Population changes of the vertebrate community during a snowshoe hare cycle in Canada's boreal forest — Source link ↗

Stan Boutin, Charles J. Krebs, Rudy Boonstra, Mark R. T. Dale ...+18 more authors

Related papers:

- Impact of food and predation on the snowshoe hare cycle.

- Functional responses of coyotes and lynx to the snowshoe hare cycle

- Numerical responses of coyotes and lynx to the snowshoe hare cycle

- Dynamics of snowshoe hare populations

- Ecosystem dynamics of the boreal forest: the Kluane project.

Population changes of the vertebrate community during a snowshoe hare cycle in Canada's boreal forest

Stan Boutin, C. J. Krebs, R. Boonstra, M. R. T. Dale, S. J. Hannon, K. Martin, A. R. E. Sinclair, J. N. M. Smith, R. Turkington, M. Blower, A. Byrom, F. I. Doyle, C. Doyle, D. Hik, L. Hofer, A. Hubbs, T. Karels, D. L. Murray, V. Nams, M. O'Donoghue, C. Rohner and S. Schweiger

Boutin, S., Krebs, C. J., Boonstra, R., Dale, M. R. T., Hannon, S. J., Martin, K., Sinclair, A. R. E., Smith, J. N. M., Turkington, R., Blower, M., Byrom, A., Doyle, F. I., Doyle C., Hik, D., Hofer, L., Hubbs, A., Karels, T., Murray, D. L., Nams, V., O'Donoghue, M., Rohner, C. and Schweiger, S. 1995. Population changes of the vertebrate community during a snowshoe hare cycle in Canada's boreal forest. – Oikos 74: 69–80.

We measured the density changes of 22 species of vertebrates during a snowshoe cycle in northern Canada. Hares were the dominant herbivore in the system and changes in their numbers were correlated with changes in numbers of arctic ground squirrel, spruce grouse, ptarmigan, lynx, coyote, great horned owl, goshawk, raven and hawk owl. Hare numbers were not correlated with numbers of red-backed vole which showed peaks during the low, increase, and early decline phases of the hare cycle. Hawk owls were the only predator whose numbers correlated with changes in red-backed voles while boreal owls and weasels were correlated with densities of *Microtus*. Red squirrel, American kestrel, red-tailed hawk, northern harrier, wolverine, magpie, and gray jay showed no correlation with hare or vole numbers. We conclude that species in the boreal forests of Canada do not exhibit the strong synchrony found between voles and other members of the vertebrate community in northern Fennoscandia. We discuss some of the possible reasons for these differences.

S. Boutin, Dept of Biological Sciences, Univ. of Alberta, Edmonton, Alberta, Canada T6G 2E9.

In the boreal forests of North America, snowshoe hares exhibit 9–11 yr population cycles (Krebs et al. 1986, Keith 1990). Changes in numbers can range over two orders of magnitude and hares represent the dominant herbivore biomass in the community when they are at peak densities (Keith et al. 1977). Longterm Hudson Bay records clearly show that lynx are linked to the hare cycle (Keith 1963) but there is limited information on how other members of the vertebrate community respond to changes in hare numbers. Ruffed grouse show 10-yr cycles with peaks and declines preceding those of hares in the northern portion of their range (Keith and Rusch 1989). A study by Keith and co-workers on the southern edge of the boreal forest indicated that coyotes, great horned owls, and goshawks reached peak numbers at the same time as hares but declined more slowly (Keith et al.

1977 and references therein). Incidental captures in hare traps also suggested that mustelid predators were synchronized with the hare cycle while sciurids, skunks, and porcupines declined 2 yr after hares declined (Keith and Cary 1991).

In northern Fennoscandia, voles, their predators, and a number of medium-sized game species including forest grouse, mountain hares, and muskrats show synchronous 4-yr cycles (Danell 1978, Hörnfeldt 1978, Angelstam et al. 1985, Hörnfeldt et al. 1986). Recent studies suggest that voles are the key component of the system with changes in their numbers generating cycles in their predators who in turn, transfer the cycle to other herbivores by prey-switching (Marcstrom et al. 1988, 1989, Lindström et al. 1994). In North America, red-backed voles are sympatric with snowshoe hares. Gilbert et al. (1986) and
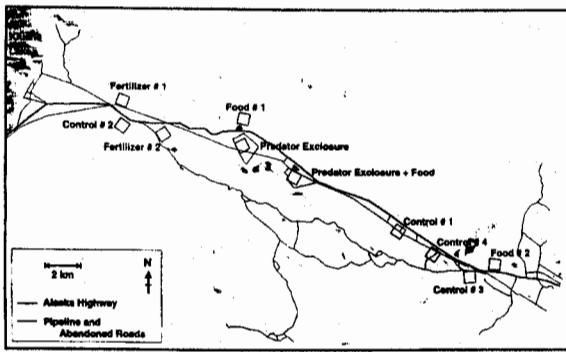
Fig. 1. Location of main study areas at Kluane Lake, Yukon, Canada. Stippled areas represent lakes.

of the vertebrate community in Canada's northern coniferous forest. In this paper we document changes in density of 22 vertebrate species during a snowshoe hare cycle. Our intention was to determine how the decline in hare numbers is correlated with density changes of other members of the community. We wished to determine if hare cycles affect most other species as voles do in northern Fennoscandia. Our approach here is descriptive and the intention is to provide background changes in density of all species for interpretation of experimental results to be published in the future. Ours is the first study to provide actual density estimates of all of the major vertebrates in a community dominated by fluctuating herbivores.

Gilbert and Krebs (1991) compared fluctuations of voles and hares in the southwestern Yukon over a 16-yr period. They observed three vole peaks, two of which occurred two years after hares reached peak densities. No one has investigated how vole fluctuations affect vole predators in North America.

There have been two general approaches to studying the linkages between members of a community. The most common involves a description of the community food web (see Lawton 1989 and Abrams 1993 for a summary of these) while the second involves experimental manipulation of trophic levels (Paine 1966, Power 1992). Neither approach has been applied to North American boreal forest vertebrate communities. The Kluane Boreal Forest Ecosystem study has been in operation since 1986 and was designed to determine the structure and function

Study area

We worked at Kluane Lake (60°57'N, 138°12'W) in a 350-km² portion of the Shakwak Trench, a broad glacial valley bounded by alpine areas to the northwest and southeast (Fig. 1). The valley bottom averages about 900 m above sea level and is mostly covered with white spruce (*Picea glauca*) forest (50%), with an understory of willow (*Salix* sp.) and birch (*Betula glandulosa*). Other vegetation types include aspen forest (*Populus tremuloides*), shrub thickets (33%), and meadows (7%). The climate is cold continental with the growing season being from mid-May through mid-August and snow cover occurring from October through early May. Average January temperatures are −18°C. Precipitation is low with most of it falling as snow. Snow depths average about 55

Table 1. List of species for which we measured density indices and/or density at Kluane Lake, Yukon. The number of years during which data were collected for each species is also provided.

Species	Common name	Index	Density	Years
Lepus americanus	snowshoe hare	No	Yes	1977–94
Clethrionomys rutilus	red-backed vole	No	Yes	1976–94
Microtus spp.	meadow vole	No	Yes	1989–94
Spermophilus parryii	arctic ground squirrel	No	Yes	1987–94
Tamiasciurus hudsonicus	red squirrel	No	Yes	1987–94
Ondatra zibethicus	muskrat	Yes	No	1988–94
Dendragrapus canadensis/Bonasa umbellus	spruce grouse/ruffed grouse	Yes	Yes	1988–94
Lagopus lagopus	willow ptarmigan	No	Yes	1980–92
Lynx canadensis	lynx	Yes	Yes	1986–94
Canis latrans	coyote	Yes	Yes	1986–94
Bubo virginianus	great horned owl	No	Yes	1988–94
Accipiter gentilis	goshawk	Yes	No	1988–94
Bubo jamaicensis	red-tailed hawk	Yes	Yes	1988–94
Surnia ulula	hawk owl	Yes	Yes	1987–94
Aegolius funereus	boreal (Tengmalm's) owl	No	Yes	1990–94
Circus cyaneus	northern harrier	Yes	Yes	1989–94
Falco sparverius	American kestrel	Yes	No	1988–94
Mustela nivalis/erminea	weasel	Yes	No	1987–94
Gulo gulo	wolverine	Yes	No	1987–94
Corvus corax	raven	Yes	Yes	1988–94
Pica pica	magpie	Yes	Yes	1990–94
Perisoreus canadensis	gray jay	Yes	No	1991–94

cm by late winter (Krebs et al. 1986, Murray and Boutin 1991).

Table 1 shows the species for which we obtained density estimates or indices of abundance. Study grids were located along 30 km of the Alaska Highway which runs through the base of the valley and over the length of the study area (Fig. 1). Willow ptarmigan were censused in the Chilkat Pass area of northwestern British Columbia (59°50'N, 136°30'W; see Hannon 1983 for a description) which was roughly 200 km from the main study site. Studies of population dynamics of various species have been ongoing at Kluane since 1973 (Krebs and Wingate 1976, Krebs et al. 1986, Gilbert and Krebs 1991). We report information for the period 1986–1994 and supply previously published information for voles and hares back to 1976.

We did not monitor some species. Moose densities were relatively low (<0.1/km² , Yukon Game. Branch unpubl.). Tracks of single wolves and one pack were observed infrequently in the study area. Grizzly bears were common but spent much of their time in the alpine surrounding the study area. Fox used our study area sporadically but spent the majority of their time in the alpine. Marten and their tracks were only rarely seen and there were no fisher in the area. Porcupines were virtually absent from the area during the study although they had been observed regularly before 1984. Flying squirrels were present but were rare as very few were captured in hare or squirrel traps. *Peromyscus* was also relatively rare from 1988 through 1994 although common before this (see Gilbert and Krebs 1991). We did not attempt to monitor density changes of passerines, woodpeckers, shrews, bats or wood frogs.

Methods

Herbivores

Densities of mammalian herbivores were estimated by mark-recapture using live-traps. Snowshoe hares were trapped on three 32.5-ha grids (Control 1, 2, 3 (Fig. 1); 86 traps per grid). Traps were baited with apple and alfalfa for an average of five nights every March and November. Numbers were estimated by the Jackknife procedure using Program Capture (Otis et al. 1978, Boulanger 1993) and densities were calculated for a 60-ha area (to account for edge effect).

Arctic ground squirrels were live-trapped in Tomahawk traps baited with peanut butter and set adjacent to burrows on three 7.5-ha grids. Control 1 (open spruce, low shrub cover) was trapped from 1987 to 1994 and Control A and Control B (open spruce, well developed shrub understory) were trapped from 1990 to 1994. Control A was located 150 m east of the Food 1 grid and Control B was located 500 m north of the food addition/ predator exclosure grid (Fig. 1). Traps were pre-baited for 5–7 d before the first trapping of each year. Trapping

occurred for two consecutive days on each grid during late May and late July. Population size was estimated by the model selected by Program Capture and density was estimated assuming an 8-ha grid.

Red squirrel densities were estimated by the number of squirrels captured during repeated live-trapping (over 5000 captures) on three 7.5-ha grids (Control 1, Control 4, Control R-1) during May and August beginning in 1987 (see Boutin et al. 1993 and Boutin and Larsen 1993 for more details). Control R-1 was located directly across the Alaska Highway from Control 1 (Fig. 1). Traps were placed at middens and baited with peanut butter. We were certain that virtually all animals present on the grids were captured as we color marked all animals caught and spent considerable time doing behavioural observations on the grids (Boutin et al. 1993). Density was calculated by assuming that animals caught on the grid covered 12 ha as determined by visual observation of how far animals ranged from their midden to be captured on the grid (Boutin et al. 1993).

Redbacked voles were estimated by minimum number alive. In spring of 1987, we set up two live-trapping grids in open spruce with stations spaced 15.2 m apart in a 10 × 10 grid. These grids were nested within the Control 1 and 2 hare grids. Each grid was trapped in spring (May) and late summer (August) with 50 Longworth traps placed at alternate stations and baited with oats. Densities were calculated for 2.8 ha grids. *Microtus* spp. (*M. pennsylvanicus, M. oeconomus*) were trapped on two meadow grids beginning in spring of 1989. The meadow grids were located on or beside the Fertilizer 1 grid (Fig. 1). *Microtus* comprise a relatively small component of the vole community because only 7.5% of our study area was *Microtus* habitat (meadow or marsh).

Estimates of resident spruce grouse during the breeding season were obtained using a systematic census at dawn (0430–0630 h) in late April-early May with standardized playback techniques using the female cantus call (Herzog and Boag 1977). Two transects, evenly spaced over the Control 1 and Control 4 hare grids and spanning their length, were walked on three separate occasions. Male spruce grouse flutter flights and female cantus calls were recorded as were drumming ruffed grouse males. Numbers of grouse were estimated by assuming an equal sex ratio of breeding birds (Boag and Schroeder 1992) and density was determined for a 40-ha area. The dawn censuses began in 1990. In 1988 grouse searches with a dog and banding were used. We used both techniques in 1990 and found good concordance between the methods.

Densities of willow ptarmigan were accurately known because all birds were colour banded and their territories plotted each spring (Hannon 1983). For this paper we present numbers of territorial males counted on a 57 ha control plot from 1980 through 1992 (with the exception of 1983). A male had to have at least half of his territory on the plot to be counted as resident on the plot.

Muskrats were indexed by counting pushups from air-

craft (Boutin and Birkenholz 1987) in spring on eight of the largest lakes shown in Fig. 1 (excluding Kluane Lake). Flights were taken over the lakes in late April when most of the snow had melted from the ice. Counts began in 1988 but we were unable to count pushups in 1989 because melting of the ice coincided with melting of the snow so pushups were not visible.

Mammalian predators

We estimated lynx and coyote density for the entire study area in November–December. The procedure was to determine home range size by taking weekly locations of collared individuals. Group size within these ranges was estimated by tracks (coyote family groups, lynx female/kit units) and records of howling (coyotes). We assumed exclusive family groups for coyotes and exclusive intrasexual territories (but overlapping intersexual territories) for lynx. We used searches for tracks and howl surveys to determine if areas that were not occupied by collared individuals were occupied. If they were we assumed the occupants had similar-sized territories to collared animals. All estimates were made by the same individual throughout the study and we provide a range around each estimate to account for situations when we were uncertain as to whether one or two lynx inhabited an area.

Raptors and corvids

Great-horned owls were censused by mapping territories and nest searches during the February–May breeding season in a 100-km² portion of the study area (see Rohner and Doyle 1992 for more details). Goshawk, red-tailed hawk, northern harrier, hawk owl, raven, and magpie were monitored in the same 100-km² area by searching intensively for nests along with using playbacks, telemetry and other indicators (see Rohner and Doyle 1992, Doyle and Smith 1994). Boreal owls were censused using playbacks in a 12 × 2 km strip along the Alaska Highway. Kestrels were indexed along a 12 × 1 km strip of the Alaska highway by locating active nests. Most birds could be detected within 500 m of the road. We are confident that we could estimate actual densities of great horned owls, red-tailed hawks, northern harriers, hawk owls, boreal owls, ravens, and magpies. For the other species the number of nests found was a reliable index of density change.

Track and sighting surveys

We attempted to obtain indices of population change on a broad scale by systematically recording tracks and observations of animals. We counted lynx, coyote, wolverine,

and weasel tracks on a series of snowmobile trails running along the base of the valley (Murray and Boutin 1991). All tracks that crossed our trails (except those where it was obvious that the same animal crossed more than once) were counted and marked after fresh snowfall and each day thereafter until conditions were such that tracks could be missed (5–7 d after snow). There were nine transects and the number of track crossings/100 km/night was calculated for each. The values were averaged for each transect over the entire winter and these nine average values were used to calculate a standard error for all transects combined. The total number of kilometers travelled each year ranged from 779 to 2128.

All project field personnel were trained to identify local raptors and corvids. These observers spent a total of 58 647 h in the study area on foot during both summer and winter doing project work, and 12 942 additional h driving vehicles on the Alaska Highway and tracks in the study area. At the end of each field day, each worker recorded the number of raptors seen on foot or from a vehicle while in the study area and the number of foot- or vehicle-hours accumulated each day. We present these observations as sightings per 100 observer hours. The number of each species seen per hour was tallied separately each month and we averaged monthly estimates over various periods to produce a mean and standard error. For spruce grouse we used the months of September through April. For goshawk, red-tailed hawk, northern harrier, magpie, and gray jay we used the months of May, June, and July while for ravens the months of April, May, and June as well as September, October, and November were used. These months were chosen to avoid seasonal migrations and maximize observer hours. In all cases, the observations made while on foot are presented.

Statistical analysis

Wherever possible we have tried to report changes on individual study areas rather than average values and standard deviations because the number of replicates was low (three or less). Many of the population estimates derived from mark-recapture had their own measures of variance associated with them and it was not possible to combine these from different areas. Reporting each study area separately shows both the variance around the estimate and the variation among sites. We performed correlation (Pearson correlation) analysis between indices or densities of other species in the community and hare densities in the current year as well as one and two years previous. We also did a similar analysis using vole densities. Where multiple measures of density for the same time period were available, we used average values. In many cases the sample size of the correlation analysis was small (4–7) and we view the correlation coefficients as guides only.
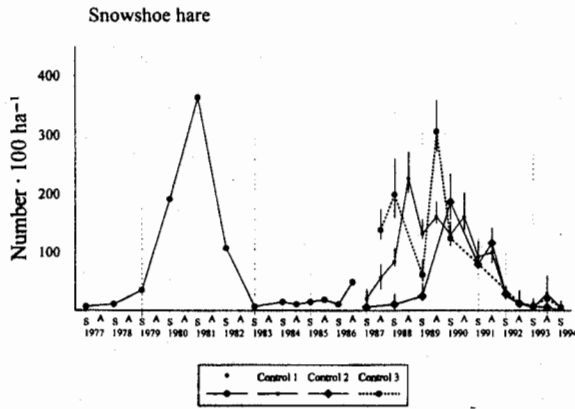
Fig. 2. Density estimates of snowshoe hares on three study sites in spring (March) and autumn (October). *Estimates from Krebs et al. 1986: Table 4. Bars represent 95% confidence limits.

Results

Hares showed two population peaks, the first occurring in 1981 and the second in 1988–90 (Fig. 2). Hares began to increase in 1987 on some grids and reached high densities as early as 1988 in some cases. All sites were high by 1990. Numbers began to decline in winter 1990–91 (spring estimates were 43–70% of the previous year) and did so precipitously in winter 1991–92 (16–20% of 1990 values). There was no population recovery in summer 1992 and a further decline in winter 1992–93. The amplitude of change (maximum autumn density/minimum spring density) from 1984 through 1994 was 26–44 fold. In general then, hare numbers showed 1) local concentrations of high density from autumn 1987 through spring 1989, 2) high densities on all areas from autumn 1989 through autumn 1990, 3) declining but relatively abundant densities in 1991, 4) low densities thereafter.

Redbacked voles were high in 1984, 1987, 1991, and 1992 (Fig. 3). They were very low in intervening years (no voles were captured on one site in 1990 and 1991). The amplitude of change was 10–50-fold in spring and 7–9-fold in autumn. Thus two peaks occurred when hare numbers were very low or declining while the third occurred as hares were increasing and locally abundant. Red-backed vole densities were not correlated with hare densities ($r = 0.26$, $P = 0.17$). Densities of *Microtus* were high in 1993 and 1994 (Fig. 3).

Densities of red squirrels were relatively constant during the study (Fig. 4). Spring densities varied from 1.7-fold on Control 1 to 4.5-fold on Control 4. The larger range on Control 4 was due to very low densities in 1991. In general, spring populations were constant from 1987 through 1990. They then declined on two grids in 1991 and 1992. All sites reached maximum spring numbers in 1994. Red squirrel densities were not correlated with hare

(maximum $r = 0.41$, $P = 0.31$ spring densities only) or vole densities ($r = 0.19$, $P = 0.49$).

Arctic ground squirrels showed density changes of 4–6-fold on open forest grids with high shrub cover (Control A and B). Spring densities were high in 1990 and 1991 but declined steadily to low levels by 1993 (Fig. 4). There was a slight recovery in 1994. Numbers on Control 1 (low shrub cover) were lower than on the other grids. Densities began to decline one year earlier than on other areas and no animals were caught in 1993. Ground squirrel densities were positively correlated with hare densities ($r = 0.69$, $P = 0.03$).

Spruce grouse were highest in 1990 as suggested by sightings and number of birds observed during the dawn census but declined drastically over winter 1990–1991 to very low levels (Fig. 5). Numbers appeared to begin to recover in 1993–94. Changes in numbers during the breeding season were about 6-fold. Our density estimates are only crude estimates as grouse are patchily distributed and our study grids were relatively small compared to grouse home ranges. However, the pattern of population change seems robust as the number of birds observed while on foot during September through April showed very similar changes. Grouse sightings were correlated with changes in hare numbers ($r = 0.94$, $P = 0.08$) but not with vole numbers ($r = 0.46$, $P = 0.34$).

Willow ptarmigan were at high density from 1980–81 and we know from work in the area on other plots, that the density was also comparably high in 1979 (Fig. 6). Numbers declined to a low in 1984 and 1985 and rose to a second, lower peak in 1990 and declined immediately in 1991 and 1992. The peak in 1990 corresponds with the peak density in spruce grouse at Kluane and both declines occurred at the same time as the declines in snowshoe hares. Changes in ptarmigan density were strongly correlated with changes in hare densities ($r = 0.84$, $P = 0.0005$).
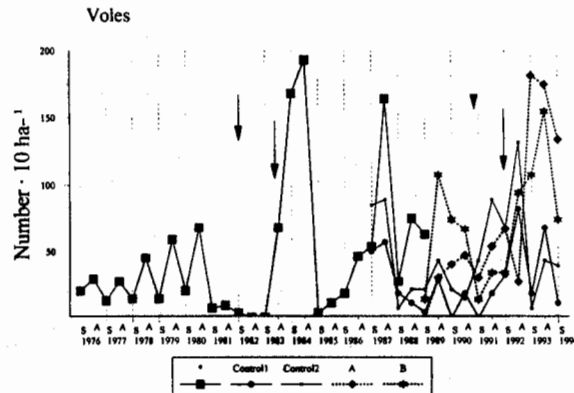
Muskrats remained roughly constant from 1988 (145

Fig. 3. Density estimates of red-backed voles (solid lines) and *Microtus* spp. (dotted lines) as determined by minimum number alive. *Estimates from Gilbert and Krebs (1991: Table 1). Arrows represent the first two years of population decline from peak densities of snowshoe hares.

Red squirrels
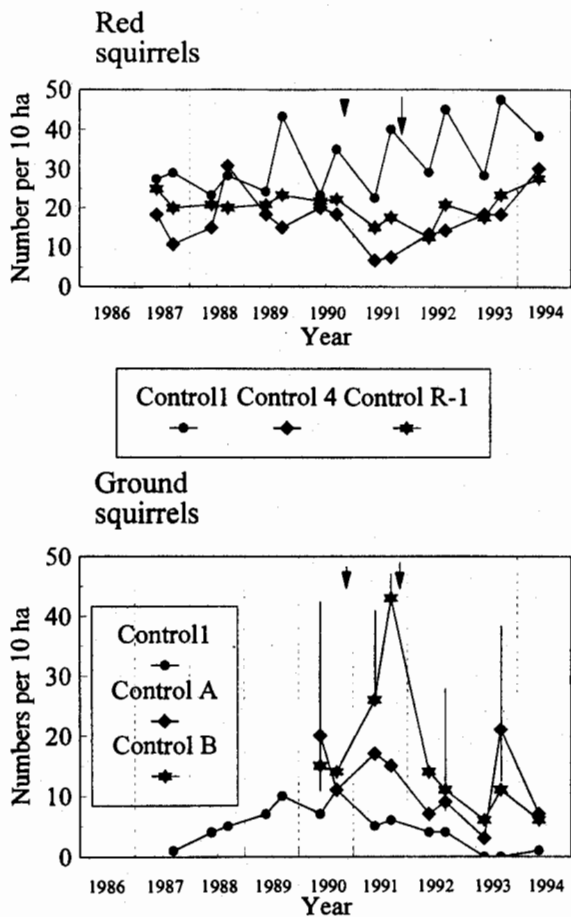

Ground squirrels

Fig. 4. Density estimates of red squirrels and arctic ground squirrels. Red squirrel densities were estimated by complete enumeration in May and August of each year. Ground squirrel densities were estimated by complete enumeration on Control 1 and by the model selected by Program Capture (Otis et al. 1978) for Control A and B. Error bars are 95% confidence limits. In cases where there are no error bars for estimates on Control A and B there was no detectable variance around the estimate. Arrows as in previous figures.

pushups) to 1990 (110) and 1991 (126) but showed a major decline from 1991 to 1992 (39). Their numbers continued to be low through 1992–93 (17) but recovered somewhat in 1994 (91).

Predators

Lynx and coyote numbers peaked in 1990–91 which coincided with the beginning of the hare decline (Fig. 7). Our density estimates suggested that numbers declined by 50% over the next year but track counts indicated that the decrease was less severe. Numbers were still relatively high in 1991–92 but by 1992–93 numbers had dropped to 20% of peak levels for lynx and 30% for coyotes. Densities continued to drop in 1993–94. The
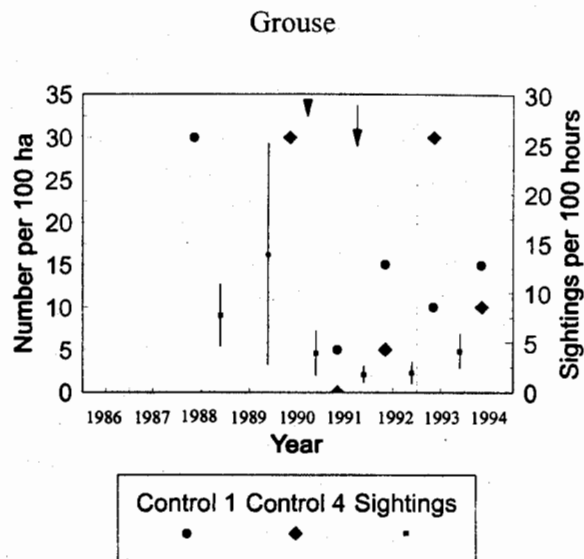
Grouse

Fig. 5. Density estimates for grouse (spruce and ruffed) as determined by dawn censuses in late April early May. Sightings are observations made by personnel while on foot during the months of September through April. Error bars are 95% confidence limits. Arrows as in previous figures.

amplitude of change for lynx was 8.5-fold and for coyotes it was 5.7-fold. Track counts of these species showed similar patterns but the amplitude of change was slightly greater being 11.5-fold for lynx and 26.3-fold for coyote. Densities of both coyotes and lynx were strongly
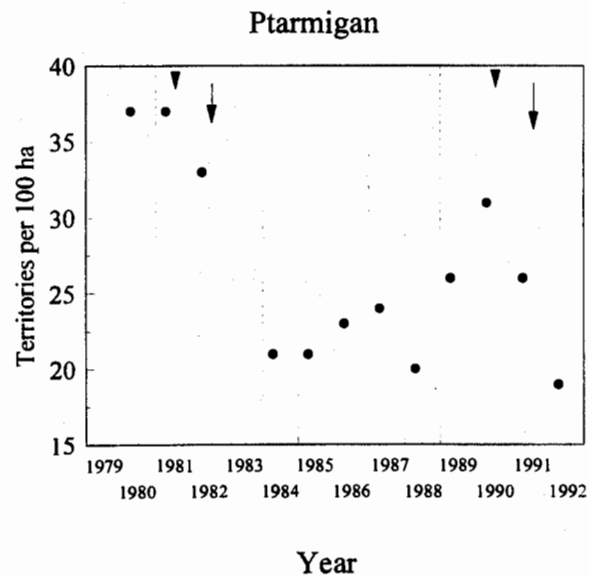
Ptarmigan

Fig. 6. The number of territorial pairs of willow ptarmigan observed on a 75-ha study area in the Chilkat Pass (see Hannon 1983). Arrows as in previous figures.
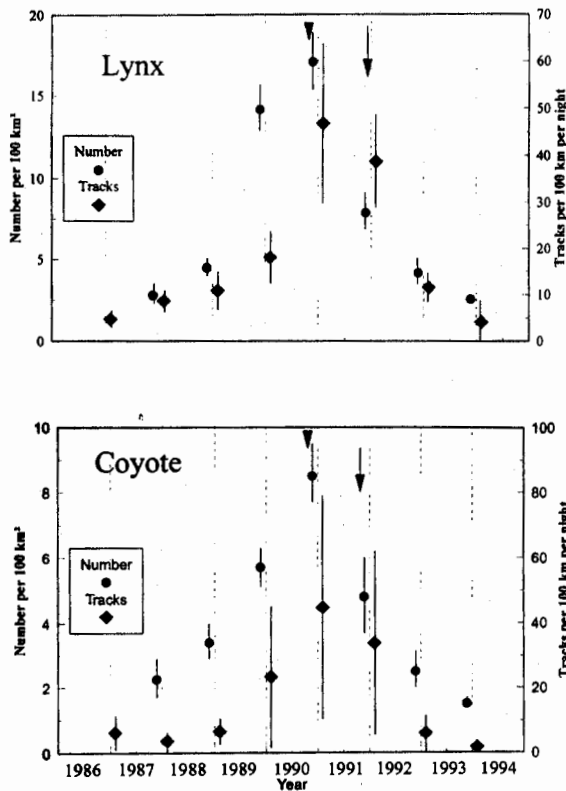
74

Fig. 7. Density estimates of lynx and coyotes in November. Tracks are the number of track crossings counted per night per 100 km travelled on snowmobile routes throughout the study area. Error bars represent a range for density estimates and 95% confidence limits for track counts. Arrows as in previous figures.

correlated with hare densities in the previous year (r = 0.94, P = 0.001 for lynx and r = 0.92, P = 0.002 for coyote).

Weasels were low from 1986–87 through 1990–91 (Fig. 8). They then increased slightly in 1991–92 and 1992–93 and were extremely abundant in 1993–94. Weasel tracks were not correlated with hare densities (r = −0.55, P = 0.15) or red-backed vole densities (r = 0.33, P = 0.41) but they were correlated with *Microtus* densities (r = 0.88, P = 0.04). Wolverine showed little change over the study with the possible exception of 1991–92 when tracks were roughly 3 times more abundant than in other years (Fig. 8).

Great horned owls were the most abundant raptor in the study area. Unlike lynx and coyotes, the number of territorial pairs continued to increase for two years into the hare decline (Fig. 9) to reach a peak in 1992. They then declined by 36% in 1992–93 and another 19% in 1993–94. Densities of great horned owls were strongly correlated with hare densities one (r = 0.80, P = 0.02) and two (r = 0.85, P = 0.01) years earlier. Breeding numbers of goshawks peaked in 1990 but the most sightings oc-

curred in 1991. Numbers and sightings declined to low levels by 1992 (Fig. 9). Sightings were correlated with hare numbers one year earlier (r = 0.80, P = 0.04). Red-tailed hawks remained constant over the study (Fig. 9).

Hawk owls were present in 1988–90 but virtually absent in other years (Fig. 10). Numbers of hawk owls were highly correlated with hare densities (r = 0.84, P = 0.008) and weakly correlated with vole densities (r = 0.68, P = 0.06). Boreal owls were low to absent in 1989–92 before becoming very abundant in 1993 and 1994 (Fig. 10). Their numbers were not correlated with red-backed voles (r = 0.002, P = 0.96) but they were correlated with *Microtus* densities (r = 0.89, P = 0.01). Northern harriers were constant and kestrels declined over the study period (Fig. 10).

Ravens were the only corvid that showed any major density change during the study (Fig. 11). These changes were most pronounced in autumn sightings which reflect reproductive performance. Sightings of ravens were highly correlated with hare numbers one year earlier (r = 0.89, P = 0.0001). We had two pairs of ravens per 100 km² in all years except 1991 and 1992 when there were
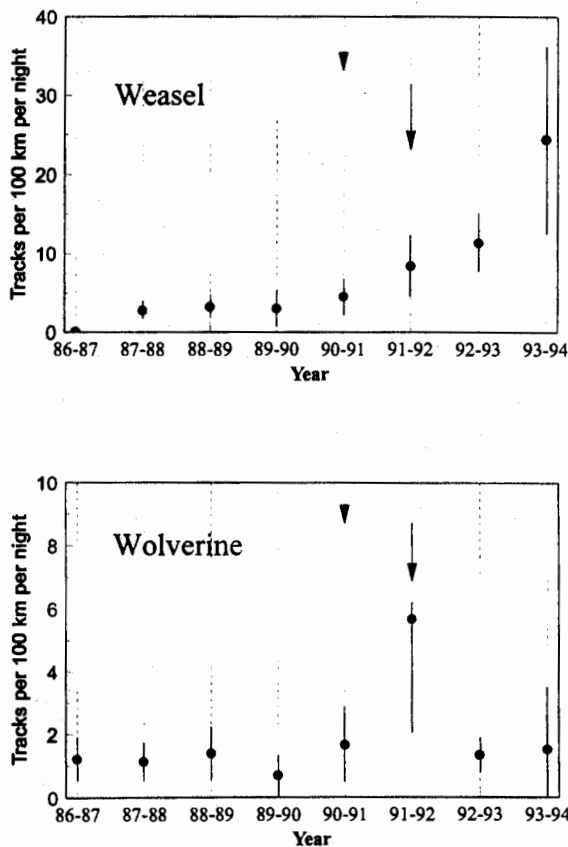

Fig. 8. Indices of weasel and wolverine abundance as determined by track crossings on snowmobile trails throughout the study area (as above). Error bars are 95% confidence limits. Arrows as in previous figures.
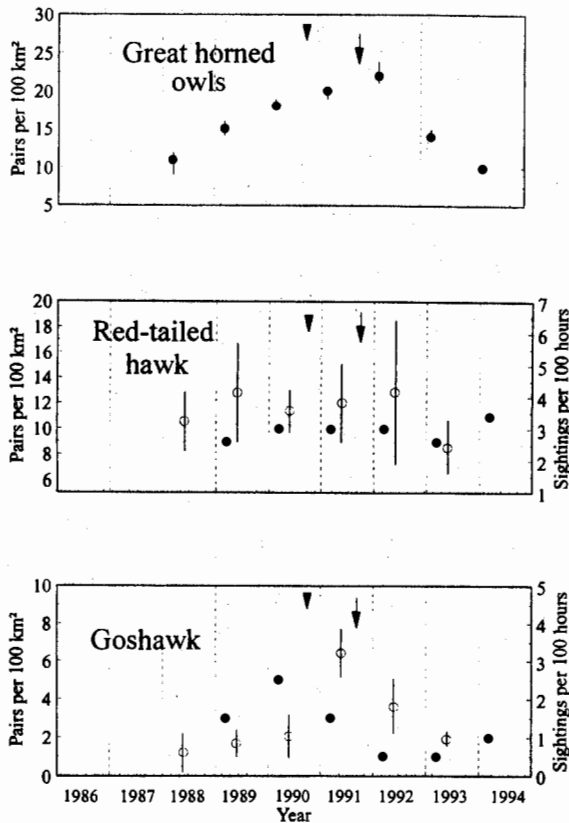
Fig. 9. Density estimates during the breeding season of great horned owls, red-tailed hawks, and goshawks. Solid circles represent the number of pairs found in a 100-km² portion of our study area. Bars on the solid circles represent a range. Open circles represent the sightings while on foot during May through July. Error bars represent 95% confidence limits. Number of pairs of goshawks should be treated as a population index rather than a true estimate of density because pairs may have been missed. Arrows as in previous figures.

three. There were three pairs of magpies in the intensive study area from 1990–94. We did not monitor nests of gray jays but sightings suggested that their numbers changed little from 1991 through 1993.

Discussion

Correlations between hares and voles

We were able to measure densities for 17 species of vertebrates and obtain indices of density for another 5 species during a snowshoe hare peak and decline. We first address the relationship between hare and vole densities. Our results, combined with previous data from the same area (Gilbert et al. 1986, Krebs et al. 1986, Gilbert and Krebs 1991), span 20 yr during which snowshoe hares reached two population peaks in 1980–81 and 1990 while red-backed voles had six high yr, 1973, 1975, 1984

(Gilbert and Krebs 1991), 1987, 1991, and 1992. Based on earlier results, Gilbert et al. (1986) suggested that vole peaks occurred 2–3 yr after hare peaks when hare predators had declined. The high red-backed vole densities in 1992 and high *Microtus* densities in 1993 refutes this argument since hare densities were declining while predator numbers were still high. Predation pressure on voles from hare predators should have been intensifying rather than declining at this time. Our results suggest that hares and voles fluctuated independently of one another since vole peaks occurred at virtually ever phase of the hare cycle with the exception of the actual peak. Adamcik et al. (1979) reported two vole peaks during a hare increase and another one year after a hare peak in central Alberta. Thus, it seems that the lack of correlation be-
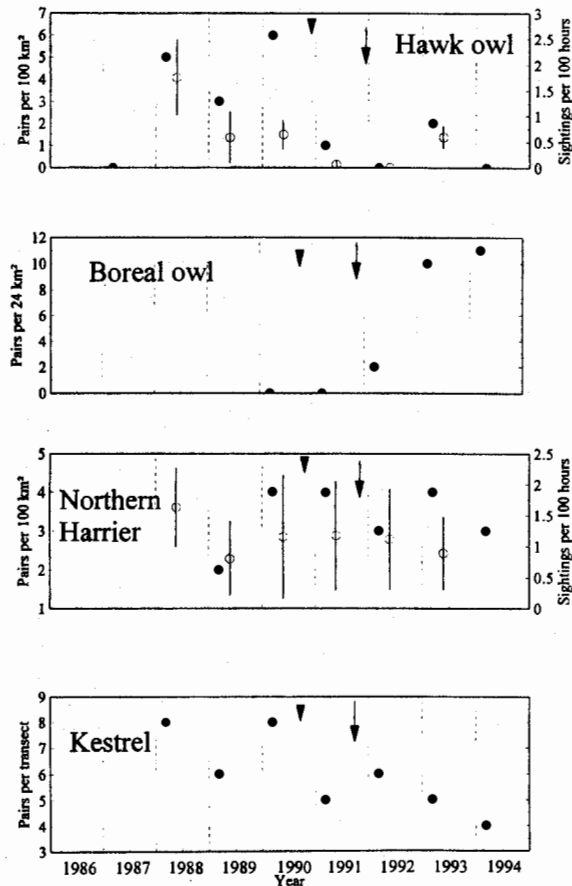

Fig. 10. Density estimates during the breeding season of hawk owls, boreal owls, and northern harriers (solid circles). For kestrels the solid circles represent the number of pairs found in a 12×1 km transect along the Alaska Highway. These values should be viewed as a density index rather than a true estimate as pairs may have been missed. Open circles are derived from sightings made while on foot during May through July. Error bars represent 95% confidence limits. Arrows as in previous figures.
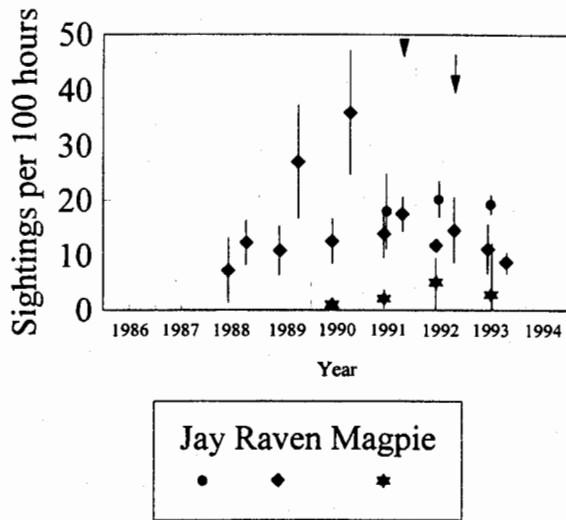
76

Corvids

Fig. 11. Sightings made while on foot during May through July for gray jays and magpies and April through June for ravens. Error bars are 95% confidence limits. Arrows as in previous figures.

tween hares and voles may be consistent throughout the boreal forests of Canada.

Species correlated with hare densities

Our data on species other than hares and voles span only a single hare peak but because hares and voles peaked at completely different times it provides an opportunity to define groups of species based on whether their densities were correlated with hares or voles. These groups are shown in Fig. 12. Five predators, one scavenger, and four herbivores showed density changes that were correlated with those of hares. Only one of these, the hawk owl, showed any correlation with red-backed vole densities. Lynx and coyotes peaked and declined with snowshoe hares whereas goshawks may have lagged by one year and great horned owls by two years. We found that indices of recruitment in these species changed immediately after hares began to decline. The number of lynx family groups that were snow-tracked by our research personnel dropped from 129 in 1990–91 to 29 in 1991–92 and there was a further drop to 2 in 1992–93 (O'Donoghue and Boutin unpubl.). The number of goshawk pairs found and the proportion that fledged young dropped from 8 of 11 (73%) in 1990 to 4 of 7 (57%) in 1991 to 0 of 3 in 1992 (Doyle and Smith 1994). No great horned owls pairs produced any fledglings in 1992. Keith et al. (1977) found that lynx, coyotes, great horned owls, and goshawks reached peak densities at the same time as

hares but the rate of decline was considerably slower than that of hares.

The correlation between hawk owl and hare densities is somewhat surprising. Hawk owls did not respond to red-backed vole peaks but our results and the analysis by Rohner et al. (unpubl.) suggest that hawk owls may be critically dependent on juvenile hares during nesting stages when voles are moderate to low.

In the case of herbivores, densities of willow ptarmigan, spruce grouse, and arctic ground squirrels were strongly correlated with that of hares. Our data are scant but it also appears that ruffed grouse were affected similarly. Keith and Rusch (1989) found that ruffed grouse populations in northern boreal areas tended to peak and decline one year before hares and they attributed this to heavy predation by hare predators on grouse eggs and chicks. We have little data on egg and chick mortality but we did find a large number of grouse kills on our grids during winter of 1990–91 which suggests that adult mortality may be important in our area. In Fennoscandia, grouse and ptarmigan fluctuate with vole densites but we found no relationship between these species.

There is scant previous information on the correlation between ptarmigan and hares (Keith 1963). We found that peaks and declines in these species were highly synchronized. In fact, the amplitude of the two peaks shown by these species were also similar with the 1980 peak being about twice as high as the 1990 peak. Ptarmigan were monitored at considerable distance away from our main study sites but previous monitoring of hares within 30 km of the ptarmigan site indicated that hares there were in synchrony with those in our area (Krebs et al. 1986).

Arctic ground squirrels showed major decreases in numbers from 1991 to 1992 and from 1992 to 1993. This was in part, due to low overwinter survival during the

Fig. 12. Relationships between fluctuating hares and voles and other members of the vertebrate community at Kluane Lake. An arrow indicates that changes in number of the species were significantly correlated with changes in hares or voles. The thickness of the arrow indicates the relative strength of the correlation.

winter of 1991–92. Since ground squirrels hibernate, these losses could not be related to hare numbers or related predators. However, adult squirrels did show reduced survival rates due to higher predator mortality from 1990 to 1992 (Hubbs and Boonstra unpubl.). Keith and Cary (1991) also recorded a major decline in Franklin's ground squirrels two yr after a hare peak. Erlien and Tester (1984) reported 10-yr cycles in this species in northern Minnesota.

Although indices of muskrat numbers were not correlated with hare numbers we did find that muskrats showed a major drop in synchrony with the hare decline. Elton and Nicholson (1942) reported a 10-yr cycle in muskrat numbers after analyzing Hudson Bay fur records. Errington (1957) found no clear association between muskrat and hare populations in Iowa while Danell (1978) reported close agreement between a vole cycle and muskrat densities in northern Sweden.

We thought members of the corvid community may fluctuate with hares because of the potential increase in carrion available during the decline and the ability of all these species to take juvenile hares. Raven breeding densities changed slightly with an extra pair of individuals breeding in the intensive study area during the hare peak. The proportion of pairs that fledged young was more variable however with all pairs monitored being successful in 1990 (n = 4) and none being successful by 1993 (n = 3). We did not monitor nesting success of gray jays or magpies but the number of sightings of these species did not drop after the hares crashed.

Species correlated with vole densities

Only hawk owls were weakly correlated with red-backed vole density changes while weasels and boreal owls were strongly correlated with *Microtus* densities (Fig. 12). In summer 1994, boreal owls utilized *Microtus* almost exclusively (90%) as evidenced by their presence in pellets found at nest sites (Doyle unpubl.). Weasel populations did not appear to be related to the hare cycle as was found by Keith and Cary (1991). The lack of correlation between vole densities and most medium-sized vertebrates in the community contrasts sharply with studies in northern Fennoscandia where virtually all vertebrates in the community fluctuate with voles.

Species that showed constant densities

The third group of species in the Kluane community was characterized by relative population stability and no correlation with hare or vole fluctuations. These included red squirrels, four species of predators, and two corvids. Red squirrel densities appeared to be unaffected by the hare cycle. Stuart-Smith and Boutin (1995) showed that predation on adult squirrels did increase as hares declined but only slightly and this was not enough to cause major

changes in density. These results are surprising since red squirrels represent the only major alternative prey biomass available to predators during winter. Keith and Cary (1991) found that red squirrels declined to 25% of maximum densities three yr after a hare peak and suggested that this was due to predator switching. Our results suggest that squirrel densities are affected little by hare cycles although squirrels may affect hare numbers by preying on juveniles when hares are at high densities (O'Donoghue 1994).

Two potential hare predators, red-tailed hawks and wolverine, did not show any increase or decline with changes in hare numbers. Our results for red-tailed hawks are similar to those obtained by Adamcik et al. (1979). This migratory raptor appears to be buffered from declines following hare crashes by feeding on a variety of alternate prey. We found that two vole predators, kestrels and northern harriers, showed no response to the red-backed vole or *Microtus* fluctuations. This may be partially due to predation by other raptors that normally rely on snowshoe hares (Smith and Doyle unpubl.).

Comparisons with other boreal communities

Our findings in the boreal forest of northern Canada differ strikingly from findings in northern Fennoscandia in two ways. Firstly hares replace voles as the predominant herbivore in the system. There are few studies which have measured actual densities of most of the herbivores in the community and thus allow calculation of biomass pyramids. However, it appears that in communities where hares dominate, they not only create a different size distribution of available prey but total herbivore biomass is also considerably higher than in vole-dominated communites. Keith et al. (1977) measured peak spring snowshoe hare biomasses of 614 kg/100 ha while we obtained values of 177 kg/100 ha. In each case, hares represented at least 50% of the small herbivore biomass present. Angelstam et al. (1985) calculated a peak spring biomass of voles of 20 kg/100 ha in the Grimsö area of central Sweden. This comprised 67% of the total small herbivore biomass present. In northern Fennoscandia Henttonen et al. (1987) reported peak vole densities of roughly 40 per ha. This would give biomasses on the order of 100 kg/100 ha, well above the biomasses of other herbivores present but still less than those observed in Canada. In central Finland, Korpimäki and Norrdahl (1989) recorded vole and shrew bimasses of roughly 50 kg/100 ha during a vole peak. They did not measure densities of other small mammals. Marcstrom et al. (1989) cite reports of arctic hare densities as high as 60 (180 kg)/100 ha in Russia. Thus, it seems that the boreal forests of Canada, and possibly Russia. differ from those in northern Fennoscandia in that small herbivore biomasses reach much higher levels and are dominated by species of hare rather than voles.

The second major difference between boreal Canada

78

and northern Fennoscandia is that densities of many fewer species in the boreal forest of Canada are correlated with the dominant herbivore relative to the situation in Fennoscandia. In Fennoscandia where voles fluctuate, their changes in density are strongly correlated with density changes of a wide range of other species. We found that only three species of herbivore were correlated with hares and two predominant alternate prey, red squirrels and voles, were not.

Why is there less synchrony of population changes in the Canadian vertebrate community? One possibility is that the numerical dominance of hares has allowed for the evolution of large-bodied hare specialists like lynx and great horned owls. These species are not efficient at switching to small alternative prey such as voles and squirrels and consequently do not act to synchronize populations. Small predators may be unable to take advantage of abundant juvenile hares because their numbers are limited by winter conditions when hares are not accessible because of their size. In Fennoscandia, the lower overall herbivore biomass and rarity of larger-bodied herbivores leads to a situation whereby predators are small and specialize on voles (Hanski et al. 1991) but are capable of switching to alternative prey when voles crash.

Another explanation may have to do with the species composition of the vole communities in each area. In our study, red-backed voles were the predominant microtine species because only 7% of the area was *Microtus* habitat. In contrast, *Microtus agrestis* is the dominant or codominant microtine along with *Clethrionomys glareolus* in Fennoscandia (Erlinge et al. 1983, Henttonen et al. 1987, Korpimäki and Norrdahl 1989). *Microtus* are larger and live in more open habitats than do *Clethrionomys*. This, along with their folivorous food habits, may make them more susceptible to predators (Henttonen et al. 1987). We found that even though *Microtus* were restricted to a small portion of our study their peak densities led to a strong numerical response in some smaller predators, and all predators, with the exception of lynx, hunted extensively in open areas. In Fennoscandia, the greater abundance of *Microtus* may allow more small predators to respond numerically than was the case in our study. *Clethrionomys rutilus* may not be accessible to many predators.

In this paper we have documented the changes in density of members of the boreal forest vertebrate community during a snowshoe hare fluctuation. The major change in herbivore community composition created by changes in hare numbers can be viewed as a natural perturbation which allows us to investigate the linkages between different members of the community. However, because hares fluctuate over wide areas there are no true controls and any arguments about cause and effect are tentative. In future publications we will present the results of large-scale experimental manipulations of plant, herbivore, and predator densities to test for causal linkages suggested by the correlations described in this paper.

References

Abrams, P. A. 1993. Effect of increased productivity on the abundances of trophic levels. – Am. Nat. 141: 351–361.

Adamcik, R. S., Todd, A. W. and Keith, L. B. 1979. Demographic and dietary responses of great horned owls during a snowshoe hare fluctuation. – Can. Field Nat. 93: 16–27.

Angelstam, P., Lindström, E. and Widen, P. 1985. Synchronous short-term population fluctuations of some birds and mammals in Fennoscandia – occurrence and distribution. – Holarct. Ecol. 8: 285–298.

Boag, D. A. and Schroeder, M. A. 1992. Spruce grouse. – In: Poole, A. F., Stettenheim, P. and Gill, F. (eds), The birds of North America, No. 5. The American Ornithologist's Union. Washington, D.C., pp. 361–383.

Boulanger, J. 1993. Evaluation of capture-recapture estimators using a cyclic snowshoe hare population. – M.Sc. thesis, Dept of Zoology, Univ. of British Columbia.

Boutin, S. and Birkenholz, D. 1987. Muskrat and round-tailed muskrat. – In: Novak, M., Baker, J. A., Obbard, M. E. and Malloch, B. (eds), Wild furbearer management and conservation in North America. Ontario Ministry of Natural Resources, Toronto, pp. 315–325.

– and Larsen, K. W. 1993. Does food availability affect growth and survival of males and females differently in a promiscuous small mammal, *Tamiasciurus hudsonicus*? – J. Anim. Ecol. 62: 364–370.

– , Tooze, Z. and Price, K. 1993. Post-breeding dispersal by female red squirrels (*Tamiasciurus hudsonicus*): the effect of local vacancies. – Behav. Ecol. 4: 151–155.

Danell, K. 1978. Population dynamics of the muskrat in a shallow swedish lake. – J. Anim. Ecol. 47: 697–709.

Doyle, F. I. and Smith, J. N. M. 1994. Population responses of northern goshawks to the 10-year cycle in numbers of snowshoe hares. Condor (in press).

Elton, C. and Nicholson, M. 1942. The ten-year cycle in numbers of the lynx in Canada. – J. Anim. Ecol. 11: 215–244.

Erlien, D. A. and Tester, J. R. 1984. Population ecology of sciurids in northwestern Minnesota. – Can. Field Nat. 98: 1–6.

Erlinge, S., Göransson, G., Hansson, L., Högstedt, G. H., Liberg, O., Nilsson, I. N., Nilsson, T., von Schanz, T. and Sylven, M. 1983. Predation as a regulating factor on small rodent populations in southern Sweden. – Oikos 40: 36–52.

Errington, P. L. 1957. Of population cycles and unknowns. – Cold Springs Harbour Symposium on Quantitative Biology 22: 287–300.

Gilbert, B. S. and Krebs, C. J. 1991. Population dynamics of *Clethrionomys* and *Peromyscus* in southwestern Yukon 1973–1989. – Holarct. Ecol. 14: 250–259.

– , Krebs, C. J., Talarico, D. and Cichowski, D. B. 1986. Do *Clethrionomys rutilus* females suppress maturation of juvenile females? – J. Anim. Ecol. 55: 543–552.

Hannon, S. J. 1983. Spacing and breeding density of willow ptarmigan in response to an experimental alteration of sex ratio. – J. Anim. Ecol. 52: 807–820.

Hanski, I., Hansson, L. and Henttonen, H. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. – J. Anim. Ecol. 60: 353–367.

Henttonen, H., Oksanen, T., Jortikka, A. and Haukisalmi, V. 1987. How much do weasels shape microtine cycles in the northern Fennoscandian taiga? – Oikos 50: 353–365.

Herzog, P. W. and Boag, D. A. 1977. Seasonal changes in aggressive behaviour of female spruce grouse. – Can. J. Zool. 55: 1734–1739.

Hörnfeldt, B. 1978. Synchronous population fluctuations in voles, small game, owls, and tularemia in northern Sweden. – Oecologia 32: 141–152.

– , Löfgren, O. and Carlsson, B.-G. 1986. Cycles in voles and small game in relation to variations in plant production indices in northern Sweden. – Oecologia 68: 496–502.

Keith, L. B. 1963. Wildlife's ten-year cycle. – Univ. of Wisconsin Press, Madison, WI.

– 1990. Dynamics of snowshoe hare populations. – In: Genoways, H. H. (ed.), Current mammalogy. Plenum Press, New York, pp. 119–195.

– and Rusch, D. H. 1989. Predation's role in the cyclic fluctuations of ruffed grouse. – Acta XIX Congr. Int. Ornithol., pp. 699–732.

– and Cary, J. R. 1991. Mustelid, squirrel, and porcupine population trends during a snowshoe hare cycle. – J. Mammal. 72: 373–378.

– , Todd, A. W., Brand, C. J., Adamcik, R. S. and Rusch, D. H. 1977. An analysis of predation during a cyclic fluctuation of snowshoe hares. – Int. Congr. Game Biol. 13: 151–175.

Korpimäki, E. and Norrdahl, K. 1989. Predation of Tengmalm's owls: numerical responses, functional responses and dampening impact on population fluctuations of microtines. – Oikos 54: 154–164.

Krebs, C. J. and Wingate, I. 1976. Population fluctuations in the small mammals of the Kluane region, Yukon Terrritory. – Can. Field Nat. 99: 51–61.

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

Lawton, J. 1989. Food webs. – In: Cherrett, J. M. (ed.), Ecological concepts. Blackwell, Oxford, pp. 43–78.

Lindström, E. R., Andren, H., Angelstam, P., Cederlund, G., Hörnfeldt, B., Jaderherg, L., Lemnell, P., Martinsson, B., Sköld, K. and Swenson, J. E. 1994. Disease reveals the predator: sarcoptic mange, red fox predation, and prey populations. – Ecology 75: 1042–1049.

Marcstrom, V., Kenward, R. E. and Engren, E. 1988. The impact on boreal tetraonids during vole cycles: an experimental study. – J. Anim. Ecol. 57: 859–872.

– , Keith, L. B., Engren, E. and Cary, J. R. 1989. Demographic responses of arctic hares (Lepus timidus) to experimental reductions of red foxes (Vulpes vulpes) and martens (Martes martes). – Can. J. Zool. 67: 658–668.

Murray, D. L. and Boutin, S. 1991. The influence of snow on lynx and coyote movements in the southwestern Yukon: Does morphology affect behaviour? – Oecologia 88: 463–469.

O'Donoghue, M. 1994. Early survival of juvenile snowshoe hares. – Ecology 75: 1582–1592.

Otis, D. L., Burnham, K. P., White, G. C. and Anderson, D. R. 1978. Statistical inference from capture data on closed animal populations. – Wildl. Monogr. 62: 1–135.

Paine, R. T. 1966. Food web complexity and species diversity. – Am. Nat. 100: 65–75.

Power, M. E. 1992. Top-down and bottom-up forces in food webs: do plants have primacy? – Ecology 73: 733–746.

Rohner, Ch. and Doyle, F. I. 1992. Methods of locating Great Horned Owl nests in the boreal forest. – J. Raptor Res. 26: 33–35.

Stuart-Smith, A. K. and Boutin, S. 1995. Predation on red squirrels during a snowshoe hare decline. – Can. J. Zool. (in press).

80