Numerical Responses of Coyotes and Lynx to the Snowshoe Hare Cycle

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Oikos, Vol. 80, No. 1. (Oct., 1997), pp. 150-162.

OIKOS 80: 150–162. Copenhagen 1997

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O'Donoghue, M., Boutin, S., Krebs, C. J. and Hofer, E. J. 1997. Numerical responses of coyotes and lynx to the snowshoe hare cycle – Oikos 80: 150–162.

Coyotes and lynx are the two most important mammalian predators of snowshoe hares throughout much of the boreal forest in North America. Populations of hares cycle in abundance, with peaks in density occurring every 8–11 yr, and experimental results suggest that predation is a necessary factor causing these cycles. We measured the numerical responses of coyotes and lynx during a cyclic fluctuation of hare populations in the southwest Yukon, to determine their effect on the cyclic dynamics. We used snow-tracking, track counts, and radio telemetry to directly examine changes in the numbers, population dynamics, and movements.

Numbers of coyotes varied 6-fold and those of lynx 7.5-fold during a 26–44-fold fluctuation in numbers of hares, and the abundances of both predators were maximal a year later than the peak in numbers of snowshoe hares. Cyclic declines in numbers of coyotes were associated with lower reproductive output and high emigration rates. Likewise, few to no kits were produced by lynx after the second winter of declining numbers of hares. High emigration rates were characteristic of lynx during the cyclic peak and decline, and low in situ survival was observed late in the decline. The delayed numerical responses of both "generalist" coyotes and "specialist" lynx were therefore similar, and would contribute to the cyclic dynamics.

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Populations of snowshoe hares (*Lepus americanus*) undergo regular cycles in abundance throughout the northern boreal forest in North America, with amplitudes over two orders of magnitude, and 8–11 yr between cyclic peaks (Elton and Nicholson 1942, Keith 1990). These cycles have major effects on predators of hares, as well as on other herbivores in the relatively simple boreal ecosystem (Finerty 1980).

There have been many different hypotheses put forward to explain population cycles of hares, involving weather, disease, plant-herbivore interactions, and predation (reviews in Finerty 1980, Keith 1990). The most widely accepted hypothesis was put forward by Lloyd Keith and colleagues, based on studies spanning two complete cycles in Alberta (Keith and Windberg 1978, Keith et al. 1984, Keith 1990). This hypothesis proposed that the cycle in hare numbers was generated by an interaction between the hares and their winter food supply, with predation playing a key role during the decline phase of the cycle. At peak numbers, hares overbrowse the woody shrubs they depend upon, and this leads to malnutrition, low reproductive output, and outright starvation, which initiates the decline in densities of hares. Predators, which respond numerically and functionally to hare abundance (Keith et al. 1977), kill a large percentage of hares during the cyclic decline, and act to deepen and lengthen the low phase of the cycle.

Accepted 14 January 1997

ISSN 0030-1299

This view of the role of predation in generating population cycles was summarized by Finerty (1980), who concluded that predation was unlikely to be the sole cause of cycles in the abundance of small mammals, but that it likely did 1) hasten the decline of herbivore populations already declining for other reasons (e.g., food shortage); 2) increase the amplitude of cycles by driving prey populations to very low numbers; 3) increase the period of cycles, due to a lag effect of predators persisting into periods of low prey numbers (delayed density-dependence); and 4) possibly synchronize cycles over large geographic areas due to the high mobility of many predators.

Studies conducted in the southwest Yukon, however, have suggested that predation may play a larger role (Krebs et al. 1995). Populations of hares supplied with supplemental food still declined in synchrony with control populations (Krebs et al. 1986, 1995); there was no evidence of absolute food shortage (Sinclair et al. 1988, Smith et al. 1988), and predators killed virtually all of the animals that died during two cycles (Boutin et al. 1986, Trostel et al. 1987, Krebs et al. 1995). However, a population of hares experimentally protected from terrestrial predators also declined from the cyclic peak, so a simple predator-prey interaction is an inadequate description of the hare cycle (Krebs et al. 1995). Only when hares were both provided with supplemental food and protected from mammalian predators did the dynamics of the cycle change, suggesting that a three-trophic level explanation must be invoked (Krebs et al. 1995). This agrees with Keith's conceptual model of the hare cycle (Keith 1990), except that there is no evidence that absolute food shortage is necessary to initiate the cyclic decline. Hik (1995) presented evidence that sub-lethal effects of predation may also influence the population dynamics of hares (e.g., hares may choose poorer habitats in the face of high risk of predation, thus leading to lower condition and depressed reproductive output), which may account for lower recruitment in the face of apparently adequate food supplies.

Recent mathematical models have supported the proposal that predation is a necessary factor in the hare cycle (Akçakaya 1992, Royama 1992, Stenseth 1995). Likewise, Fennoscandian researchers have presented theoretical (Hanski et al. 1991, 1993, Hanski and Korpimäki 1995) and empirical (Henttonen et al. 1987, Korpimäki 1993) evidence that predation is an essential factor in generating 3–4-yr cycles of microtine rodents in northern Fennoscandia. Strong functional responses by a large suite of generalist predators may regulate vole numbers in southern regions (Erlinge et al. 1983, 1984, 1988, Hanski et al. 1991), while delayed numerical responses of specialist predators – mostly weasels – cause a lag and cyclic dynamics in the north.

The main predators of snowshoe hares are the same through much of their range – lynx (*Lynx canadensis*), coyotes (*Canis latrans*), great horned owls (*Bubo virginianus*), and goshawks (*Accipiter gentilis*). Keith and colleagues (Keith et al. 1977) estimated the population sizes and predation rates of these predators during a complete hare cycle in order to analyze the effects of predation on hare dynamics. They found that both coyotes and lynx responded to the increase in hare numbers with approximately 4-fold increases in their population sizes, followed by a 6-fold decrease in coyote numbers, and a 3–4-fold decrease in lynx numbers, during the decline phase of the cycle. Further north, Poole (1994) noted a 10-fold change in lynx density during the decline of hare populations in the Northwest Territories, and Slough and Mowat (1996) found a 10–17-fold fluctuation of lynx numbers in south–central Yukon over a hare cycle.

Lynx are usually considered prototypical specialists on snowshoe hares, and virtually all studies of their food habits have shown hares to be their predominant prey (Saunders 1963, Brand and Keith 1979, Parker et al. 1983, Ward and Krebs 1985). They are morphologically well adapted to hunting in the deep snows of the north (Murray and Boutin 1991), and their geographic range overlaps almost exactly with that of hares (Banfield 1974).

Coyotes, in contrast, are often considered prototypical generalists. Over their large and expanding range in North America, they are adapted to a wide variety of habitats, climates, and foods (see papers in Bekoff 1978). Morphologically, coyotes are not well suited for hunting in deep, soft snow, having a relatively high foot-load (Murray and Boutin 1991). Coyotes are fairly recent immigrants into the far north, appearing in the Yukon between 1910 and 1920 (G. Lotenberg, 1994, unpublished report for Parks Canada).

The effects of generalist and specialist predators on prey populations are likely to be very different, based on theoretical (Murdoch and Oaten 1975, Hassell and May 1986) and empirical (e.g., Erlinge et al. 1983, Henttonen et al. 1987, Korpimäki 1993) evidence. Rapid functional responses of generalist predators may increase the stability of predator-prey interactions, while the delay in the numerical responses of specialists may introduce lags and dynamic instability.

While there is ample evidence that the hare cycle has persisted since long before coyotes immigrated into the north (Elton and Nicholson 1942), there is little quantitative evidence of their effect on hare populations, populations of alternative prey, and other predators. There have been very few studies conducted of coyotes in true boreal forest (Theberge and Wedeles 1989, Murray and Boutin 1991, Murray et al. 1994, 1995) – Keith's Alberta study area was approximately one-third agricultural land, which was used by coyotes extensively during periods of low hare numbers (Todd et al. 1981).

Objectives, hypotheses and predictions

The goal of this paper is to present and contrast the numerical responses of coyotes and lynx to the snowshoe hare cycle, and examine the demographic mechanisms behind these responses. Boutin et al. (1995) presented data showing that numbers of these two predators cycle in synchrony with populations of snowshoe hares, with a 1-yr time lag. This research is aimed at meeting part of a larger objective of evaluating the total impact of mammalian predators on the dynamics of hare populations. Both carnivores are approximately the same size (9–12 kg adult body size in the southwest Yukon), and they are therefore reliant on essentially the same prey base.

From the data of Keith and co-workers, we assume that 1) food is not limiting for coyotes or lynx at high hare density, 2) at low hare density, food does become a limiting factor, and 3) snowshoe hares are the preferred food for both coyotes and lynx (the percent biomass of hares in the diets of coyotes and lynx was greater than the percent available at all phases of the cycle in this study; O'Donoghue 1997).

As a null hypothesis, we postulate that the rates of population change of the two carnivores are determined solely by the abundance of snowshoe hares. Since both coyotes and lynx have similar potential rates of population increase (Brand et al. 1976, Nellis and Keith 1976), populations of the two species should respond numerically to changes in hare numbers with cyclic fluctuations of similar amplitude and timing. Alternatively, since lynx are considered to be specialists on hares, they may respond with fluctuations of greater amplitude (higher highs or lower lows), and may persist longer when hare densities decline. Another alternative prediction is that coyote populations may decline at a slower rate than those of lynx due to more efficient use of alternative prey.

Study area

This study was conducted in the southwest Yukon Territory, Canada (60° 57′ N, 138° 12′ W), in a broad glacial valley approximately 350 km² in area (Fig. 1). The study area was bounded to the north and south by alpine tundra, to the west by Kluane Lake, and to the east by Kloo Lake and the Jarvis River. Elevation ranges from approximately 830 m to 1170 m. The dominant vegetation of the area is white spruce forest (*Picea glauca*) with scattered aspen stands (*Populus tremuloides*), and a dense but patchy understory of willow (mostly *Salix glauca* and *S. alaxensis*), bog birch (*Betula glandulosa*), and soapberry (*Shepherdia canadensis*) (Douglas 1974). The climate is cold continental, with mean January temperatures of −18°C, and about 65 cm average snow accumulation. Snow cover is usually continuous from October through May.

Methods

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

Estimation of prey densities

We estimated densities of snowshoe hares, red squirrels (*Tamiasciurus hudsonicus*), Arctic ground squirrels (*Spermophilus parryi*), and small mammals (mostly *Clethrionomys rutilus*, *Microtus oeconomus*, and *M. pennsylvanicus*) by live-trapping (Boutin et al. 1995). Snowshoe hares were trapped on 1–3 60-ha grids each March and October-November; population estimates were made using the jackknife estimator in program CAPTURE (White et al. 1982). Squirrels were trapped on 1–3 8-ha grids each May and August; population estimates were made using the estimators recommended by the model selection procedure of program CAPTURE. *Clethrionomys* were trapped on two 2.8-ha grids, and *Microtus* on two 1.5-ha grids each May and August; population estimates were made

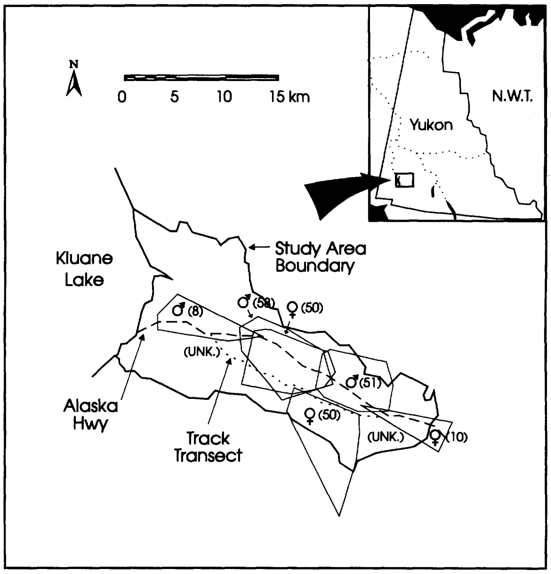

Fig. 1. Location of study area, and an example of how predator numbers were estimated. The polygons represent the home ranges of adult radio-collared lynx during the winter of 1994–95, calculated using 95% minimum convex polygons. Numbers in parentheses represent the total number of relocations. Based on tracks and movements of radio-collared animals, we estimated that there were two untagged animals in the study area ("UNK"), probably a female in the west, and a male in the east.

based on the minimum number of animals alive (MNA; Krebs 1966). Available biomass of each prey species was calculated by averaging the "fall" and "spring" estimates each winter, and multiplying these abundances by 1500 g for hares, 250 g for red squirrels, and 20 g for small mammals.

Track counts

We counted all tracks of coyotes and lynx along a 25-km transect that traversed our study area (Fig. 1). We ran the transect by snowmobile, starting each day after fresh snowfalls from October-April, and continuing on subsequent days for as long as fresh tracks could be distinguished. The transect was sub-divided into eight segments, based on topographic features. We recorded every track that crossed our transect that could not be visually connected to another crossing, and recorded the species, group size, location and habitat type at each track.

We analyzed the track-count data by calculating least squares means (Searle et al. 1980) for each year and species in an analysis of covariance model (Wilkinson 1990), with transect segment, date, days since last snowfall, and temperature and cloud cover on the night before the count as covariates. Least squares means are the expected values of cells (in this case, years) if all covariates were at their mean values, and the model design were balanced. In other words, they are estimates of mean track counts, controlling for time of year, weather, and location. The distributions of track-count data were severely skewed, so we log-transformed the data before analysis, and entered only transect segments with counts >0 into the analysis. We used logistic regression (Trexler and Travis 1993) to estimate the probability of encountering any tracks in a transect segment, and multiplied the least squares means by these probabilities to give our yearly means.

Live-trapping and radio-tracking of predators

We live-trapped coyotes and lynx, mostly during the fall and winter months, using padded foot-hold traps (No. 3 Soft-catch® traps, Woodstream Corp., Lititz, PA, USA), cable snares (Fremont leg snares®, Fremont Humane Traps, Candle Lake, SK, Canada), and box traps (techniques similar to Mowat et al. 1994). We checked traps at least once per day, and locked traps open when the temperature was less than −20°C. During the first 4 yr of the study, we immobilized captured animals using a 7:1 mixture of ketamine hydrochloride and xylazine hydrochloride, but we switched to using a mixture of tiletamine hydrochloride and zolazepam hydrochloride (Telazol®, A. H. Robbins Co., Richmond, VA, USA) since then (Poole et al. 1993). We subjectively classified all captured animals as adults, yearlings, or kits, based on body size and tooth wear, and after 1990, we pulled lower incisors from most animals, and determined their ages from cementum annuli (Crowe 1972).

We fitted animals with radio-collars weighing 250–350 g (Telonics, Inc., Mesa, AZ, USA); most of these had internal mercury switches sensitive to movement, which allowed us to monitor the activity of collared animals. Using ground-based telemetry, we attempted to get at least one radio-location per week of each radio-collared coyote and lynx. We periodically monitored the activity of most animals much more intensively. We calculated locations and error ellipses using the program LOCATE II (Nams 1990), and plotted home ranges using 95% minimum convex polygons (Mohr 1947) with the program CALHOME (Kie et al. 1994).

Estimates of predator populations

We estimated the numbers of coyotes and lynx in the study area each December, from 1987 to 1995, using data from several sources. We kept detailed records of the home ranges and movements of radio-collared animals from telemetry locations and snow-tracking. Each winter, we also had extensive snow-tracking programs, in which we followed the tracks of coyotes and lynx throughout the study area (O'Donoghue 1997). During 8 winters, from 1987 to 1995, we tracked coyotes an average of 237 km, and lynx an average of 279 km per winter. These data, supplemented by track data from our transect counts, allowed us to estimate the number of uncollared animals in our study area. We also kept records of the locations and group sizes of all howling by coyotes throughout the year, which gave us a further check on the size of family groups of coyotes. An example of our method is illustrated in Fig. 1 for lynx during the winter of 1994–95.

Results

Prey populations

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

Population trends of other potential prey species varied. Numbers of red squirrels stayed relatively stable,

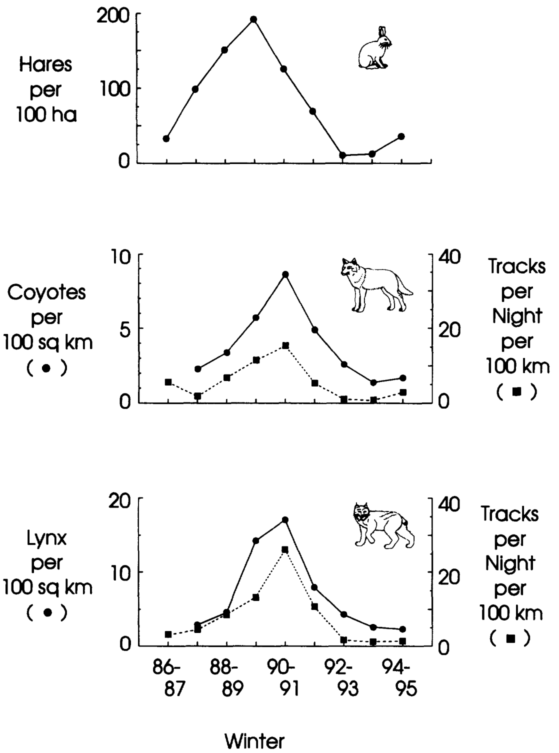

Fig. 2. Estimated densities of snowshoe hares (means of autumn and late winter estimates from live-trapping on 1–3 60-ha grids), coyotes, and lynx from 1986 to 1995 in the southwest Yukon. Counts of predator tracks along a 25-km transect are presented as least squares means; raw track counts were adjusted for covariates track location, date, days since last snowfall, and temperature. Mean 95% confidence intervals of track counts were ±13%.

with a slight increase during the last two winters of the study (Fig. 3). Populations of small mammals fluctuated with a 10–50-fold amplitude, with the highest numbers occurring from 1991 to 1993 (Fig. 3). Densities of ground squirrels increased to a peak in 1991 (a year after the cyclic peak of hares), declined to low numbers by 1993, and increased again in 1994 (Fig. 3). During the winter, ground squirrels hibernate, and they are therefore not available as prey. There were few other alternative prey species. Spruce grouse (*Dendragapus canadensis*), ruffed grouse (*Bonasa umbellus*), and ptarmigan (mostly *Lagopus lagopus*) were present (Boutin et al. 1995), but were seldom utilized by predators (2% of all kills in winter from 1987 to 1995; O'Donoghue 1997).

Snowshoe hares were by far the most abundant potential food source during winter for predators from 1987 to 1992, comprising 63–81% of the total biomass of the main prey species (Fig. 4). Red squirrels were the second largest food source during these years. During the last three winters of the study (1992–93 to 1994–95), however, once hare numbers had crashed, red squirrels comprised 58–72% of the total biomass (Fig. 4). Small mammals represented less than 10% of the total biomass of prey in all winters except 1992–93 (14%; Fig. 4). From the winter of 1989–90 to winter 1992–93, there was an approximately 4-fold decrease in the total prey biomass available. Snowshoe hares are the only one of these prey species with no arboreal or subnivean refuge from predation, so the decrease in effective availability of prey during this time was likely considerably greater.

Predator populations

Coyotes increased in numbers from 1987 to 1990, and then decreased to low numbers again by 1992–93 (Fig. 2). The density of coyotes was highest, at about 9/100 km^2, in 1990–91, the first winter of declining hare numbers (Fig. 5). The low density of coyotes was 1.4/100 km^2, and the cyclic amplitude was approximately 6-fold. Over the whole cycle, coyote numbers were strongly correlated with hare numbers the previous year (Fig. 5; Spearman rank correlation coeffi-

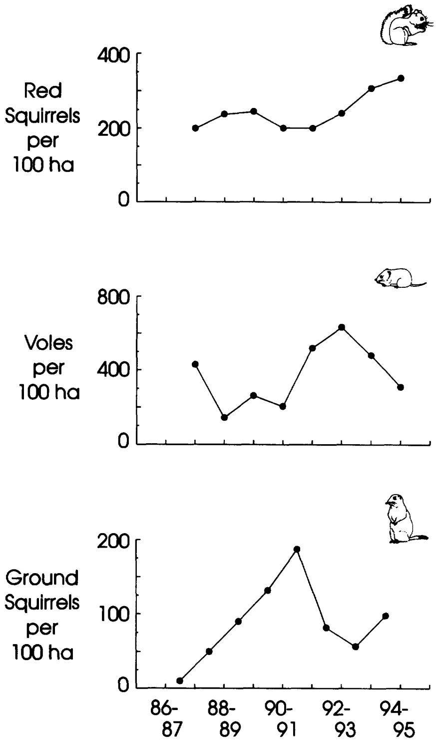

Fig. 3. Estimated densities of red squirrels (means of late summer and spring estimates from live-trapping on 2–3 8-ha grids), small mammals (means of late summer and spring estimates from live-trapping on two 2.8-ha grids for *Clethrionomys rutilus*, and on two 1.5-ha grids for *Microtus oeconomus* and *M. pennsylvanicus*), and Arctic ground squirrels (means of spring and late summer estimates from live-trapping on 1–3 8-ha grids) from 1986 to 1995 in the southwest Yukon. Arctic ground squirrels hibernate during the winter, and are therefore not available to predators.

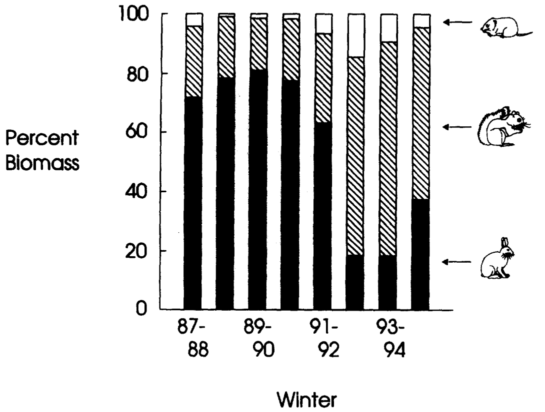

Fig. 4. Percent prey biomass of hares, red squirrels and small mammals available to predators in winter from 1987 to 1994. These species made up 97% (666/689) of all kills by coyotes and lynx during the winters of these years.

cient = 1.00, $P < 0.001$). The trend in track counts, based on 11 140 km of transect sampled, closely mirrored the trend suggested by our population estimates (Spearman rank correlation coefficient = 0.88, $P = 0.01$).

The trend in lynx numbers was similar to that of coyotes (Fig. 2). Populations of lynx increased from 1987 to 1990 to a peak density of about 17/100 km^2, and then declined by 1992–93 to a low of about 2.3/100 km^2. The cyclic amplitude was 7.5-fold. Lynx numbers were also highly correlated with densities of hares during the previous year (Fig. 6; Spearman rank correlation coefficient = 0.98, $P = 0.001$). As with coyotes, the trend in track counts closely followed our population estimates of lynx (Spearman rank correlation coefficient = 0.95, $P < 0.005$).

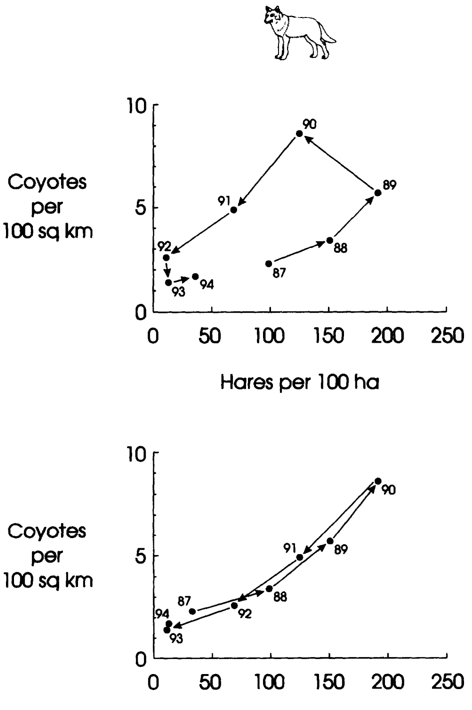

Fig. 5. Numerical response of coyotes to changes in the density of snowshoe hares from 1987 to 1995. Coyote density was highly correlated with density of hares during the previous winter. Numbers next to the data points indicate years.

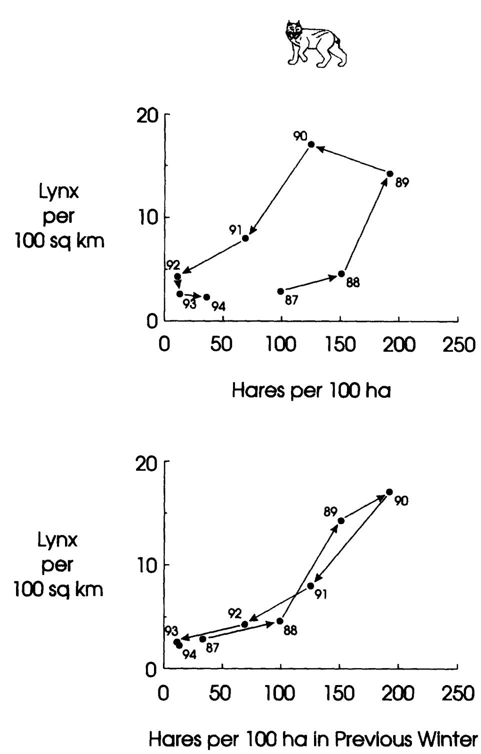

Fig. 6. Numerical response of lynx to changes in the density of snowshoe hares from 1987 to 1995. Lynx density was highly correlated with density of hares during the previous winter. Numbers next to the data points indicate years.

Survival and emigration of predators

We live-trapped and radio-collared 21 different coyotes and 56 different lynx between 1986 and 1995 (Tables 1 and 2). In general, we were able to capture a greater percentage of the coyotes and lynx present in the study area during the second half of the study. The mean weights of trapped animals were: adult male coyotes = 12.2 kg ($n = 11$), adult female coyotes = 10.7 kg ($n = 6$), adult male lynx = 10.8 kg ($n = 26$), and adult female lynx 9.6 kg ($n = 18$).

Over-winter survival of radio-collared lynx varied widely during the study (Fig. 7). Survival was high (> 70% per winter) during the increase phase of the hare cycle, slightly lower (45–63% per winter) during the early decline phase, and most (8 of 11) animals died in 1992–93, the first winter of very low hare numbers. Those animals that did survive into the next winter

Table 1. Numbers of radio-collared coyotes, and estimates of untagged animals, during winter from 1986 to 1995. Some coyotes were radio-tracked during more than one winter. Numbers of untagged animals were estimated from intensive snow-tracking and recording howling year-round.

Winter	Estimated population	Number of collared coyotes	Number of adult males	Number of adult females	Number immature males	Number immature females	Estimated number of uncollared coyotes
1986–87	–	0	–	–	–	–	?
1987–88	8	3	1	1	1	0	5
1988–89	12	2	0	2	0	0	10
1989–90	20	0	0	0	0	0	20
1990–91	30	6	4	1	0	1	24
1991–92	17	8	2	2	1	3	9
1992–93	9	4	1	2	1	0	5
1993–94	5	3	3	0	0	0	2
1994–95	6	0	0	0	0	0	6

(1993–94) survived quite well. Overall, survival of lynx was lower during the cyclic decline than at other phases of the cycle ($\chi^2 = 7.29$, d.f. = 1, $P = 0.007$). Causes of mortality of radio-collared lynx in the study area were mostly human-caused (fur-trapping) in all years except during the decline phase of the cycle when predation/scavenging ($n = 5$) and starvation ($n = 2$) were of greater or equal importance (Fig. 7). We confirmed three cases of predation on lynx (by a wolf, a wolverine, and another lynx), and suspected predation by wolverines in two other cases. We recorded only 5 mortalities of coyotes, and 4 were human-caused.

Yearly emigration rates of lynx varied from 0 to 32%, with the highest rates occurring at the peak and in the decline phase of the hare cycle (Fig. 7; emigration here is defined as leaving the study area), although the frequency of emigration was not significantly higher in this period than during the cyclic low and increase ($\chi^2 = 1.86$, d.f = 1, $P = 0.17$). In contrast, 62% of all coyotes radio-collared emigrated or were lost (and presumed to have emigrated) from our study area, and there was no clear relationship between the timing of emigration and the abundance of prey. Emigration rates of both adults (coyotes = 56%, lynx = 44%) and juveniles (coyotes = 80%, lynx = 58%) were high for both species.

We determined the minimum emigration distances for 2 coyotes and 10 lynx, most of which were captured by fur-trappers (Table 3). Distances between capture and mortality sites varied from 23 to 40 km for coyotes, and 24 to 830 km for lynx. Six lynx emigrated further than 200 km from their capture sites – one of these was trapped in the Northwest Territories, and the other 5 were trapped in Alaska.

Recruitment of predators

While we did not directly measure reproduction of coyotes or lynx, we recorded the mean group sizes for all observations of tracks along our track transect (Figs 8 and 9). We defined "family groups" of coyotes as all groups with more than 2 animals, and of lynx as all groups with kittens present (determined by track size). Groups of coyotes were noted only during the 4 winters from 1988–89 to 1991–92, and groups of more than 3 only during the first two winters of the hare decline (Fig. 8). Family groups of lynx were seen in all winters except the last two years of the study, but there were very few sightings after 1990–91 (Fig. 9). Groups of larger than 4 animals were seen only in the three winters from 1988–89 to 1990–91.

Discussion

Coyotes and lynx showed similar responses to changes in prey abundance over the cycle in numbers of snowshoe hares. The 6-fold change in coyote numbers was slightly less than the 7.5-fold fluctuation of the lynx population, but measures of amplitude are strongly affected by estimates at the low of the cycle, so small changes in numbers at the low can translate into large differences in amplitude. Populations of both carnivores peaked in 1990–91, the year following the highest hare densities, and both declined at a similar rate; coyote abundance was 30% of peak density 2 yr afterwards, compared to 25% for lynx. Populations of the main species of alternative prey did not fluctuate in synchrony with snowshoe hares (Boutin et al. 1995). Therefore, our null hypothesis, that the densities of coyotes and lynx in the boreal forest are largely determined by the abundance of snowshoe hares, is supported by these data.

Densities of predators

The peak density of coyotes in our study area (9/100 km^2) was much lower than that observed in Alberta (44/100 km^2), and more comparable to their low density (8/100 km^2; Keith et al. 1977, Todd et al. 1981). Populations of coyotes in Alberta also declined at a

Table 2. Numbers of radio-collared lynx, and estimates of untagged animals, during winter from 1986 to 1995. Some lynx were radio-tracked during more than one winter. Numbers of untagged animals were estimated from intensive snow-tracking.

Winter	Estimated population	Number of collared lynx	Number of adult males	Number of adult females	Number immature males	Number immature females	Estimated number of uncollared lynx
1986–87	–	4	2	2	0	0	?
1987–88	10	7	2	2	0	3	3
1988–89	16	6	2	1	2	1	10
1989–90	50	11	4	3	2	2	39
1990–91	60	22	13	5	1	3	38
1991–92	28	16*	8	5	2	0	12
1992–93	15	11	8	3	0	0	4
1993–94	9	6	4	2	0	0	3
1994–95	8	6	3	3	0	0	2

* The sex of one adult was not noted in 1991–92.

much slower rate than those in the Yukon after the cyclic peak (22% decline after 2 yr relative to 70% decline in the Yukon), despite similar trends in hare abundance. Coyotes made heavy use of livestock carcasses during periods of low prey abundance in Alberta (Todd et al. 1981), which were not available to coyotes in our study. Further south in their range, densities of coyotes can range as high as 50–100/100 km^2 (Camenzind 1978, Andelt 1985), so the densities we observed in the boreal forest are quite low.

Densities of lynx at the cyclic peak in our study area (17/100 km^2) were higher than those observed in Alberta (10/100 km^2; Brand et al. 1976, Keith et al. 1977), but considerably lower than in south–central Yukon (50/100 km^2; Slough and Mowat 1996) or in the Northwest Territories (30/100 km^2; Poole 1994). The peak abundances of hares were greater in all 3 other study sites (Alberta: 17/ha, Brand et al. 1976; south–central Yukon: 8/ha, Slough and Mowat 1996; Northwest Territories: 8/ha, Poole 1994; vs 2/ha at Kluane). Despite apparently higher prey density further south in their range then, lynx attain higher densities in the north. In our study area, densities of lynx were approximately double those of coyotes at all phases of the cycle. The reverse was true in the Alberta study area (Brand et al. 1976, Keith et al. 1977, Todd et al. 1981).

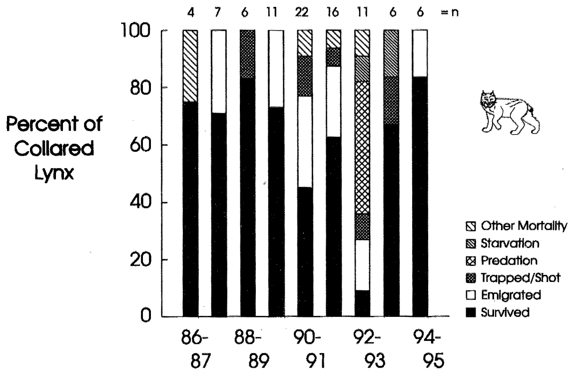

Fig. 7. Survival and causes of mortality of radio-tagged lynx during winter, from 1986 to 1995. Sample sizes are given above each bar. Of the 5 mortalities classified as due to "Predation" in 1992–93, 3 were confirmed, and two suspected, based on signs at the sites of mortality. Sample sizes were too small for a comparable figure for coyotes, but 62% of all radio-tagged coyotes emigrated from the study area, and only 5 mortalities, 4 of them human-caused, were recorded.

Numerical responses of specialist predators such as lynx are usually delayed, and they therefore tend to destabilize predator-prey interactions, while the functional responses of generalists are stabilizing (Murdoch and Oaten 1975, Hassell and May 1986, Crawley 1992). However, strong numerical responses of generalist predators to cyclic prey have also been reported for coyotes (approximately 10-fold change) responding to changes in the abundance of black-tailed jackrabbits (*Lepus californicus*) in Utah (Clark 1972, Wagner and Stoddart 1972, Knowlton and Stoddart 1992), bobcats (*Lynx rufus*; 9-fold change) in relation to jackrabbit densities in Idaho (Knick 1990), and red foxes (*Vulpes vulpes*) to European vole populations (Goszczynski 1977, Angelstam et al. 1985, Small et al. 1993).

Survival of predators

The decline in lynx numbers in our study area was in part due to lower survival of adults during the decline phase of the cycle. Our results are comparable to the two other concurrent studies of lynx in northern Canada (Poole 1994, Slough and Mowat 1996). Survival of radio-collared lynx was high (75–90% per year) in both of these studies during all years except for the decline phase of the cycle. In our study, only 1 of 11 lynx (9%) survived the second winter after the cyclic peak, while 40% ($n = 30$) survived in the south–central Yukon (Slough and Mowat 1996), and 27% ($n = 16$) survived in the Northwest Territories (Poole 1994) during the same time period. In Idaho, the annual survival

Table 3. Known emigration distances, from capture sites to sites of mortality, of radio-collared coyotes and lynx from 1986 to 1995.

Species	Age* when last in study area-sex	Date of last location in study area	Days from last location to mortality	Total emigration distance (km)	Fate
Coyote	A–F	18 Nov 91	1117	40	Trapped
Coyote	A–M	10 Mar 94	0	23	Shot
Lynx	Y–M	26 Mar 90	660	140	Trapped
Lynx	Y–M	01 Jul 90	858	355	Shot
Lynx	A–F	15 Jul 90	167	320	Trapped
Lynx	A–M	16 Feb 91	296	830	Trapped
Lynx	A–M	02 Apr 91	680	405	Trapped
Lynx	A–M	30 Sep 91	483	300	Trapped
Lynx	Y–F	18 Oct 91	58	130	Trapped
Lynx	A–M	02 Nov 92	202	245	Trapped
Lynx	A–F	10 Feb 93	0	24	Unk. cause
Lynx	A–M	04 Mar 93	11	40	Trapped

* A = adult, Y = yearling.

of bobcats declined from 78% to 16% during a cyclic decline in numbers of jackrabbits (Knick 1990).

These are the first studies to document causes of mortality in untrapped or lightly trapped populations of lynx. Both other studies in northern Canada noted that starvation, predation, and cannibalism were the main causes of mortality that they could identify (Poole 1994, Slough and Mowat 1996). Predation among predators (intraguild predation) has been recorded among many species of carnivores (e.g., Elsey 1954, Eaton 1979, Stephenson et al. 1991, O'Donoghue et al. 1995). Intraguild predation may have important consequences in some predator-prey systems (review in Polis et al. 1989), but it is not known whether the lynx killed in our studies would have survived or starved had they not been killed by predators.

In our study, and in the study of Poole (1994, 1995), there was a complete turn-over of resident lynx in the study area during the population decline. We know of only 1 animal which survived on our study area from the previous cyclic peak (1981) until the most recent decline (1992). We therefore have little evidence supporting the "core population hypothesis", which proposes that a cohort of permanent residents persist through cyclic lows in relatively stable home ranges (Breitenmoser et al. 1993). In south–central Yukon, the majority of animals surviving into the low phase of the cycle were born in the study area (Slough and Mowat 1996), but it remains to be seen whether they survive to breed during the next cyclic increase.

We have insufficient data on the survival of radio-collared coyotes during the hare cycle, since most animals emigrated out of range before they died. The few mortalities that we did identify were all human-caused.

Recruitment of predators

The decline in populations of both predators was associated with lower recruitment. We did not directly

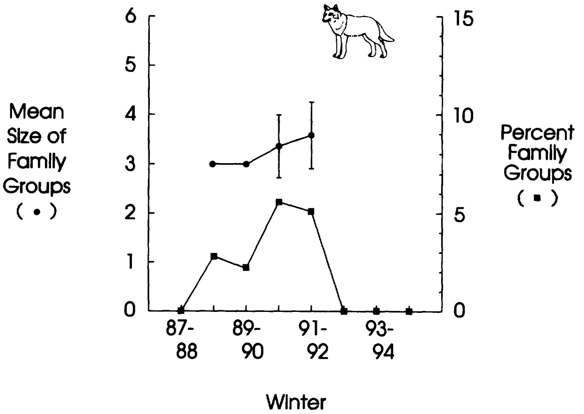

Fig. 8. Mean group sizes of family groups (±S.D.) of coyotes (defined as groups with more than 2 individuals), and percent of total number of track observations comprised of family groups, along the 25-km track transect, from 1987 to 1995.

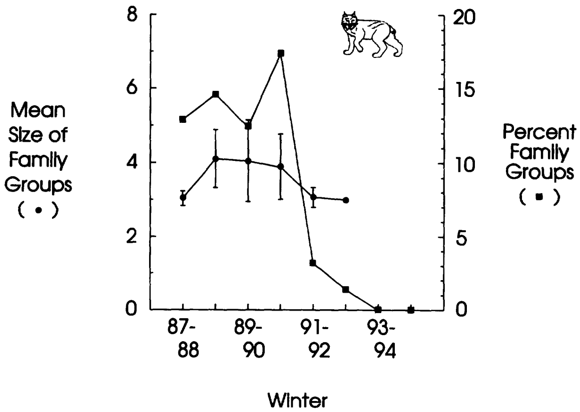

Fig. 9. Mean group sizes of family groups (±S.D.) of lynx (defined as groups with kittens present), and percent of total number of track observations comprised of family groups, along the 25-km track transect, from 1987 to 1995.

measure the reproductive output of either species, but since we failed to hear howling by any family groups of coyotes after 1991, and lynx kits stay with their mother through their first winter (Mowat et al. 1996), we propose that the changes in group sizes that we observed were due to lower recruitment rather than early dispersal of young.

There is ample evidence that cyclic declines in lynx numbers are associated with drastic declines in their reproductive output (Brand et al. 1976, Brand and Keith 1979, Parker et al. 1983, O'Connor 1986, Poole 1994, Mowat et al. 1996, Slough and Mowat 1996). During the low phase of the hare cycle, recruitment is generally zero. Declines in litter sizes, pregnancy rates, reproduction by yearlings, and kitten survival all contribute to the lower recruitment. Bailey (1974) and Knick (1990) also documented drops in recruitment by bobcats during crashes in jackrabbit numbers in Idaho.

Likewise, although coyotes select a broader range of prey species across their range, cyclic declines of snowshoe hares (Todd et al. 1981, Todd and Keith 1983) and jackrabbits (Clark 1972), have also been associated with lower body condition and decreased reproductive output. Lower recruitment has also been noted for red foxes during cyclic declines in vole numbers (Lindström 1989), and wolves (*Canis lupus*) during a decline in deer populations (Mech 1977). Canids in general have higher reproductive potential than felids, and can thus take greater advantage of short-term fluctuations in food abundance (Eisenberg 1986), but lynx have one of the largest potential litter sizes of felids and do not differ from coyotes in their potential rate of population increase.

Emigration of predators

The cyclic decline of hares on our study area was accompanied by high rates of emigration of lynx. This was also the case in studies in the south–central Yukon (Slough and Mowat 1996) and Northwest Territories (Poole 1994). Mech (1980) reported influxes of lynx into Minnesota that were associated with declining populations of hares to the north. Likewise, bobcats in Idaho went on long forays and emigrated at higher rates during periods of declining and low jackrabbit populations in Idaho (Knick 1990). Lynx are quite vulnerable to trapping mortality (Ward and Krebs 1985), and because of this, we were able to learn the eventual mortality sites of some very long-distance dispersers. Slough and Mowat (1996) also reported emigration distances of up to 1100 km for radio-tagged lynx. Although emigration was biased towards male kits in the south–central Yukon, we did not observe a sex-bias in our study.

Most of the loss of coyotes from our study area was due to emigration. Few trappers concentrate their effort on coyotes in the north, so we received collar returns from only two dispersers, both less than 50 km from their capture sites. Long-distance natal dispersal by coyotes may be typical, however (Harrison 1992).

High mobility of predators has been cited as a potential factor in causing regional synchrony of cyclic populations (Finerty 1980, Ims and Steen 1990), and in allowing nomadic avian predators to track and dampen local outbreaks of vole numbers in Fennoscandia (Korpimäki and Norrdahl 1991). Long-range movements of mammalian predators during cyclic declines may also act to keep the fluctuations of local hare populations in synchrony.

How accurate are our estimates of predator density?

Our estimates of the numbers of coyotes and lynx in our study area were based on a comparison of the locations of radio-tagged animals with the locations and numbers of tracks found by extensive snow-tracking, as well as howling for coyotes. Since we did not estimate densities of predators using a statistical model, we can put no confidence limits on our estimates. During years of low hare numbers, the task of estimating the number of animals in the study area was relatively easy, since there were very few animals present (5 coyotes and 8 lynx at the cyclic low). At peak predator densities though, there were a great many tracks, and we were not as certain of our estimates.

We based our estimates of lynx numbers on the assumption that the core areas of lynx home ranges were relatively intrasexually exclusive. Based on our radio-telemetry locations, this assumption was valid for all years except for the decline winters of 1991–92 and 1992–93 (U. Breitenmoser unpubl.). Data from the Northwest Territories also support this assumption at cyclic peaks, and the social system of lynx seemed to break down at low hare densities there as well (Poole 1995). We had an additional check on monitoring the numbers of resident females at the peak of the cycle, since each traveled with their kits, which often differed in number.

Our estimates of coyote numbers were based on the assumption that coyotes lived in relatively exclusive family group territories. This assumption has been supported by numerous studies (Bowen 1982, Messier and Barrette 1982, Bekoff and Wells 1986); most studies have also noted that a portion of coyotes persists as transients or solitary residents though, with home ranges that overlap those of resident pairs and packs. Since we recorded howling throughout the year, it is not likely that we misjudged the numbers of residents, but we may have missed an unknown number of transients.

In summary, our estimates of predator numbers were likely very accurate before and after the peak and early decline phases of the cycle. During the peak and early decline though, greater movement of animals (Ward and Krebs 1985, Slough and Mowat 1996), a possible increase in the number of transients and "floaters", and a break-down of the social system (Brand et al. 1976, Poole 1995) may have caused us to miss animals. Therefore, our estimates of the peak densities of predators may be conservative, although we do not believe we underestimated by more than 5 animals.

Our indices of predator numbers, track counts, were closely correlated with our estimates of population sizes. Although we used tracks to make our assessment of predator numbers, we only used the locations and group sizes of these tracks, rather than their abundance, in estimating populations of predators, and so the two methods were essentially independent. Track counts suggest that we may have overestimated the number of lynx on our study area during the winter of 1989–90 (Fig. 2).

Track counts have been often used as indices of animal numbers (e.g., Stephenson and Karczmarczyk 1989, Thompson et al. 1989). In an evaluation of the method for lynx, Stephenson and Karczmarczyk (1989) found a poor correlation between the index and an estimate of lynx numbers based on radio telemetry, especially at low densities of lynx. They postulated that increased movements of lynx during cyclic lows (Ward and Krebs 1985) would bias track counts as indicators of population trends. However, these authors counted tracks for only 2–5 weeks each year on an average of 542 km, and factors such as weather, location of the transect, and time of year could have introduced a great amount of variability among years. We ran our transect throughout each winter, for an average of 1238 km per year. By controlling for factors such as date, track location, and weather in our analysis, we were also able to factor out some of the year-to-year variance which would have affected our counts.

Conclusions

Coyotes and lynx responded numerically in much the same way to the fluctuation in numbers of hares in our study area. The limited availability of alternative prey in the boreal forest gave both predators restricted options when densities of hares were low. Lynx were apparently more skilled at capturing red squirrels than coyotes (O'Donoghue 1997), and although coyotes killed more small mammals than lynx, the total biomass and availability of voles was quite low. "Generalist" predators may behave as specialists in such low-diversity systems. Based on work in Idaho, Johnson and Hansen (1979) concluded that coyotes were highly selective predators of rabbits rather than opportunistic predators. The relatively low density of coyotes in our study area suggests that the boreal forest is not optimal habitat for them.

We found evidence that changes in survival, recruitment, and dispersal rates all contributed to changes in the populations of predators. Numerical responses which are due to changing rates of reproduction are likely to be more de-stabilizing to predator-prey interactions than those based on aggregation or changes in survival (Crawley 1975). The time-lag of the decline of predator numbers also tends to lead to cyclic dynamics (May 1973). Although, as a rule, numerical responses are more pronounced in specialist than generalist predators (Crawley 1992), and generalists tend to stabilize predator-prey interactions (Hanski et al. 1991), both coyotes and lynx responded numerically to the cycle in hare numbers more in the manner of hare specialists, which would contribute to the cyclic behavior of the system.

Acknowledgements – This paper is based on 8 years of field work, as a part of the Kluane Boreal Forest Ecosystem Project. Many people contributed their time, work, and ideas to the predator research. S. Antpoehler, C. Bell, J. Bishop, M. Blower, R. Buck, E. Claus-Sinclair, M. Connor, T. Heakes, T. Hucal, A. Milani, D. L. Murray, S. Schweiger, I. Sinclair, P. Upton, and J. Wilmshurst tracked coyotes and lynx. D. L. Murray started the predator studies, and V. O. Nams developed the data entry protocols. U. Breitenmoser and C. Breitenmoser-Wursten monitored radio-collared lynx for several years. C. Doyle, F. Doyle, and S. Schweiger gathered much of the data on prey populations. W. Hochachka developed the statistical analyses of track count data, and I. Wingate helped with logistics. S. Erlinge, L. D. Mech, F. Messier, D. L. Murray, A. R. E. Sinclair, J. N. M. Smith, and S. Stuart offered helpful criticisms of this manuscript. The Kluane project was supported by a Collaborative Special Project grant from the Natural Sciences and Engineering Research Council of Canada. This is paper No. 104 from the Kluane Boreal Forest Ecosystem Project.

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