

Christoph Rohner · Charles J. Krebs

Owl predation on snowshoe hares: consequences of antipredator behaviour

Received: 19 January 1996 / Accepted: 15 April 1996

Abstract We show evidence of differential predation on snowshoe hares (*Lepus americanus*) by great horned owls (*Bubo virginianus*) and ask whether predation mortality is related to antipredator behaviour in prey. We predicted higher predation on (1) young and inexperienced hares, (2) hares in open habitats lacking cover to protect from owl predation, and (3) hares in above average condition assuming that rich food patches are under highest risk of predation. Information on killed hares was obtained at nest sites of owls and by monitoring hares using radio-telemetry. The availability of age classes within the hare population was established from live-trapping and field data on reproduction and survival. Great horned owls preferred juvenile over adult hares. Juveniles were more vulnerable to owl predation before rather than after dispersal, suggesting that displacement or increased mobility were not causes for this increased mortality. Owls killed radio-collared hares more often in open than in closed forest types, and they avoided or had less hunting success in habitats with dense shrub cover. Also, owls took hares in above average condition, although it is unclear whether samples from early spring are representative for other seasons. In conclusion, these results are consistent with the hypothesis that variation in antipredator behaviours of snowshoe hares leads to differential predation by great horned owls.

Key words *Bubo virginianus* · Differential predation · *Lepus americanus* · Population cycles · Predation risk

Introduction

Keith et al. (1984) proposed an interaction between predation and food to explain the 10-year population cycle of snowshoe hares (*Lepus americanus*) across the boreal forest in North America, and subsequent experiments have supported this hypothesis (Krebs et al. 1995). Hik (1995) proposed how this interaction of factors, based on predation risk and resource distribution across different habitats, can exacerbate the decline of cyclic hare populations.

Prey animals have conflicting demands of being active and avoiding predation (for a review see Lima and Dill 1990), and depending on their current state, they can vary the sensitivity of their behaviour to predation risk (e.g. McNamara and Houston 1990). Predators, on the other hand, choose the most profitable prey (review in Stephens and Krebs 1986), and differences in antipredator behaviours of prey are predicted to reflect in a predator's diet (e.g. Dickman et al. 1991; Longland and Price 1991).

In recent years, aviary experiments have dramatically increased our understanding of the processes involved in differential predation (e.g. Metzgar 1967; Kaufman 1974; Kotler et al. 1991; Longland and Price 1991). Testing such predictions in the field, however, is extremely difficult and evidence for the effect of antipredator behaviours on mortality patterns in natural systems is rare (e.g. Dickman et al. 1991; Dickman 1992; FitzGibbon and Lazarus 1995; Sinclair and Arcese 1995). Simultaneous and intensive collaborative effort on both predator and prey (Krebs et al. 1992) provided an opportunity to test predictions on differential predation in a natural situation.

If snowshoe hares adopt foraging behaviours to minimise predation risk (Hik 1995), the following predictions will apply to the biases in samples of

C. Rohner (✉)¹ · C. J. Krebs
Centre for Biodiversity Research, Department of Zoology,
University of British Columbia,
Vancouver B.C., Canada, V6T 1Z4

Present address:

¹Mitrani Centre for Desert Ecology,
Blaustein Institute of Desert Research,
Ben Gurion University of the Negev,
Sede Boqer Campus, 84990 Israel
e-mail: rohner@bgumail.bgu.ac.il,
fax: 972-7-655-7829

individuals killed by great horned owls. Young animals, which are not experienced or have not been selected against, should be exposed to a higher predation risk than adults (prediction 1). High predation losses could also be an effect of high mobility of subordinates (Metzgar 1967; Kaufman 1974; Dickman et al. 1991), but if so, younger juveniles should be relatively safe before their movements begin to increase at the age of about 30 days (O'Donoghue and Bergman 1992, prediction 1a).

Snowshoe hares prefer dense forest with abundant cover, and they only use open habitats at highest densities during the peak of the cycle, possibly accepting a higher risk of predation because safer food patches are being depleted (Wolff 1980; Hik 1994, 1995). If this is true, the probability of being killed by an owl should be greater for hares in open habitat classes with less cover than in closed forest (prediction 2).

Predators are commonly assumed to kill prey in poor condition more frequently than expected (Errington 1946; review in Temple 1987), but this is different for a patchy situation with varying habitat structure (Hik 1994). Individuals foraging in rich patches under high predation risk should be in better body condition than individuals tolerating poor forage quality at safer sites (prediction 3).

Several approaches were necessary to test these predictions. The proportions of different age classes were identified in pellets and prey remains collected at great horned owl nests, and then compared to the availability in the hare population as obtained from an estimate based on densities from live-trapping and field data on reproduction and survival. The distribution of predation mortality across different habitat types was assessed by monitoring hares by radio-telemetry, and was then compared to a null-model of expected mortalities based on the availability of these habitat types in the environment. Body condition of snowshoe hares was determined from the fat content of bone marrow, and fresh remains at owl nests were compared to a shot sample from the hare population.

Materials and methods

The study system

We worked at Kluane Lake (60° 57'N, 138° 12'W) in the south-western Yukon, Canada, and the data reported here were collected during 1989–1993. The study area comprised about 350 km² of the Shakwak Trench, a broad glacial valley bounded by alpine areas to the north-west and the south-east. The valley bottom averages about 900 m above sea level and is covered mostly with spruce forest (*Picea glauca*), shrub thickets (*Salix* sp.), some aspen forest (*Populus tremuloides*) grassy meadows with low shrub (*Betula glandulosa*), old burns, eskers, marshes, small lakes and ponds.

Snowshoe hares are widely distributed throughout Northern Canada and Alaska; they have a high fecundity, are heavily preyed-upon, and their abundance oscillates 15- to 200-fold in a 10-year cycle (e.g. Keith 1963, Keith et al. 1984; Boutin et al. 1986; Krebs

et al. 1992). Their diet in winter and spring is dominated by *Betula glandulosa*, *Salix glauca*, and to a lesser extent, by *Picea glauca* (Smith et al. 1988). Great horned owls are large and long-lived predators, which are distributed throughout the continent and show a strong numerical response to the population cycle of snowshoe hares in the boreal forest where hares are their main prey (Keith 1963; Adamcik et al. 1978; Houston and Francis 1995; Rohner 1995, 1996).

Predation on different age classes

The diet of great horned owls was sampled during the breeding season from the beginning of May to mid-July as follows. Nest sites were located in early spring (Rohner and Doyle 1992) and owlets were transferred shortly before fledging to elevated tethering platforms, where the parents kept feeding them (Peterson and Keir 1976; Rohner and Smith 1996). The platforms were about 3.5 m above ground, and pellets fell between the slats into a sheet of burlap, which was attached underneath. The owlets were checked 2–4 times/week with a ladder, and then released after 3–5 weeks at a maximum age of 80 days. We report the results from ten platforms for each year from 1989–1991 (14 individual territories).

Two different methods were used to identify the age of snowshoe hares in owl diets. For the first method, lengths of right hind feet were directly measured in a sample of killed hares found on platforms. Since growth in hind foot length is nearly linear for younger juveniles, a linear regression was used to calculate their age ($y = 1.49x + 34.93$, $r^2 = 0.93$, $n = 844$; M. O'Donoghue, unpublished data). A second method was based on measurements of bones found in owl pellets. Femurs were chosen because they were most abundant and least biased compared to other bones in pellets (C. Rohner, unpublished data). We measured the width of proximate ends of right femurs, and then transformed this to hind foot length by applying a regression from a known sample ($y = 8.49x - 5.15$, $r^2 = 0.96$, $n = 43$).

The density of snowshoe hares in the environment was estimated by separate methods for juveniles and adults. Adult snowshoe hares were live-trapped during 5–6 days in March and April (4–6 grids of 34 ha in size), and closed population methods were used for calculating numbers (Otis et al. 1978). The abundance of juveniles from May to July was estimated with a simple population model with discrete time intervals of 1 day (Walters 1986). The number of juveniles N per adult at time j was calculated separately for each litter i :

$$N_{ij} = [P_i * b_i * (1 - m_i) * s_{ij}] / 2 \quad (1)$$

with p as the pregnancy rate of females, b as the birth rate or litter size, and $(1 - m)$ as the stillborn rate (parameter values in Table 1). The proportion of surviving juveniles s at time j was obtained from curve-fitting to survival data measured by O'Donoghue (1994). The following Eqs. 2 and 3 were used for litters 1 and 2:

$$s_{1j} = 0.53 * \exp [-0.14 * (d_j - d_1)] + 0.47 \quad (2)$$

$$s_{2j} = 0.85 * \exp [-0.27 * (d_j - d_2)] + 0.15 \quad (3)$$

with $(d_j - d_i)$ as the age of juveniles obtained from the current date j and the mean parturition date of litter i (Table 1). To calculate the total number of juveniles per adult at any given time j , N_{1j} and N_{2j} were simply added. Because the parameter values were not different in 1989 and 1990, the data were pooled for these two years. The data from 1991 were excluded for this detailed phenological analysis, because the density and reproduction of snowshoe hares were lower and more variable in this first year of population decline (Hik 1994) and diet information from pellets was incomplete because of drastically reduced survival of juvenile owls (Rohner and Hunter 1996).

Table 1 Parameter values for estimating the abundance of juvenile snowshoe hares at Kluane Lake, Yukon. All parameters were calculated per female and averaged for 1989 and 1990 (data from O'Donoghue and Krebs 1992; O'Donoghue 1994; C. Doyle and D. Hik, unpublished data)

Parameter	First litter	Second litter
Parturition date (d_i)	25 May	30 June
Pregnancy rate (p_i)	0.94	0.98
Litter size (b_i)	3.78	5.88
Stillborn rate (m_i)	0.04	0.07

Predation in different habitat types

During 1989–1993, a total of 1570 snowshoe hares on 10 grids of 34 ha size were equipped with radio collars that included a mortality sensor. The hares were checked daily, and in case of mortality the proximate cause was identified according to diagnostic tracks and other circumstantial evidence at the kill site (Einarsen 1956; C. Doyle, unpublished data). During this field check, the habitat was assessed within a circle of 15 m radius of the kill site and classified according to the amount of cover by trees and shrubs. For estimating the availability of different habitat features, 400 points were sampled according to a checkerboard design on all grids (20 × 20 with 30.5 m spacing). The habitat in a circle of 15 m radius of each point was classified as for kill sites of radio-collared hares.

Predation on hares in different body condition

The body condition of snowshoe hares was assessed by measuring fat levels in the marrow of long bones (Keith et al. 1984). Between 1 May and 10 June 1989–1991, fresh hind legs of adult hares were collected from nests or tethering platforms ($n = 85$) and compared to a shot sample in the population ($n = 180$). Bone marrow was extracted from tibias and fat levels were estimated by the oven-dry percentage of the fresh weight (Keith et al. 1984).

Data analysis

We used SYSTAT for statistical analysis. Correlation coefficients refer to the Spearman rank correlation. Percentages were arcsine-transformed and tested for deviations from normality before analyses of variance were calculated. If not indicated otherwise, all probabilities are two-sided. To calculate preferences for specific age classes in the diet, we used Manly's alpha, which is an index that ranges from 0 to 1 and is robust to density changes (Chesson 1983; calculation according to Krebs 1989).

Results

Prediction 1: High risk for young hares

The phenology in relative abundance of juvenile hares in the population was bimodal (Fig. 1). First litters showed as a moderate peak at the end of May, and second litters followed as a more pronounced peak with both higher productivity and higher early mortality. The third litter was born after the end of our sampling period.

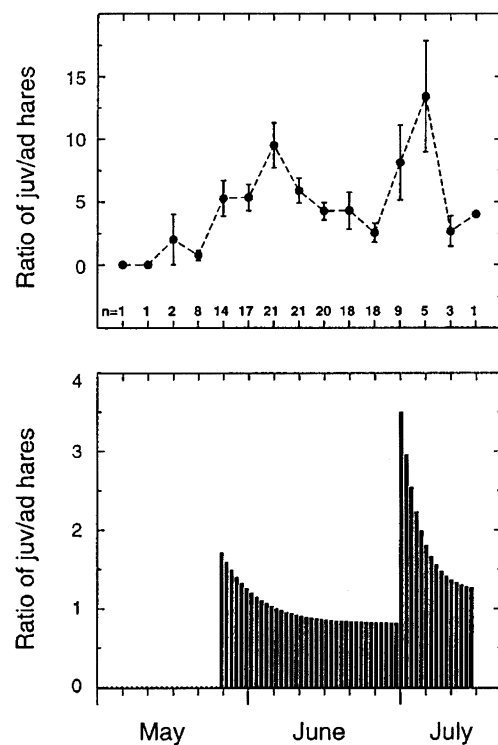
Owl predation mirrored the same phenological pattern: the occurrence of juvenile hares in pellets was

bimodal both in 1989 and 1990. The peaks in the use of juvenile hares in the owl diet showed a time lag in the response to the two litters of newborn hares.

The population model predicted a maximum ratio of 3–4 juvenile hares per adult hare in the population. This is likely to be an overestimate because we did not include any natural variation in parturition dates for our model. (Natural variation would result in smoothed peaks and a lower value of newborn hares at any time during the season). Figure 1 shows a clearly higher use of juvenile hares by owls, with peaks of 5–10 juveniles per adult hare. We calculated Manly's alpha as a preference index for the diet samples from 30 territories during 1989–1991 (total of 14 different territories). The preference of great horned owls for juvenile hares was much higher than the preference for adult hares ($a_{juv} = 0.68$ vs $a_{ad} = 0.32$, $SE = 0.04$, $P < 0.001$, Wilcoxon rank test for paired samples).

Hind foot length was used as an indicator of age to investigate whether great horned owls preferred older or younger juveniles within the first-litter cohort (Fig. 2a). The elongated horizontal scatter of points with maximum values stems from adult hares. Young hares appear in distinct clusters around the mean parturition dates (arrows), and can be recognised as two

Fig. 1a,b Phenology in the relative abundance of juvenile snowshoe hares 1989–1990. **a** Killed by great horned owls as determined from pellets collected at tethering platforms. Data are grouped in 5-day intervals, with means ± SE and n of sampled territories. **b** Available in the environment, as estimated from field data of density, reproduction, and survival (see Materials and methods for details)



similar-sized cohorts growing over time. A regression line, obtained from first-litter juveniles in the population (M. O'Donoghue, unpublished data), was overlaid onto the sample killed by owls in Fig. 2a. The slopes of the two samples were not significantly different, but the intercept of the kill sample was greater than in the population ($n = 181$, $t = 3.07$, $P < 0.01$).

At the end of June, when the first-litter cohort was on average 44 days old and second litters were born, we tested if the two distinct age classes were at equal risk to owl predation using a similar method as above. As an index of age, hind foot lengths were calculated from bone measurements in pellets. This method is less precise than measuring hind feet directly, but pellets are a more systematic and complete source of information than leftovers on platforms, and therefore more data points were available. This data presented in

Fig. 2a,b Phenology in the development of hindfoot length of snowshoe hares killed by great horned owls in 1989–90. **a** Direct measurements from hare remains found on tethering platforms. **b** Calculated from the proximate width of femurs found in pellets. Arrows indicate average parturition dates for first and second litters. Solid line represents predicted regression from first-litter juveniles in the hare population ($y = 1.42x + 35.49$, $r^2 = 0.94$, $n = 176$; M. O'Donoghue, unpublished data). Dashed line shows shifted regression, separating first and second litters

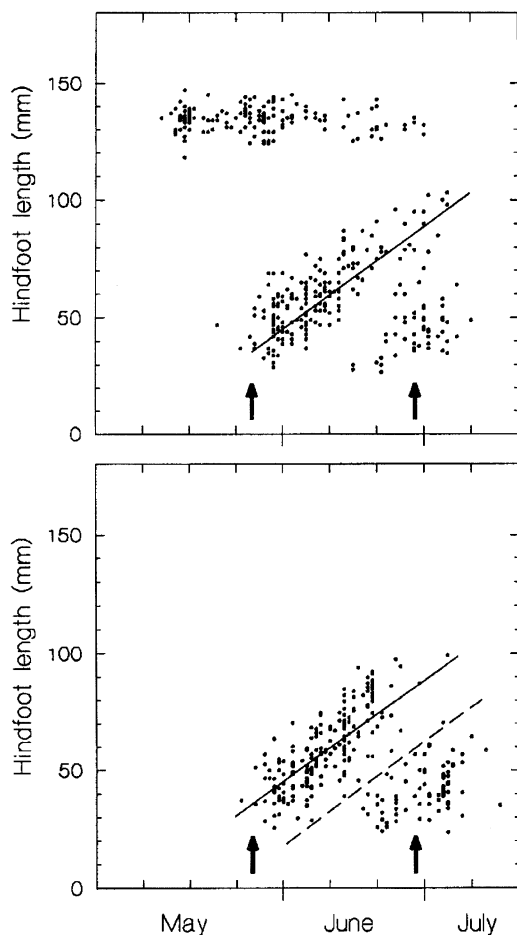
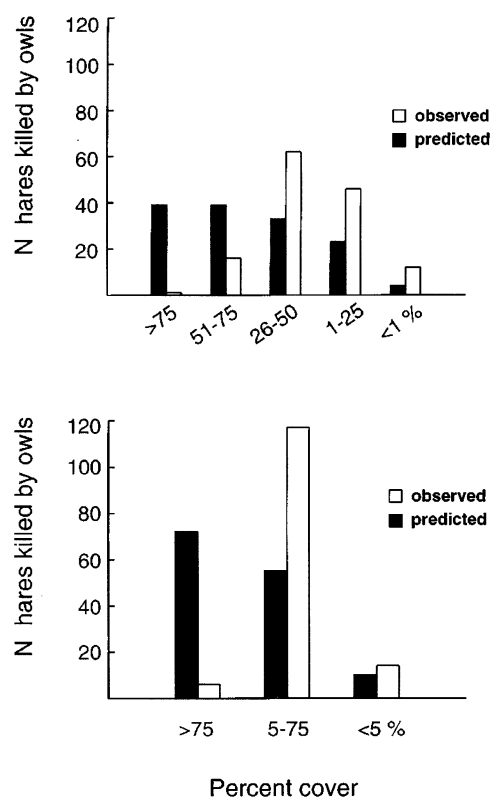


Fig. 2b was overlaid by the same regression line as in Fig. 2a (solid line). In order to separate first and second litters we shifted this regression line in between the two intercepts given by the average parturition dates for first and second litters (broken line). We then chose time windows with a width of 5–20 days around the average parturition date, and calculated the proportion of the newborn and the 6-week-old cohort during this period. Depending on the exact time window chosen around the end of June, the maximum percentage of the older first-litter cohort was 25–30% in the environment (data from Fig. 1b), but only 7–15% in the owl pellets (data from Fig. 2b). This difference was significant ($\chi^2 = 3.86 - 12.08$, $df = 1$, $n = 99-159$, $P < 0.05$), indicating a clearly higher predation risk for very young hares.

Prediction 2: High risk in open habitat

Great horned owls killed more hares in open forest types than expected from the availability in the study area (Fig. 3a). Comparing the location of owl kills to a null-model based on habitat availability assumes that hares have equal densities in all habitat types. This is

Fig. 3a,b Distribution of 137 radioed snowshoe hares killed by great horned owls in different habitat types, compared to the expected distribution from a null-model of habitat availability (assuming equal habitat use by hares). **a** Effect of tree cover. **b** Effect of shrub cover in open forest types (tree cover $\leq 50\%$, representing 88% of kill data)



a conservative assumption, because snowshoe hares are well known to prefer habitat types with abundant cover (e.g. Wolff 1980; Hik 1995).

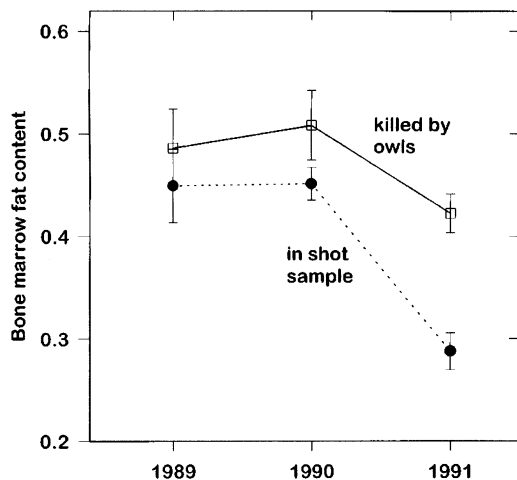
There was also an effect of shrub cover: great horned owls avoided or had less hunting success where shrub cover was dense (Fig. 3b). Because shrub cover was negatively affected by tree cover (presumably by reduced sunlight), data from closed forest types (tree cover >50%, 22% of the sum of kills) were not included in Fig. 3b.

All interactions of tree cover, shrub cover, and kill sites (used vs available) were significant with $P < 0.001$ in a log-linear model ($df = 24$).

Prediction 3: High risk for hares in good condition

Indices of body condition are presented in Fig. 4. There were significant effects of year (ANOVA $F_{2,259} = 14.32$, $P < 0.001$) and of fate (killed by owls or shot sample, $F_{1,259} = 7.70$, $P < 0.01$), but the interaction of year and fate was not significant ($F_{2,259} = 1.92$, $P = 0.15$). Because body mass of snowshoe hares declines over winter and then recovers from May onwards during spring and summer (Keith et al. 1984; Hik 1995), some of the differences in Fig. 4 may have resulted from biases in sampling dates. During the collection period from early May to early June, the index for condition increased over time in the shot sample ($r = 0.225$, $P < 0.01$, $n = 180$) but not in the owl sample ($r = 0.064$, $P > 0.2$, $n = 85$). We tested a possible effect of collection date on fat content using ANCOVA, but only the effect of the covariates year and fate were significant (overall $r^2 = 0.139$, $F_{3,261} = 14.02$, $P < 0.001$).

Fig. 4 Fat content in bone marrow of snowshoe hares killed by great horned owls (squares, $n = 85$) and in a shot sample from the population (circles, $n = 180$). Data from May and June 1989–1991, with means \pm SE



Discussion

High predation risk for juveniles

Juvenile snowshoe hares were at least twice as vulnerable to great horned owl predation as adult hares, and this result confirms prediction 1. If young individuals are predator-naive and have to learn how to reduce their exposure to predation risk (Curio 1993), we expect a bias in predation rates towards juveniles. Dickman (1992) found that the survival of predator-experienced house mice (*Mus domesticus*) was 2.5 times higher than of predator-naive mice, because predator-experienced mice used sites with greater vegetation cover. Janes and Barss (1985) did not find a preference of great horned owl predation on any particular size class of pocket gophers (*Thomomys talpoides*), perhaps because this fossorial prey species does not experience failed attacks, which may be necessary for learning. Donazar and Ceballos (1989) found that eagle owls (*Bubo bubo*) preferred juvenile rabbits (*Oryctolagus cuniculus*). According to Mykytowycz et al. (1959), young rabbits behave naively towards predators. Beside the effects of active learning, predator avoidance by juveniles may simply be limited by growth processes, and essential organs like brain (predator detection) or hind limbs (predator escape) may not have reached full efficiency (see also Curio 1993). Future work is needed to separate active learning of antipredator behaviours from developmental constraints on detection and escape from predators.

An alternative hypothesis to explain high predation rates on juvenile and subadult mammals is based on increased movement because of exploration, dispersal, or displacement (Metzgar 1967; Ambrose 1972; Kaufman 1974; Halle 1988). For example, adult house mice appear to confine juveniles to open vegetation where they are more vulnerable to predation (Dickman et al. 1991). Snowshoe hares begin to increase their movements after weaning at about 30 days of age (O'Donoghue and Bergman 1992), thus allowing an accurate prediction when predation mortality should increase according to this hypothesis. In contrast to prediction 1a, great horned owls killed very young hares at clearly greater proportions than older juveniles of the cohort with increased movements. This suggests that in snowshoe hares, older juveniles are more successful in avoiding predation, either because of their progressed abilities, or because predators have already removed less successful juveniles at a younger age.

The small differences in age within a litter cohort did not reveal results as clear as above. The slope in hind foot growth was not flatter for owl kills as expected if younger hares are easiest to capture. The difference in intercepts could also result from a bias in the measurements (if hind feet of dead hares are easier to stretch than of live-trapped juveniles, this would lead

to a consistent size difference across all ages). Because of the extreme synchronisation of first litters (O'Donoghue and Boutin 1995), the contrast in age and size within a cohort is probably too small for detailed analysis.

Predation risk in patchy habitat

Wolff (1980) developed a conceptual model of changing habitat use by snowshoe hares over the population cycle, and proposed that closed spruce forest, open spruce forest, and open shrub habitat represent habitats with increasing predation risk. Predation mortality by great horned owls was clearly biased towards open habitat classes, and these results confirm prediction 2.

Hik (1994) found that food was more abundant in habitat types with little cover, and he presented experimental evidence that the absence of predators led to high body mass in female snowshoe hares (Hik 1995). Our results (prediction 3) suggest better condition in hares killed by owls and are consistent with a trade-off in food availability and predation risk for foraging hares.

In contrast, Keith et al. (1984) proposed that limited resources lead to poor condition and increased predation rates in snowshoe hares. They found that 10 of 16 snowshoe hares killed by great horned owls were in poor condition, whereas only 13% of the hare population was malnourished. Despite a much larger sample size, we could not confirm that great horned owls selected snowshoe hares in poor condition at our study site. Although predators are commonly thought to capture starving or diseased individuals in higher than expected proportions, the evidence for this hypothesis is inconsistent in many species (Temple 1987; see also Sinclair and Arcese 1995). A variety of factors may account for diverging results, for example in our case, Keith's winter data (December to April 1981–82) may not be comparable to our spring sample. High availability of food alone does not necessarily result in higher body mass of foraging individuals, since the energetic balance is also affected by other costs such as exposure to unfavourable weather, increased movement, or physiological stress when exposed to higher risk of predation (Boonstra and Singleton 1993; Hik 1995).

An alternative explanation for the results in Fig. 4 would entail that our shot sample was biased. Although shot samples are a standard technique to assess the average condition of individuals in wildlife populations (e.g. Temple 1987), animals in poorer than average condition may accept a higher risk of predation and may therefore tolerate a closer distance to an approaching person or a mammalian predator before escaping. Further research should compare the vulnerability to different predators in more detail (see also Keith et al. 1984) and test the responses of individual hares to standardised risks.

Population consequences for predators and prey

Great horned owls may actively select more profitable prey when given a choice (see also Marti and Hogue 1979), but it appears that these predators using a sit-and-wait approach from exposed and elevated perches (Rudolph 1978; C. Rohner, unpublished data) are largely dependent on prey animals leaving safe cover and crossing open habitat (see also Kotler et al. 1991; Longland and Price 1991; Brown et al. 1992; Hughes et al. 1995). This reflects in higher hunting success in open habitat as indicated by our results, and in higher productivity of great horned owl populations in mixed habitat compared to contiguous forests (Bosakowski et al. 1989). Johnson (1993), who studied the effects of logging in the Pacific Northwest, found that great horned owls intruded in higher densities into forests fragmented by clear-cuts, and possibly increase predation rates on animals of mature forests such as the spotted owl (*Strix occidentalis*).

In snowshoe hares, failure of avoiding predators may not only become apparent in differential predation, but the costs of successfully avoiding predators may also have consequences on population dynamics (Hik 1995; see also Abrams 1984; Ives and Dobson 1987; Brown et al. 1992; FitzGibbon and Lazarus 1995; Sinclair and Arcese 1995). Adopting foraging behaviours that minimise predation risk may lead to a decline in condition and fecundity (Hik 1994, 1995). Recent field data and experiments emphasise the trade-off between predation risk and reproduction (e.g. Magnhagen 1991), and there is evidence for reduced reproduction through behavioural changes or detrimental effects because of high physiological stress levels (e.g. Ylönen 1989; Takahashi et al. 1990; Boonstra and Singleton 1993; Korpimäki et al. 1994; Ylönen and Ronkainen 1994; Hik 1995). The strong preference of great horned owls and possibly other predators for juvenile hares may also have a cumulative effect on the reduced recruitment typical for declining snowshoe hare populations (Keith et al. 1984; Hik 1994).

In conclusion, the results of all three predictions were consistent with the hypothesis that individual differences in antipredator behaviour of snowshoe hares lead to differential predation by great horned owls under natural conditions. This, however, does not mean that all possible alternative explanations have been excluded. More work is needed to understand how young animals learn to adopt foraging behaviours that minimise predation risk (see also Sullivan 1989; Skutelsky 1996) and to separate active learning of antipredator behaviours from developmental constraints on detection and escape from predators (e.g. Curio 1993). Future studies may identify the exact mechanism of how resource distribution and predation risk or social behaviour affect stress levels, body condition, and reproduction in snowshoe hares, and may therefore assess the potential effect on population dynamics.

Acknowledgements This study is the result of a collaborative project and would not have been possible without the contributions of many. We thank F. Doyle, C. Schmid, K. Russenberger, B. Zimmermann, C. Kullberg, S. Wagnière, J. Stroman, and T. Wellicome for their help with often strenuous field work on great horned owls. Samples and unpublished data were contributed by R. Boonstra, S. Boutin, C. Doyle, D. Hik, M. Nams, and M. O'Donoghue. Special thanks to C. Doyle and S. Schweiger for their tireless effort in monitoring radio-collared hares. J. Stroman and C. Frye analysed most owl pellets. Mary Price, B. Kotler, J. Brown, L. Metzgar, E. Korpimäki, A. R. E. Sinclair, J. N. M. Smith, C. S. Houston, and R. Ydenberg improved the manuscript with valuable comments. Our study was funded by a J.R. Thompson Wildlife Fellowship and a Graduate Fellowship of the University of British Columbia to C. Rohner, and a grant of the Natural Sciences and Engineering Council of Canada to C. J. Krebs. This is contribution 34 of the Kluane Boreal Forest Ecosystem Project.

References

- Abrams PA (1984) Foraging time optimization and interactions in food webs. *Am Nat* 124: 80–96
- Adamcik RS, Todd AW, Keith LB (1978) Demographic and dietary responses of great horned owls during a snowshoe hare cycle. *Can Field Nat* 92: 156–166
- Ambrose HW (1972) Effect of habitat familiarity and toe-clipping on rate of owl predation in *Microtus pennsylvanicus*. *J Mammal* 53: 909–912
- Boonstra R, Singleton GR (1993) Population declines in the snowshoe hare and the role of stress. *Gen Comp Endocrinol* 91: 126–143
- Bosakowski T, Speiser R, Smith DG (1989) Nesting ecology of forest-dwelling great horned owls, *Bubo virginianus*, in the eastern deciduous forest biome. *Can Field Nat* 103: 65–69
- Boutin S, Krebs CJ, Sinclair ARE, Smith JNM (1986) Proximate causes of losses in a snowshoe hare population. *Can J Zool* 64: 606–610
- Brown JS, Morgan RA, Dow BD (1992) Patch use under predation risk. II. A test with fox squirrels, *Sciurus niger*. *Ann Zool Fenn* 29: 311–318
- Chesson J (1983) The estimation and analysis of preference and its relationship to foraging models. *Ecology* 64: 1297–1304
- Curio E (1993) Proximate and developmental aspects of antipredator behaviour. *Adv Study Behav* 22: 135–238
- Dickman CR (1992) Predation and habitat shift in the house mouse, *Mus domesticus*. *Ecology* 73: 313–322
- Dickman CR, Predavec M, Lynam AJ (1991) Differential predation of size and sex classes of mice by the barn owl, *Tyto alba*. *Oikos* 62: 67–76
- Donazar JA, Ceballos O (1989) Selective predation by eagle owls *Bubo bubo* on rabbits *Oryctolagus cuniculus*: age and sex preferences. *Ornis Scand* 20: 117–122
- Einarsen AS (1956) Determination of some predator species by field signs. *Oreg State Monogr* 10: 1–34
- Errington PL (1946) Predation and vertebrate populations. *Q Rev Biol* 21: 221–245
- FitzGibbon CD, Lazarus J (1995) Antipredator behaviour of Serengeti ungulates: individual differences and population consequences. In: Sinclair ARE, Arcese P (eds) *Serengeti II: dynamics, management, and conservation of an ecosystem*. University of Chicago Press, Chicago, pp 274–296
- Halle S (1988) Avian predation upon a mixed community of common voles (*Microtus arvalis*) and wood mice (*Apodemus sylvaticus*). *Oecologia* 75: 451–455
- Hik DS (1994) Predation risk and the 10-year snowshoe hare cycle. Ph.D. Thesis, University of British Columbia, Vancouver
- Hik DS (1995) Does risk of predation influence population dynamics? Evidence from the cyclic decline of snowshoe hares. *Wildl Res* 22: 115–129
- Houston CS, Francis CM (1995) Survival of great horned owls in relation to the snowshoe hare cycle. *Auk* 112: 44–59
- Hughes JJ, Ward D, Perrin MR (1995) The effects of predation risk and competition on habitat selection and activity in gerbils in the Namib desert. *Ecology* 75: 1397–1405
- Ives AR, Dobson AP (1987) Antipredator behaviour and population dynamics of simple predator-prey systems. *Am Nat* 130: 431–447
- Janes SW, Barss JM (1985) Predation by three owl species on northern pocket gophers of different body mass. *Oecologia* 67: 76–81
- Johnson DH (1993) Spotted Owls, Great Horned Owls, and forest fragmentation in the Central Oregon Cascades. MSc Thesis, Oregon State University, Corvallis, Ore
- Kaufman DW (1974) Differential predation on active and inactive prey by owls. *Auk* 91: 76–81
- Keith LB (1963) *Wildlife's ten year cycle*. University of Wisconsin Press, Madison
- Keith LB, Cary JR, Rongstad OJ, Brittingham MC (1984) Demography and ecology of a declining snowshoe hare population. *Wildl Monogr* 90: 1–43
- Korpimäki, Norrdahl K, Valkama J (1994) Reproductive investment under fluctuating predation risk: microtine rodents and small mustelids. *Evol Ecol* 8: 357–368
- Kotler BP, Brown JS, Hasson O (1991) Factors affecting gerbil foraging behavior and rates of owl predation. *Ecology* 72: 2249–2260
- Krebs CJ (1989) *Ecological methodology*. Harper and Row, New York
- Krebs CJ, Boonstra R, Boutin S, Dale M, Hannon S, Martin K, Sinclair ARE, Smith JNM, Turkington R (1992) What drives the Snowshoe Hare cycle in Canada's Yukon? In: McCullough D, Barrett R (eds) *Wildlife 2001: populations*. Elsevier, London, pp 886–896
- Krebs CJ, Boutin S, Boonstra R, Sinclair ARE, Smith JNM, Dale RT, Martin K, Turkington R (1995) Impact of food and predation on the snowshoe hare cycle. *Science* 269: 1112–1115
- Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68: 619–640
- Longland WS, Price MV (1991) Direct observations of owls and heteromyid rodents: can predation risk explain microhabitat use? *Ecology* 72: 2261–2273
- Magnhagen C (1991) Predation risk as a cost of reproduction. *Trends Ecol Evol* 6: 183–186
- Marti CD, Hogue JG (1979) Selection of prey by size in screech owls. *Auk* 96: 319–327
- McNamara JM, Houston AI (1990) State-dependent ideal free distributions. *Evol Ecol* 4: 298–311
- Metzgar LH (1967) An experimental comparison of screech owl predation on resident and transient white-footed mice (*Peromyscus leucopus*). *J Mammal* 48: 387–391
- Mykityowycz R, Hesterman ER, Purchase D (1959) Predation on the wild rabbit by the Australian raven. *Emu* 59: 41–43
- O'Donoghue M (1994) Early survival of juvenile snowshoe hares. *Ecology* 75: 1582–1592
- O'Donoghue M, Bergman CM (1992) Early movements and dispersal of juvenile snowshoe hares. *Can J Zool* 70: 1787–1791
- O'Donoghue, Boutin S (1995) Does reproductive synchrony affect juvenile survival rates of northern mammals? *Oikos* 74: 115–121
- O'Donoghue M, Krebs CJ (1992) Effects of supplemental food on snowshoe hare reproduction and juvenile growth at a cyclic population peak. *J Anim Ecol* 61: 631–641
- Otis DL, Burnham KP, White GC, Anderson DR (1978) Statistical inference from capture data on closed animal populations. *Wildl Monogr* 62: 1–135
- Petersen LR, Keir JR (1976) Tether platforms – an improved technique for raptor food habits study. *Raptor Res* 10: 21–28
- Rohner C (1995) Great horned owls and snowshoe hares: what causes the time lag in the numerical response of predators to cyclic prey? *Oikos* 74: 61–68
- Rohner C (1996) The numerical response of great horned owls to the snowshoe hare cycle: consequences of non-territorial 'floaters' on demography. *J Anim Ecol* 65: 359–370

- Rohner C, Doyle FI (1992) Methods of locating Great Horned Owl nests in the boreal forest. *J Raptor Res* 26: 33–35
- Rohner C, Hunter DB (1996) First-year survival of great horned owls during a peak and decline of the snowshoe hare cycle. *Can J Zool* 74: 1092–1097
- Rohner C, Smith JNM (1996) Brood size manipulations in Great Horned Owls *Bubo virginianus*: are predators food limited at the peak of prey cycles? *Ibis* 138: 236–242
- Rudolph SG (1978) Predation ecology of coexisting great horned and barn owls. *Wilson Bull* 90: 134–137
- Sinclair ARE, Arcese P (1995) Population consequences of predation-sensitive foraging: the Serengeti wildebeest. *Ecology* 76: 882–891
- Skutelsky O (1996) Predation risk and state dependent foraging in scorpions: effects of moonlight on foraging in the scorpion *Buthus occitanus*. *Anim Behav* (in press)
- Smith JNM, Krebs CJ, Sinclair ARE, Boonstra R (1988) Population biology of snowshoe hares. II. Interactions with winter food plants. *J Anim Ecol* 57: 269–286
- Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton, NJ
- Sullivan KA (1989) Predation and starvation: age-specific mortality in juvenile juncos (*Junco phaenotus*). *J Anim Ecol* 58: 275–286
- Takahashi LK, Baker EW, Kalin NH (1990) Ontogeny of behavioral and hormonal responses to stress in prenatally stressed male rat pups. *Physiol Behav* 47: 357–364
- Temple SA (1987) Do predators always take substandard individuals disproportionately from prey populations? *Ecology* 68: 669–674
- Walters CJ (1986) Adaptive management of renewable resources. Macmillan, New York
- Wolff JO (1980) The role of habitat patchiness in the population dynamics of snowshoe hares. *Ecol Monogr* 50: 111–130
- Ylönen H (1989) Weasels suppress reproduction in cyclic bank voles *Clethrionomys glareolus*. *Oikos* 55: 138–140
- Ylönen H, Ronkainen H (1994) Breeding suppression in the bank vole as antipredatory adaptation in a predictable environment. *Evol Ecol* 8: 658–666