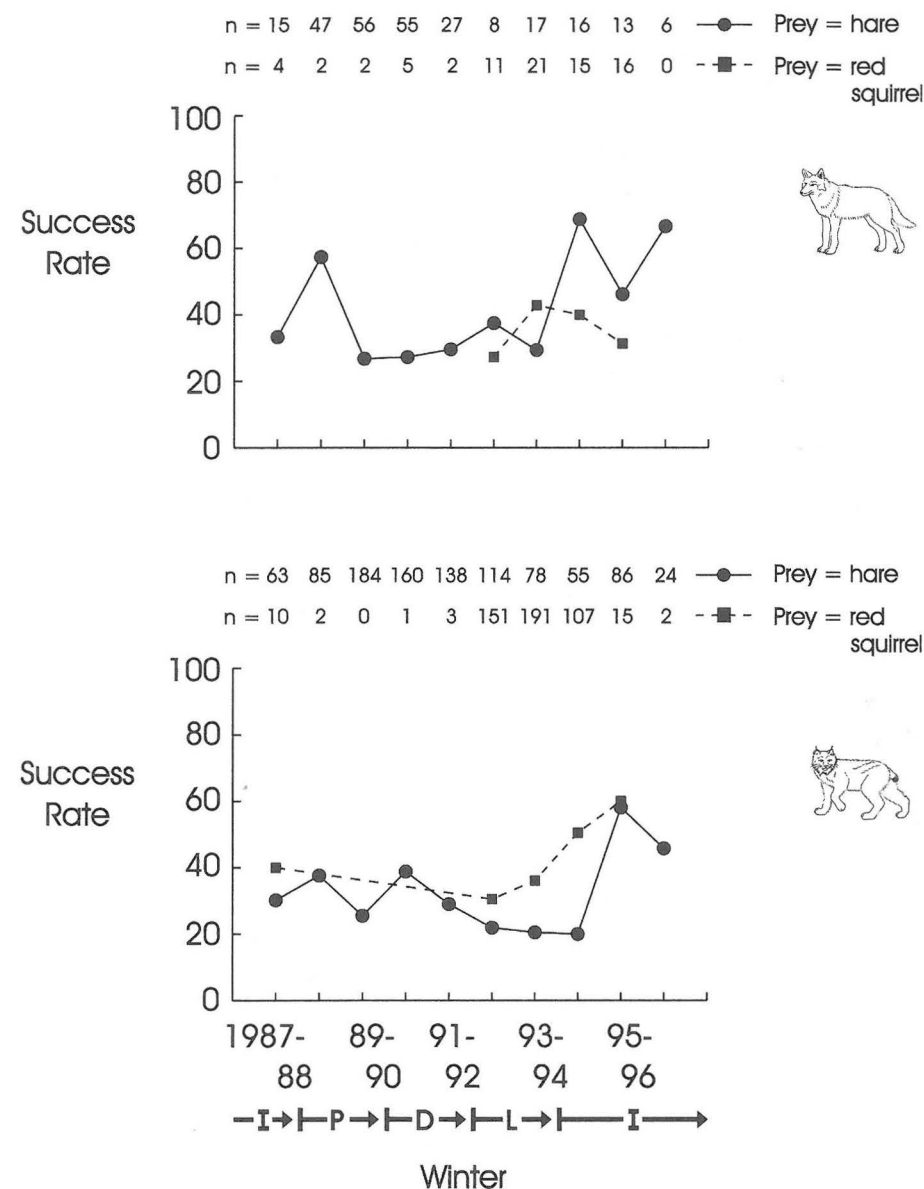


Figure 13.13 Hunting success (percentage of chases that were successful) for coyotes and lynx preying on snowshoe hares and red squirrels during winter from 1987–1988 through 1996–1997 at Kluane. Sample sizes (number of chases) are given at the top of each graph; data points are plotted only for winters with more than five chases. The phases of the hare cycle (I = increase, P = peak, D = decline, L = low) are shown by the horizontal bar below the x-axis.

1998b). Based on our verification trials, the automatic receiver with data logger was an accurate technique for remote measurement of the activity patterns of predators. The percent time active by coyotes varied little (range 44.3–49.7%) from 1990–1991, when the abundance of hares was still high, through 1993–1994, the cyclic low (O'Donoghue et al. 1998b). The frequency of resting beds along coyote trails also varied little among all winters (range 2.5–4.3 beds/10 km of trail), so we have little evidence that coyotes varied their foraging time in response to changes in the density of hares.

Likewise, the percent time active by lynx also varied little among winters (range 39.2–43.5%) and animals (mean annual CV = 4.8%) from 1990–1991 through 1994–1995. For lynx, though, the percent time active may not be a good measure of time they are exposed to prey because the use of ambush beds also increased greatly over that period (figure 13.9); during these “inactive” periods, lynx were still actively foraging. The frequency of resting beds also varied from 1.9 to 5.0 beds/10 km of trail during the 10 years of this study, with the most beds being used during winters of low abundance of hares (O'Donoghue et al. 1998b).

The activity rates of coyotes we measured were comparable to those measured elsewhere during winter (44–50%; Bekoff and Wells 1981, 1986, Bowen 1982). Several studies have found that lynx increased their daily movements as densities of hares declined (Ward and Krebs 1985, Poole 1994).

Handling Time The only component of handling time that we directly recorded was the amount of prey eaten by coyotes and lynx at each kill site (which was presumably correlated with the amount of feeding time). Coyotes consumed an average of 82–96% of each carcass of hares in all winters except for 1993–1994 (62%) and 1996–1997 (68%) (sample sizes were small, $n = 5$ and 6, respectively, during these years) (O'Donoghue et al. 1998b). Lynx ate an estimated 78–95% of hare carcasses, with the lowest consumption rate during the cyclic peak. Although partial consumption of prey may decrease handling time (Abrams 1990), the time devoted to feeding on prey is likely not the major component of total handling time.

13.5.2 Prey Switching

We investigated prey switching by coyotes and lynx by comparing their relative use of snowshoe hares, red squirrels, and small mammals with the availability of these prey items in the autumn, late winter, and the mean of these two measures (O'Donoghue et al. 1998a). The results were the same regardless of which part of the winter was considered, so we present only the data considering mean densities of prey here.

Coyotes strongly preferred snowshoe hares in all winters (mean Manly's $\alpha = 0.85 \pm 0.12$ [SD], range 0.65–1.00), so the null curve for the switching test is a convex curve for hares and concave curves for squirrels and small mammals (figure 13.14). Based on these graphs, there is no evidence that coyotes switched among prey species (relative to their innate preference for hares) as the relative frequencies of these prey changed over the hare cycle.

Lynx also preferred hares in all winters ($\alpha = 0.91 \pm 0.13$, range 0.59–1.00), but this preference was lowest in 1993–1994 ($\alpha = 0.79$) and 1994–1995 ($\alpha = 0.59$), winters in which lynx more actively pursued red squirrels. The graphical tests suggest that lynx did

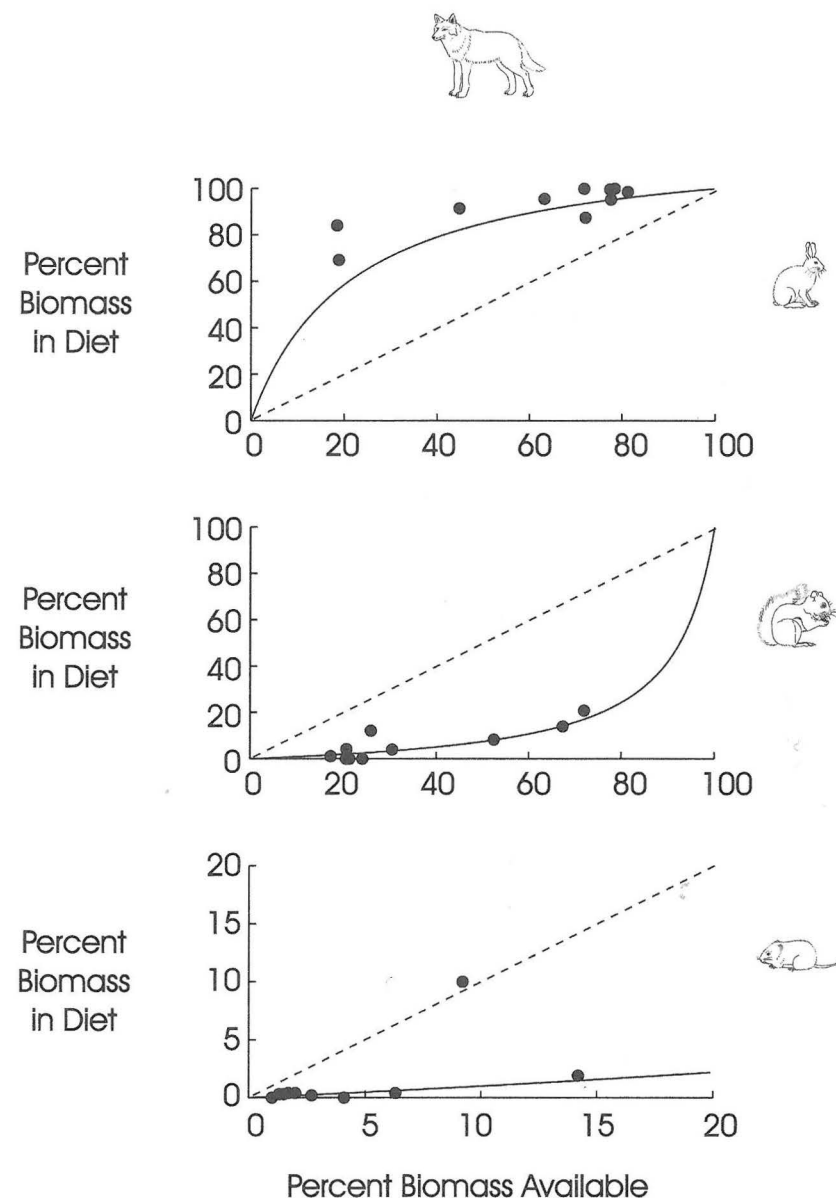


Figure 13.14 Graphical tests for prey switching by coyotes among snowshoe hares, red squirrels, and small mammals during winter from 1987–1988 through 1996–1997 at Kluane. The dashed lines represent equal availability and use of each prey, and the solid curves are the null hypotheses of no switching, taking into account the innate dietary preferences of coyotes. Evidence of switching is implied when data points lie below the null curve at relatively low (<50%) availability and above the curve at high availability.

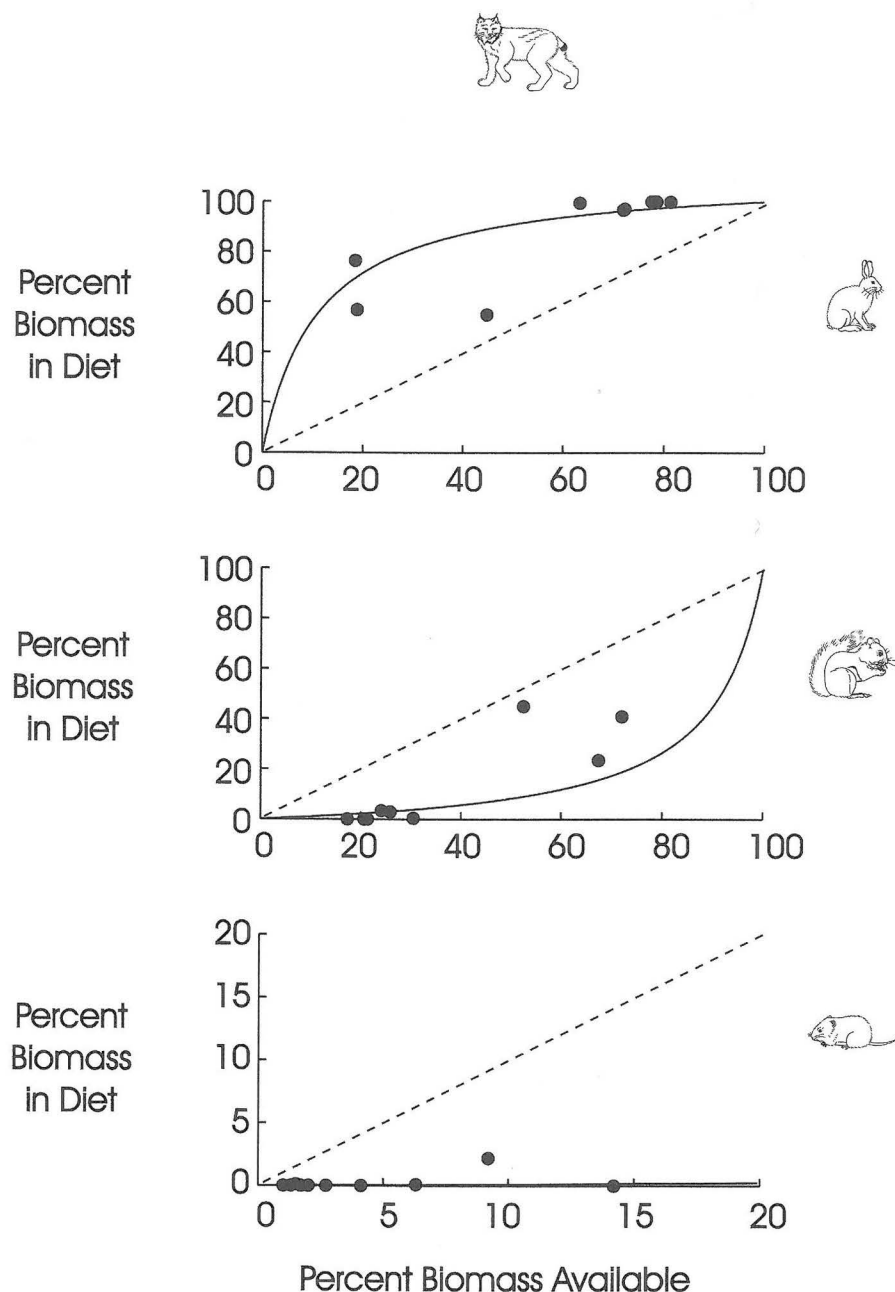


Figure 13.15 Graphical tests for prey switching by lynx among snowshoe hares, red squirrels, and small mammals during winter from 1987–1988 through 1996–1997 at Kluane. The dashed lines represent equal availability and use of each prey, and the solid curves are the null hypotheses of no switching, taking into account the innate dietary preferences of lynx. Evidence of switching is implied when data points lie below the null curve at relatively low (<50%) availability, and above the curve at high availability.

switch (sensu Murdoch 1969) to preying on red squirrels from 1992–1993 through 1994–1995, when red squirrels represented more than 50% of the prey biomass (figure 13.15). This conclusion is robust to two assumptions we made (O'Donoghue et al. 1998a). First, we assumed that the relative availabilities of prey equaled their relative densities. This is unlikely to be strictly true in any field situation, but our interpretation of switching remained the same if we considered that as little as 25% of red squirrels and small mammals were available due to arboreal and subnivean refuges, respectively. Second, we derived the null curves for these tests from our kill data, and calculated a 10-to-1 innate preference for hares. We would draw the same conclusion about switching even if this preference was as low as about 5 to 1. During the seven winters that red squirrels represented <50% of the prey biomass, the diets of lynx were composed of an average of $0.4 \pm 0.7\%$ (SD) squirrels, whereas $36.2 \pm 1.5\%$ of their diets were squirrels when squirrels composed >50% of the prey biomass present.

13.6 Synthesis and Conclusions

The main objectives of the Kluane research on mammalian predators were to determine and contrast the numerical and functional responses of coyotes and lynx to the changes in prey abundance associated with the 10-year cycle of snowshoe hares. Second, we wanted to investigate the behavioral mechanisms leading to changes in kill rates (i.e., the functional responses) of the two predators.

Coyotes and lynx responded to cyclic changes in the abundance of their main prey species, snowshoe hares, with major demographic and behavioral changes. Our main results were:

1. Coyotes and lynx responded numerically in much the same way to the 26- to 44-fold fluctuation in numbers of hares in our study area. Numbers of coyotes varied 6-fold and those of lynx 7.5-fold, and the abundances of both predators were maximal a year later than the peak in numbers of snowshoe hares.
2. Cyclic declines in numbers of coyotes were associated with lower reproductive output and high dispersal rates. Likewise, lynx produced few to no kittens after the second winter of declining numbers of hares. High dispersal rates were characteristic of lynx during the cyclic decline, and low *in situ* survival was observed later in the decline.
3. The sizes of home ranges of lynx, and possibly coyotes, increased as densities of hares declined, and the territorial organization of lynx apparently broke down after 2 years of declining abundance of prey.
4. Coyotes and lynx both fed mostly on hares during all winters except during cyclic lows. Coyotes killed more voles than hares during two winters when abundance of hares was lowest and numbers of small mammals were high. The main alternative prey of lynx was red squirrels, which they killed more than hares during the two winters of low hare numbers and during the first winter of the subsequent cyclic increase.
5. Coyotes and lynx both showed clear functional responses to changes in the densities of snowshoe hares. Coyotes responded with a ninefold change in kill rates, and their functional response is described equally well by linear and type-2 curves. Kill rates of hares by coyotes were generally lower during the cyclic decline in hare densities than during the increase. Kill rates of hares by lynx changed four- to fivefold

during the cyclic fluctuation. Their functional response is well described by a type-2 curve. Kill rates by lynx were lower during the increase phase of the hare cycle than they were during the hare decline.

6. Coyotes killed the maximum number of hares per coyote (2.3 hares/day) one year before the peak in hare abundance. During the first rise and fall of hare abundance, lynx killed the most hares (1.2 hares/day) one year after the peak in hare abundance, but as hare numbers reached high densities again, at the end of this study, lynx killed 1.6 hares/day. These kill rates are more than the estimated energetic requirements of the predators.
7. Coyotes killed more hares early in the winter and cached many of these for later retrieval.
8. Coyotes and lynx preferred hares to other prey species during all phases of the cycle. At low densities of hares, lynx switched to hunting more actively for, and preying on, red squirrels.
9. Habitat use by coyotes and lynx changed over the cycle and roughly paralleled trends in habitats used by hares. Both predators used the densest cover during the second winter of decline in hare abundance. Coyotes and lynx concentrated their activities in areas of high densities of hares during most winters. Coyotes hunted for voles in more open cover during the cyclic low in hare abundance, when voles were numerous.
10. Lynx increasingly used hunting beds for ambushing both hares and red squirrels during the cyclic decline and low. Coyotes switched their hunting tactics to active foraging for voles during only one winter. Both predators frequently traveled on the trails of hares, and coyotes also often used trails made by other predators and humans.
11. Lynx hunted in adult groups for the first time during the cyclic decline and low in hare numbers. Our data suggest the per-individual foraging success may have been higher for these groups.

Although the spatial and temporal scales of the Kluane Project were very large relative to most field studies, we could only work on the scale of the whole study area for these wide-ranging predators. We therefore have no replicates for examining variation in the demographic and behavioral parameters that we estimated. Furthermore, because we could not distinguish among individual predators while snow tracking, we could not measure variances in, for example, diets or kill rates within our study area either (although we did attempt to index variance by subdividing our data by time of winter and section of our study area). We therefore need to be conservative in the inferences we make from our analyses.

These data represent a fairly unique attempt to measure the specific parameters of predator–prey interactions among terrestrial vertebrates in the field, in a multispecies system with all of the major components quantified. Replicates will only accumulate over a period of decades. Below, we speculate on some of the implications suggested by our studies, and those of others, on the roles of coyotes and lynx in the boreal ecosystem. We see their value as much in suggesting hypotheses as in providing answers.

13.6.1 Numerical Responses

In theory, the 1-year lag in the numerical responses of coyotes and lynx should destabilize the predator–prey interaction, as is typical with the responses of many specialists,

and contribute to its cyclic behavior. The delay of 1 year between peak densities of hares and lynx appears to be consistent among our study and other field studies (Keith et al. 1977, Poole 1994, Slough and Mowat 1996). But it is shorter than the 2- to 3-year lag, frequently used in models of the hare cycle, suggested by historical fur records (Royama 1992). Increased vulnerability of lynx to fur-trapping during periods of prey shortage may bias the accuracy of fur statistics as indices of population densities. For coyotes, the only other comparable field data show no lag in their numerical responses during the cyclic increase, but a 2-year lag in their cyclic decline (Keith et al. 1977). Modelers will need to incorporate shorter lags into their models to examine the effects of predation, as shorter time lags imply shorter cyclic periodicity (May 1981).

Densities of coyotes in our study area were about half those in Alberta over the course of the cycle (Keith et al. 1977, Todd et al. 1981), whereas our densities of lynx were about double (Brand et al. 1976, Keith et al. 1977). The estimated peak abundance of hares in Alberta was approximately five times that observed at Kluane (Keith 1990, Boutin et al. 1995). In other areas of their range, coyotes may reach densities as high as 50–100/100 km² (Camenzind 1978, Andelt 1985) relative to the peak of 9/100 km² we observed at Kluane, suggesting that the boreal forest is suboptimal habitat for coyotes. In the Alberta study, coyotes extensively used livestock carcasses as alternative prey during cyclic lows, which apparently allowed them to maintain higher densities. Peak densities of lynx were higher in our study and in the two other recent northern investigations (Poole 1994, Slough and Mowat 1996) than in Alberta. The lack of synchrony between population fluctuations of coyotes and lynx with those of small mammals in our study area (Boutin et al. 1995) underscores the importance of hares to the dynamics of these predators in the north.

Cyclic declines are characterized by long-distance emigration by lynx (Slough and Mowat 1996, Poole 1997, this study), and probably by coyotes as well. High mobility by predators may be important in synchronizing population cycles on a regional scale (Finerty 1980, Ims and Steen 1990, Korpimäki and Norrdahl 1991, Korpimäki and Krebs 1996). Influxes of lynx have been noted south of their usual range during cyclic declines to the north (Mech 1980), and these dispersers may establish new home ranges far from their points of origin (Poole 1997). Likewise, long-distance natal dispersal is typical of coyotes in some areas (Harrison 1992), and we observed high rates of emigration by adults from our study area. The role of these migratory movements in synchronizing the cycle on a continental scale has not been fully explored. Cyclic peaks in populations of introduced snowshoe hares on the island of Newfoundland have been synchronous with those on the mainland, despite the island's geographic isolation, which suggests that dispersal of terrestrial predators is not necessary for regional synchrony.

The role of emigration in maintaining the local persistence of populations of predators through cyclic lows is uncertain as well. Breitenmoser et al. (1993) proposed that locally born resident lynx occupied large, stable home ranges between periods of prey abundance and that these formed core populations for subsequent cyclic increases. Between the cyclic peak in the early 1980s, we found that at least one adult male persisted until the next cyclic peak in approximately the same home range. However, in both our study during the most recent cycle and in the Northwest Territories (Poole 1994, 1995), we observed a complete turnover of resident lynx during the cyclic declines. We could not confirm the origin of any of the residents that became established during the cyclic low. Slough and Mowat (1996), in contrast, noted that two of three resident animals at the cyclic low had been born

in their study area. Local dynamics may vary consistently among source and sink areas (Pulliam 1988), or the patterns of persistence of resident lynx and settlement of dispersers may be random.

13.6.2 Functional Responses

The functional response of coyotes to changing densities of hares at Kluane showed no clear asymptote (figure 13.12), especially in the early winter (O'Donoghue et al. 1998b), whereas that of lynx had a more clearly decelerating slope. Our calculations suggest that both predators killed more hares than energetically required. Many of the hares killed by coyotes in the early winter were cached, and some of these caches were lost to scavengers or not retrieved. Storing excess food during times of plenty may guard against future periods of scarcity or a loss of caches (Vander Wall 1990). Surplus killing could then be the result, and this, in combination with some wastage (incomplete consumption) of carcasses by both coyotes and lynx (O'Donoghue et al. 1998b), apparently contributed to the high kill rates we observed. The higher proportion of juvenile hares early in winters could also have contributed to the higher kill rates. In this case, models of predator-hare interactions that assume functional responses based on energetic requirements of the predators would underestimate the impacts of predation.

We observed a 1-year lag in the functional responses of lynx to the changes in the densities of hares from the start of our study until the subsequent cyclic low. Kill rates by lynx were higher during the cyclic decline than during the increase, while the opposite was true for coyotes. Differences in kill rates between the two cyclic phases could be the result of changing age structures of predators—most offspring are born during cyclic increases and peaks, leading to progressively older mean ages (and more-experienced hunters) from the early cyclic decline to the subsequent cyclic increase (O'Connor 1986, Slough and Mowat 1996)—or result from lags in the prey preferences of predators relative to changing frequencies of prey. Phase dependency in kill rates could contribute to the asymmetry of populations cycles observed in historical time series and models (Royama 1992).

Of the basic behavioral components of functional responses (Holling 1959a, 1966), we observed large changes only in our index of the reactive distances of predators in response to changing densities of hares (O'Donoghue et al. 1998b). Reactive distances may be a function of hunger or environmental factors, such as density of habitat (Holling 1965, Abrams 1990, Bell 1991), and satiated predators have been shown to react to prey within smaller perceptual fields (e.g., Wood and Hand 1985). The increases in hunting success that we observed for coyotes and lynx during periods of cyclic increase (figure 13.13) may have been related to an older age structure in populations of animals at those times. Lack of change in travel rates and activity rates by predators relative to prey densities has been noted in several studies (Holling 1966, Schaller 1972), but changes in these parameters have been documented for other predators (Smith 1974, Bell 1991).

Our results suggest that lynx switched to hunting red squirrels during periods of low abundance of hares and that this switch persisted into the subsequent period of cyclic increase of hares. Switching is more characteristic of generalist predators, which typically have more plastic foraging behavior (MacNally 1995) than specialists. In northern boreal forests, however, the availability of alternative prey to hares is limited. Small mam-

mals were the most frequently used alternative prey of coyotes in our study area, and their availability was limited by snow cover during winter (Wells and Bekoff 1982, Halpin and Bissonette 1988) and the habitat composition of our study area (*Microtus* seem more vulnerable to predation [Henttonen et al. 1987], and meadows only composed about 7% of our study area). Coyotes killed some red squirrels, but their hunting tactics (they seldom ambushed prey) and lack of ability to climb trees likely limited the availability of squirrels.

The main alternative prey of lynx were red squirrels, which were relatively abundant at all phases of the cycle (chapter 9; Boutin et al. 1995). The increasing use of ambush beds by lynx during the cyclic decline and progressively higher hunting success by lynx chasing squirrels during the cyclic low indicate that lynx surviving into this period became skilled at catching squirrels. Even when numbers of hares began to increase in 1994–1995 and coyotes shifted their hunting effort to hares again, these lynx continued hunting mostly squirrels. The foraging decisions of predators are typically more strongly influenced by recent feeding choices than those made over a longer time frame (Shettleworth et al. 1993). Assuming there is a cost to gaining enough information to accurately track resource availability, predators may maintain dietary preferences even as the relative profitabilities of those prey change (Lewis 1986, Dukas and Clark 1995, Dall and Cuthill 1997). Patterns of dietary choice and the functional responses of coyotes and lynx in northern boreal forests are likely closely related to the local availability of alternative prey species to hares.

Prey switching may result from a number of mechanisms, including the development of search images for specific prey (Tinbergen 1960, Lawrence and Allen 1983), switches among habitat types as the relative profitabilities of foraging in them change (Royama 1970, Murdoch and Oaten 1975), and changes in foraging tactics by predators (e.g., Lawton et al. 1974, Davies 1977, Akre and Johnson 1979, Formanowicz and Bradley 1987). We documented shifts in habitat use by coyotes and lynx during the hare cycle that paralleled those by hares (Wolff 1980, Hik 1995) but saw no major switches away from denser forested areas. The densest habitats may act as refuges for hares during cyclic lows (Wolff 1980, Akçakaya 1992), and hares were found in denser cover than their predators at all phases of the cycle (O'Donoghue et al. 1998a). Aggregation of predators in patches of good densities of prey can be considered a functional or numerical response, depending on scale, but the effect on the prey (increasing rates of predation) is the same (Solomon 1949, Murdoch and Oaten 1975, Hanski et al. 1991, Korpimäki and Krebs 1996).

Several other changes in the behavior of coyotes and lynx during our study may also have affected the pattern and magnitude of kill rates. The switch by lynx to hunting red squirrels during the cyclic low was accompanied by increased use of ambush beds. Although use of these beds did not seem to increase hunting success, ambush tactics may be more energy efficient or better for hunting alternative prey during periods of low abundance of hares. Hunting in groups may have led to increased foraging success for lynx during the cyclic low, as has been shown for other group-living carnivores (Gittleman 1989). Likewise, use of trails by predators for travel helps them conserve energy and may increase encounter rates with prey; this is especially important for coyotes because of their high foot-loads for travel in the soft snows of the northern forests (Murray and Boutin 1991).

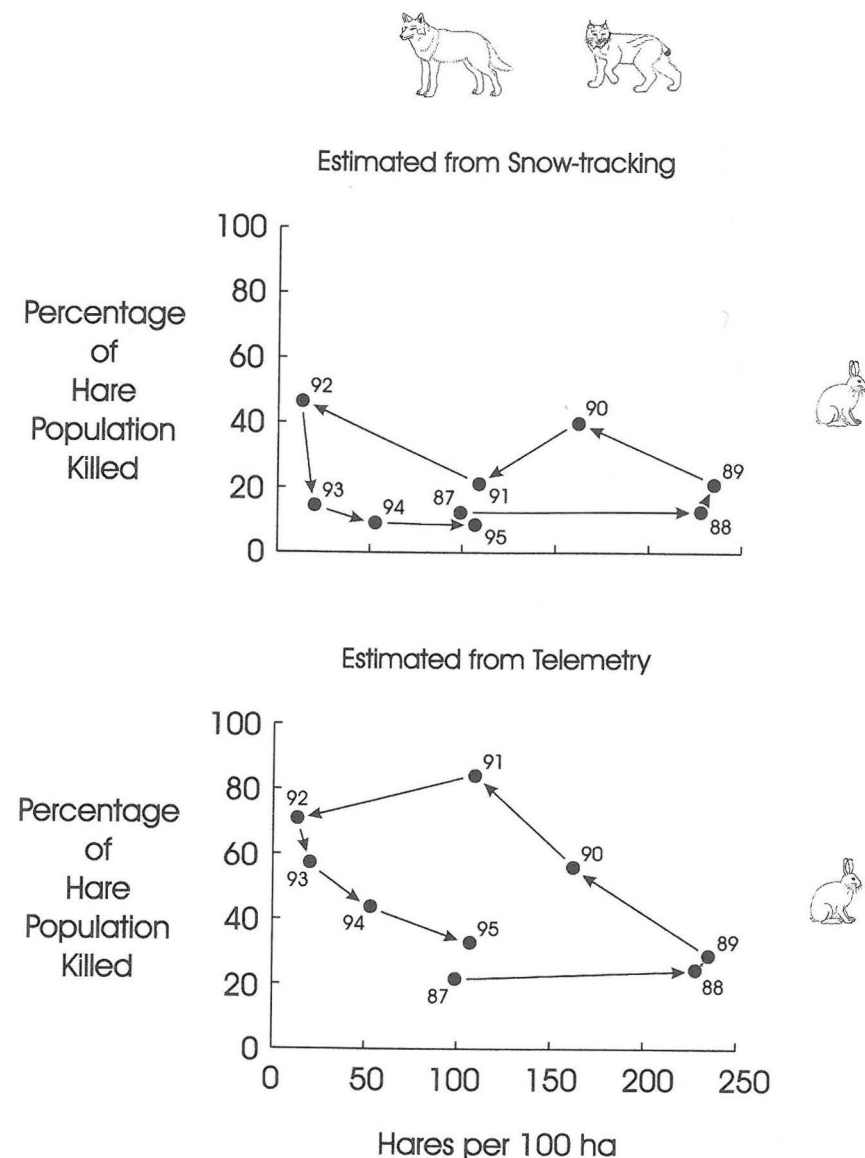


Figure 13.16 Estimated total impact of predation by coyotes and lynx during winter (October through April) on populations of snowshoe hares from 1987–1988 (labeled “87” on graph) through 1995–1996 at Kluane, as calculated from the combined numerical and functional responses of the predators and from survival rates of radio-collared hares.

13.6.3 Total Impact of Predation by Coyotes and Lynx on Hares

We estimated the total impact of predation by coyotes and lynx on populations of snowshoe hares by calculating the total number of hares killed by these predators each winter, from October through April, based on our measured functional and numerical responses. The percentage of the autumn population of hares killed by coyotes and lynx over the winter exhibits a counterclockwise temporal pattern typical of delayed density-dependent predation (Sinclair and Pech 1996; figure 13.16). However, the low predation rate calculated in 1991–1992, largely the result of rapidly declining populations of coyotes and lynx (figure 13.1), departs from the pattern expected with a simple time lag of the effects of predation.

We used data collected on the survival of radio-collared hares to make a second, independent estimate of the effects of predation by coyotes and lynx on hares. This analysis suggests that predation by these predators was 1.5–4 times higher than our estimates from this study (figure 13.16), particularly during the decline and low phases of the cycle. Rates of predation calculated from the hare survival data are likely overestimates, due to higher vulnerability of radio-collared hares to predation (Mech 1967), stress to hares caused by live trapping, or attraction of predators to trapping grids. Nonetheless, the data from the hare telemetry suggest that the effect of predation by coyotes and lynx was highest in 1991–1992, the winter we measured quite low rates from our predator data. Many radio-collared hares were killed by coyotes in October–November that winter, and we could have missed many kills because snow conditions were poor for snow tracking until November 1991.

Our estimates of the total impact of predation by coyotes and lynx ranged from 9–13% of the autumn population of hares during the cyclic increase, 21% at the peak, 21–40% during the decline, and 15–47% during the cyclic low in hare abundance (figure 13.16). These are approximately double those calculated in Alberta of 3–6% during the increase, and 9–20% during the decline of hare populations (Keith et al. 1977). We suggest that our estimates of kill rates by predators, particularly coyotes, are conservative (O’Donoghue 1998b) and that the true impact of predation by coyotes and lynx was somewhere between the two estimates calculated in figure 13.16.

The impact of all predators, in all seasons, needs to be assessed for a full evaluation of the effects of predation on the hare cycle. These data suggest that the delayed numerical (coyotes and lynx) and functional (lynx) responses of mammalian predators contributed to the cyclic dynamics of populations of hares (2- to 3-year lag in maximum predation rates) and that the magnitude of the effect of predation by coyotes and lynx is greater than previously measured. The functional and numerical responses that we have measured can be used to develop an accounting model of the whole system and to parameterize simulation models (Korpimäki and Krebs 1996).

13.6.4 Impact of Predation by Coyotes and Lynx on Alternative Prey

There is ample evidence from field studies that cyclic fluctuations of a preferred prey species may also occur in populations of alternative prey of predators (Henttonen 1985, Marcström et al. 1988, 1989, Lindström et al. 1994). In our study area, trends in populations of arctic ground squirrels, grouse, and ptarmigan were correlated with those of hares (Boutin et al. 1995), suggesting there may be a causal connection.

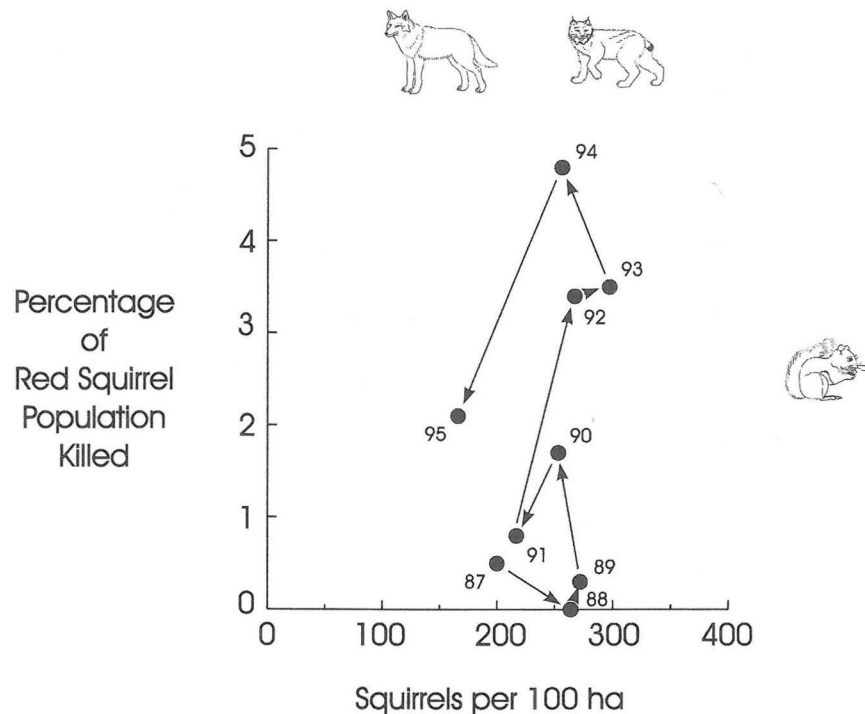


Figure 13.17 Estimated total impact of predation by coyotes and lynx during winter (October through April) on populations of red squirrels from 1987–1988 (labeled “87” on graph) through 1995–1996 at Kluane, as calculated from the combined numerical and functional responses of the predators.

We evaluated the effects of predation by coyotes and lynx during winter on populations of red squirrels using our measured numerical responses and kill rates calculated in the same manner as those for hares. We were unable to evaluate the effects of predation on numbers of small mammals because of the difficulty in judging whether attempted kills were successful, and we did not attempt to investigate predation on other prey species due to the low number of kills by coyotes and lynx. The estimated total effect of predation by coyotes and lynx on red squirrels was small (<5% of the autumn populations) in all winters and showed no pattern relative to densities of squirrels (figure 13.17). This agrees with the experimental results of Stuart-Smith and Boutin (1995), showing predation by mammals had little effect on population sizes of red squirrels.

13.6.5 Coexistence of Coyotes and Lynx

Competition between sympatric predators and how it affects partitioning of resources and breadth of resource use has been much explored and debated in the literature (Rosenzweig 1966, Schoener 1982, Wiens 1993). In general, overlap in resource use between sympatric species is less during lean times (high competition; Schoener 1982) than during periods of resource abundance. But this prediction may not hold due to complex rela-

tionships between resource abundance and species-specific thresholds of resource limitation (Wiens 1993) or different strategies of resource acquisition (Glasser and Price 1982, MacNally 1995). Accordingly, studies of patterns of overlap among predators have shown no change (Jaksic et al. 1993, Meserve et al. 1996), lower overlap (Korpimäki 1987), or higher overlap (Wiens 1993) with lower resource abundance.

We did not conduct experiments that would enable us to add empirical evidence on mechanisms permitting coexistence of coyotes and lynx. The question of how these two predators, of similar size, survive using a very limited resource base is especially interesting, given that coyotes are relatively new immigrants in the north. We summarize our observations here to suggest questions for further research.

We calculated Horn's index of overlap in diet (based on number of kills) and habitat use between coyotes and lynx for each winter of our study. Overlap in diet was high (>0.75) in all winters (figure 13.18). The lowest dietary overlap was in 1992–1993, when coyotes killed mostly small mammals and lynx killed more red squirrels, at a time when

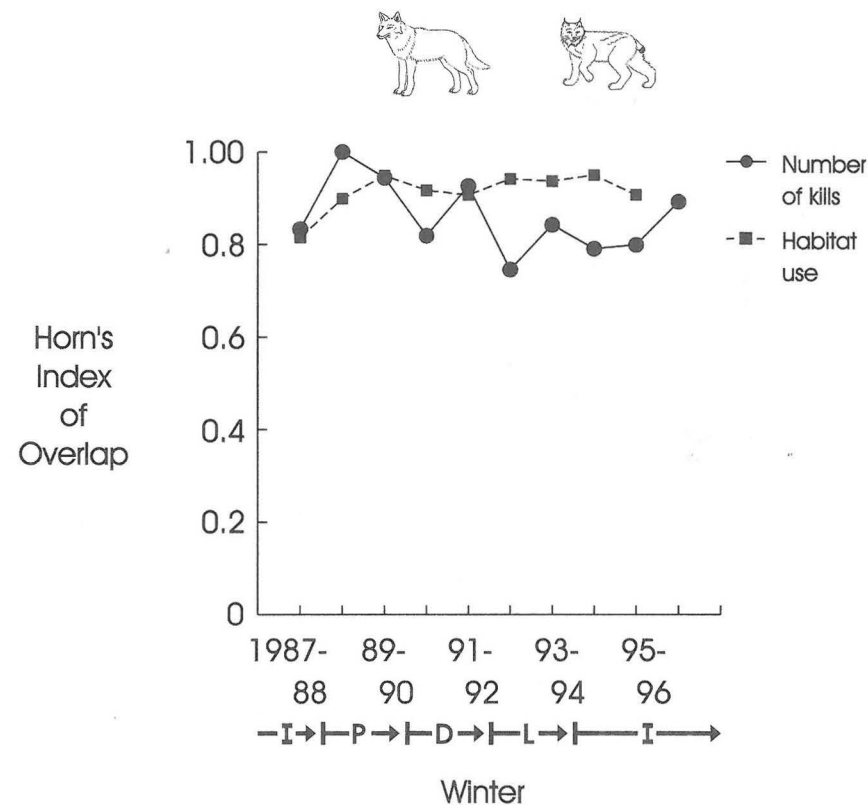


Figure 13.18 Overlap in diets (based on number of kills located during snow tracking) and habitat use by coyotes and lynx during winter from 1987–1988 through 1996–1997 at Kluane. The phases of the hare cycle (I = increase, P = peak, D = decline, L = low) are shown by the horizontal bar below the x-axis.

numbers of hares were low. Overlap in habitat use was high (range 0.82–0.95) in all winters (figure 13.18).

These observations are consistent with those made of high overlap in diets between bobcats and coyotes in areas where coyotes were relatively recent colonizers (Witmer and DeCalesta 1986, Major and Sherburne 1987, Litvaitis and Harrison 1989). There is correlative evidence that coyotes may depress numbers of bobcats in the western and north-eastern United States (Nunley 1978, Litvaitis and Harrison 1989), and both interspecific competition and intraguild predation have been suggested as mechanisms. We observed only one case of a coyote killing a young lynx (O'Donoghue et al. 1995), so the influence of predation by coyotes on lynx is not likely large in our area. Predation among predators (intraguild predation), however, has been recorded among many species of carnivores (e.g., Elsey 1954, Eaton 1979, Stephenson et al. 1991, O'Donoghue et al. 1995), and intraguild predation may have important consequences in some predator–prey systems (review in Polis et al. 1989).

The degree of overlap in the diets of coyotes and lynx during cyclic lows is likely highly dependent on the availability of alternative prey. In our study area, population fluctuations of red squirrels and voles, which are largely unrelated to cyclic hare dynamics (Boutin et al. 1995), would have a great influence on this overlap. Lynx appear better able than coyotes to take advantage of the most consistently available alternative prey species, red squirrels, and during periods when few voles or hares are available, lynx may persist in greater numbers than coyotes. In areas where other alternative food sources, such as the carrion of moose (e.g., Staples 1995) or livestock (e.g., Todd et al. 1981) are consistently available, coyotes may persist in higher numbers. Even with high or even complete overlap in resource use, though, recent models of competition have suggested that species may coexist for long periods of time (Hubbell and Foster 1986, MacNally 1995).

13.6.6 The Specialist–Generalist Contrast

The degree of versatility in resource use by any consumer is a function of species-specific constraints and external factors such as the relative availabilities of resources. Predators that are generalists, when considered over their whole geographic range, may be local specialists (MacNally 1995). Clearly, in a low-diversity environment such as the boreal forest in our study area, dietary options are limited for terrestrial predators. Given the limited availability of voles and other alternative prey, coyotes in our study area appeared to specialize on hares even during periods (1994–1995) when lynx were preying more heavily on red squirrels.

In fluctuating environments, facultative foraging strategies, in which predators concentrate their foraging efforts on the most profitable prey, which may vary in time, should be favored over obligate strategies (Glasser 1982). Over their geographic range, North American lynx can certainly be said to be more dependent on snowshoe hares than are coyotes—on this basis, they can be considered hare specialists. Locally, though, at least some individual lynx can specialize on preying on red squirrels during periods of low hare abundance, and so they may perhaps better be called facultative specialists. We do not know whether the changes that we observed during the hare cycle were due to all or only some individuals shifting their foraging behavior. Studies comparing the plasticities of in-

dividual lynx and coyotes in adjusting their patterns of resource use to changing availabilities of prey would be valuable for clarifying mechanisms behind shifts at the population level.

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