

## Does Risk of Predation Influence Population Dynamics? Evidence from the Cyclic Decline of Snowshoe Hares

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### Abstract

Like most heavily preyed-upon animals, snowshoe hares (*Lepus americanus*) have to balance conflicting demands of obtaining food at a high rate and avoiding predators. Adopting foraging behaviours to minimise predation risk may also lead to a decline in condition, and hence fecundity. Predictions of three hypotheses (condition constraint hypothesis, predator-avoidance constraint hypothesis, predation-sensitive foraging (PSF) hypothesis) were tested by comparing changes in the survival and condition of snowshoe hares on four experimental areas in winter during a cyclic peak and decline (1989–1993) near Kluane Lake, Yukon, Canada, where (i) predation risk was reduced by excluding terrestrial predators (FENCE), (ii) food supply was supplemented with rabbit chow *ad libitum* (FOOD), (iii) these two treatments were combined (FENCE+FOOD), and (iv) an unmanipulated CONTROL was used.

Different patterns of survival and changes in body mass were observed in the presence and absence of terrestrial predators. On the CONTROL area, female body mass and fecundity declined, even though sufficient winter forage was apparently available in all years. A similar decrease in body mass was observed on the FOOD treatment, but only during the third year of the population decline. In contrast, female body mass remained high throughout the decline in the absence of terrestrial predators in the FENCE+FOOD and FENCE treatments. Winter survival declined on CONTROL and FENCE areas during the first year of the population decline (1991), but remained higher on FOOD until 1992 and FENCE+FOOD until 1993. These results generally supported the PSF hypothesis where terrestrial predators were present (CONTROL and FOOD grids). Where terrestrial predators were absent (FENCE and FENCE+FOOD), the results supported the alternative condition constraint hypothesis. The evidence suggests that a cascade of sublethal behavioural and physiological effects associated with increased predation risk contribute to the population decline and delayed recovery of cyclic low-phase populations of snowshoe hares.

### Introduction

Where predation is implicated in the regulation of prey populations, anti-predator behaviour will probably play a role in the process (Abrams 1989, 1990, 1992a, 1992b, 1992c, 1993; Matsuda and Abrams 1994). The theoretical basis for exploring this problem of a trade-off between gaining energy and avoiding predation has developed rapidly in recent years (Gilliam and Fraser 1987; McNamara and Houston 1987, 1990; Ludwig and Rowe 1990; Brown 1992; Houston *et al.* 1993; Clark 1993, 1994; Oksanen and Lundberg 1994). Numerous studies have investigated the effects of increased predation risk on foraging behaviour of small mammals (Holmes 1984; Kotler 1984; Anderson 1986; Desy *et al.* 1990; Lima and Dill 1990; Cassini and Galante 1992; Dickman 1992; Kotler *et al.* 1992; Saarikko 1992; Hughes *et al.* 1994), and in most of these studies increased risk of predation resulted in a shift in patterns of habitat use, diet and time spent active or foraging. Similarly, several studies have demonstrated the importance of anti-predator behaviours in determining patterns of species coexistence (Kotler 1984; Brown 1989; Hughes *et al.* 1994). The influence of predation risk on population dynamics has been

more difficult to demonstrate (Hassell and May 1985; Ives and Dobson 1987; Brown *et al.* 1992; Abrams 1993; FitzGibbon and Lazarus 1995). In this paper I examine the population-level consequences of increased predation risk to snowshoe hares (*Lepus americanus*).

### *The 10-year Population Cycle of Snowshoe Hares*

Populations of snowshoe hares fluctuate in number, with population peaks occurring at periods of 8–11 years throughout most of their range in the North American boreal forest (Keith 1990). Several alternative hypotheses involving food, predation and social behaviour of hares have been proposed to explain the cycle (Sinclair *et al.* 1988, 1993; Keith 1990; Krebs *et al.* 1992; Royama 1992; Hik 1994). Recent studies have suggested that predation alone may be sufficient to generate the population decline of hares (Boutin *et al.* 1986; Krebs *et al.* 1986a, 1986b; Trostel *et al.* 1987; Boutin 1995). Winter food does not appear to be absolutely limiting for hares at any time during the cycle (Sinclair *et al.* 1988; Smith *et al.* 1988), although the accessibility of winter forage may be reduced when predation risk is high (Smith *et al.* 1988; Royama 1992). Previous studies have also observed a significant reduction in female fecundity during the population decline. This demographic characteristic is closely linked to the cyclic dynamics (Cary and Keith 1979; Royama 1992).

Several authors (Wolff 1980; Keith *et al.* 1984; Smith *et al.* 1988) have suggested that predation risk may influence patterns of habitat use of snowshoe hares. Hik (1994) examined this hypothesis and found that hares attempted to reduce risk of predation by reducing use of riskier, open habitats (where more food was available) in favour of safer, closed habitats (less available food) as predation risk increased during the population decline. A summary of the different factors (food, predation, habitat) that characterised the population peak and decline at Kluane (1988–1993) are shown in Fig. 1a–g. During the decline in the hare population (a) there was an increase in the predator-to-hare ratio (b), and survival of hares was reduced in the early decline (c). Available forage increased during this period (d) and, although there was no evidence that hares were absolutely food-limited, forage was more available in open-forest habitats than closed-forest habitats (negative covariance of food and safety). During the population decline female body mass (e) and reproduction (f) were reduced, even though *per capita* food availability was increasing. Concomitantly, there was a notable shift in patterns of winter habitat use by hares (g), such that hares increased the proportion of safer, closed habitats used in winter, and avoided riskier, open habitats (Hik 1994).

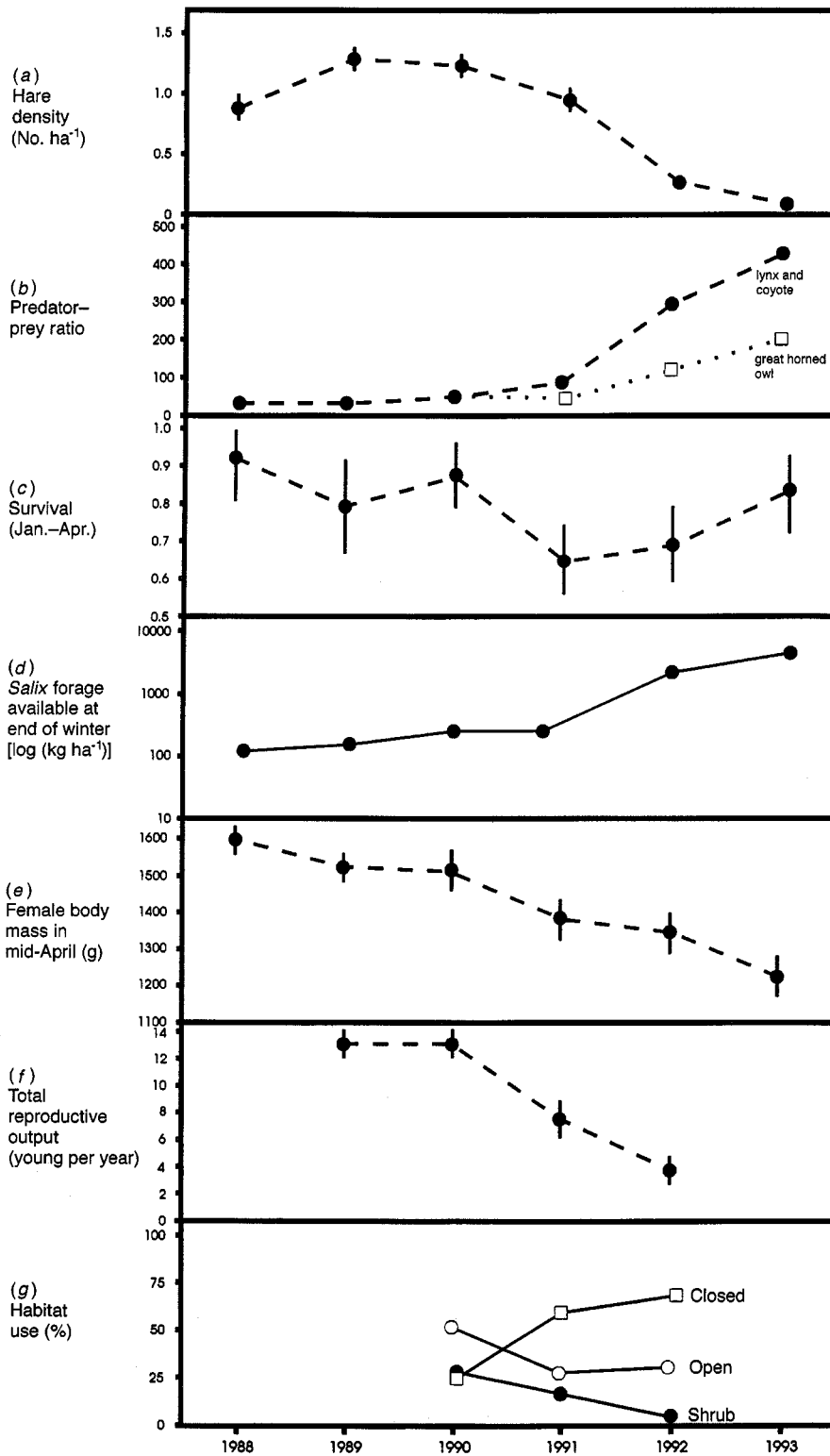
### *Hypotheses and Predictions*

The theoretical models mentioned above predict that animals choose a level of intake and predation risk that maximise individual fitness. Depending on ambient resource availability and predation risk this maximisation can be achieved by reducing condition or survival, or both, to some extent. During the population increase and cyclic peak (1989–1990), food is readily available and predators are scarce, therefore body mass (condition) and survival of hares should be high (initial state in Fig. 2). Predicted changes in condition (measured as body mass) and survival of hares during winter according to each of three hypotheses are indicated in Fig. 2.

Specific predictions of three alternative hypotheses in response to a behavioural trade-off between foraging and predator-avoidance as predation risk increases are as follows. The 'condition constraint hypothesis' predicts that hares maintain body mass (maximise intake rate),

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**Fig. 1.** Patterns of change of the main demographic, environmental and behavioural factors during a snowshoe-hare cyclic peak and decline at Kluane, Yukon, Canada (after Hik 1994). (a) Hare density (No. ha<sup>-1</sup>); (b) predator-prey ratio of terrestrial and avian predators; (c) survival of hares during January–April period, on the basis of radio-telemetry; (d) *Salix* forage availability per hare at the end of winter (kg per hare); (e) body mass of female hares in mid-April; (f) total reproductive output of female hares; and (g) use of habitat by female hares during late winter.



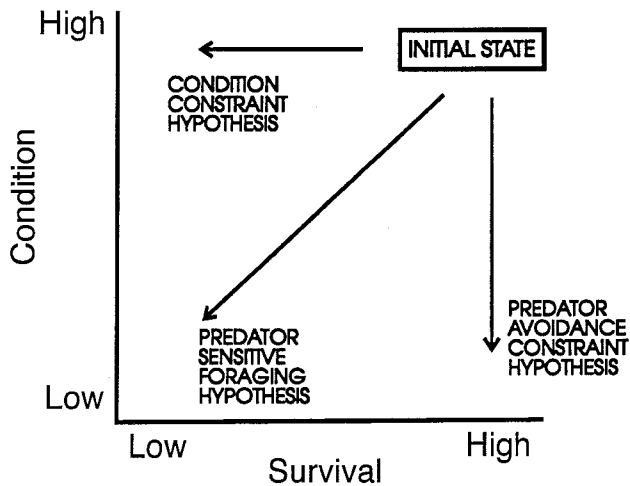


Fig. 2. Predicted changes in condition (body mass) and winter survival with increased risk of predation. The arrows indicate the direction of change from the initial state (high food, low predation risk) that supports each hypothesis.

but survive less well, relative to the initial state. The 'predator-avoidance constraint hypothesis' predicts that hares lose body mass, but still survive well (minimise predation). The 'predation-sensitive foraging hypothesis' predicts that hares adopt a strategy in which both survival and condition will decrease. Specific predictions of this hypothesis (McNamara and Houston 1987; Ludwig and Rowe 1990; Brown 1992) are (i) increased predation risk leads to decreased body mass (hence fecundity), and (ii) decreased food levels lead to increased mortality.

The predictions were examined by manipulating food and predation risk on four experimental hare-trapping grids at Kluane, Yukon, during a hare population peak and decline (1989–1993). I focused on the late winter period (January–April) when food is most limited and survival is lowest. There are also theoretical reasons to expect hares to be most sensitive to predation risk in the period immediately prior to summer breeding (Ludwig and Rowe 1990; Rowe and Ludwig 1991; Houston *et al.* 1993; Clark 1994).

## Methods

### Study Sites

This study was conducted between 1989 and 1993 as part of the Kluane Boreal Forest Ecosystem Project (Krebs *et al.* 1992). This period spanned the peak (1989–1990) and three decline years of one hare cycle. Field sites were located in the Shakwak Trench along the Alaska Highway, east of Kluane Lake, Yukon, Canada (61°N, 138°W; c. 900 m above sea level). The forest community is dominated by white spruce (*Picea glauca*), and a shrub understorey of grey willow (*Salix glauca*) and bog birch (*Betula glandulosa*). These three plant species are the primary forage of snowshoe hares during winter (Sinclair and Smith 1984; Smith *et al.* 1988).

Hares were studied on four 34-ha experimental grids, each marked by 400 grid points located in a 20 × 20 array: (i) an unmanipulated CONTROL, (ii) FENCE+FOOD, (iii) FENCE and (iv) FOOD. FENCE+FOOD was a 1-km<sup>2</sup> area surrounded by an electric fence to deter terrestrial predators, lynx (*Lynx l. canadensis*), and coyote (*Canis latrans*), and provisioned weekly with pelleted rabbit chow (16% crude protein). Chow was distributed along four cut-lines spaced evenly across the grid. Avian predators, mainly great horned owl (*Bubo virginianus*) and northern goshawk (*Accipiter gentilis*), had unrestricted access to this site. FENCE was a 1-km<sup>2</sup> area surrounded by an electric fence as above. Approximately 12 ha of this grid was covered by monofilament-line in an attempt to deter avian predators; however, much of this was buried by snow in late winter and therefore ineffective. FOOD was a 1-km<sup>2</sup> area where hares were provisioned with pelleted rabbit chow as above. Experimental areas were not replicated for logistical reasons, hence all comparisons are based on the mean response of individuals from each experimental treatment.

### Hare Trapping

Hares were live-trapped (Tomahawk Live Trap Co., Tomahawk, Wisconsin) on 34-ha trapping grids between January and May, 1988–1993. At least 86 traps were placed on four equally spaced rows across the grid. Traps were baited with alfalfa cubes, and hares were trapped over 1–6 days, at 2- to 4-week intervals between January and May. We eartagged (No. 3 monel tags, National Band and Tag Co., Newport, Kentucky), weighed, and determined the sex of all animals trapped. Body mass was determined at each capture, but only the mass recorded at the first capture during a multi-day trapping session was used in this analysis. Differences in female body mass in April between years and treatments were analysed by two-way repeated-measures ANOVA, with the program SYSTAT (Evanston, Illinois). All data passed Bartlett's test for homogeneity of group variance. Multiple-range tests with the overall comparison rate maintained at  $P < 0.05$ , using the Bonferroni procedure, were used to compare body mass in April 1990 with each decline year.

Hare densities were estimated from trapping sessions in April of each year, with mark–recapture estimators for a closed population (Boulanger 1993; Boutin *et al.* 1995). The effective trapping area was estimated to be 60 ha, which includes a buffer of one home range (about 5 ha) around the edge of the trapping grid.

### Hare Survival

During trapping sessions, some hares were fitted with 40-g radio-collars equipped with mortality sensors (Lotech Inc., Newmarket, Ontario). Radio frequencies were monitored daily to determine survivorship of hares. On the death of a radio-collared hare, details of the cause of death and the location of the kill site were recorded (C. Doyle and C. J. Krebs, unpublished data). The proportion of hares surviving was calculated by means of the non-parametric Kaplan–Meier maximum likelihood estimator described by Pollock *et al.* (1989a, 1989b), which allows for the staggered entry of animals during the study and censoring of data for lost radios. Usually 25–35 hares were radio-collared on each grid, but following the decline all hares (as few as four at any one time) were radio-collared on CONTROL and FENCE. For each grid, mean 30-day survival (January–April) in 1990 was compared with corresponding values in each year of the decline (1991–1993) by means of a Z-test statistic with  $\alpha = 0.05$  (Pollock *et al.* 1989a). Comparison of survival curves between treatments were made with the  $k$ -sample test (Lee 1992).

## Results

### Hare Density

The effects of each experimental treatment on changes in hare density are discussed in detail by Krebs *et al.* (1992). On CONTROL, the population peak occurred in 1989 and 1990 with spring hare densities of 1.25 and 1.18 hares  $\text{ha}^{-1}$ , respectively. During the three years of decline (1991–1993), spring densities were 0.93, 0.23 and 0.07 hares  $\text{ha}^{-1}$ , respectively. By comparison, the peak years inside FENCE were 1990 (1.57 hares  $\text{ha}^{-1}$ ) and 1991 (1.45 hares  $\text{ha}^{-1}$ ), and densities dropped to 0.17 hares  $\text{ha}^{-1}$  by 1993. Spring densities on the FOOD and FENCE+FOOD grids were highest in 1990 and 1991 (5–6 hares  $\text{ha}^{-1}$ ). Numbers dropped rapidly on FOOD to 0.88 and 0.20 hares  $\text{ha}^{-1}$  in 1992 and 1993, respectively. On FENCE+FOOD, numbers declined more gradually to 3.97 hares  $\text{ha}^{-1}$  in 1992 and 1.13 hares  $\text{ha}^{-1}$  in 1993.

### Body Mass

Body mass of female hares generally decreased throughout the winter and then increased rapidly after conception in mid-April (Fig. 3), except on CONTROL after 1990 and FOOD after 1991. A two-way repeated-measures ANOVA indicated a significant difference between experimental treatments ( $F = 10.47$ , d.f. = 3,19,  $P < 0.001$ ) and between years ( $F = 2.665$ , d.f. = 4,76,  $P = 0.039$ ); the interaction term was not significant ( $F = 1.576$ , d.f. = 12,76,  $P = 0.117$ ). On CONTROL, female hares were significantly lighter in each winter during the decline than at the peak, and weighed less than 1400 g at the end of winter in 1991, 1992 and 1993. On FENCE grid, body mass did not decline, and values were consistently between 1500 and 1600 g. On FENCE+FOOD, body mass was about 1600 g in all years. On FOOD, body mass was similar to that on CONTROL during the peak; during the decline body mass remained

above 1400 g, but dropped to about 1350 g in spring 1993. Significant differences in spring body mass between the population peak and each year of the decline are shown in Table 1.

#### Winter Survival

Estimates of 30-day survival in winter (January–April) were highest on FENCE, FOOD and FENCE+FOOD grids in 1989 and 1990, and were somewhat lower on CONTROL, particularly in 1989 (Fig. 4). In 1991, the first year of the decline, survival was highest on FENCE+FOOD (0.92), followed by FOOD (0.86), FENCE (0.76) and then CONTROL (0.64). Comparison of all four treatments indicated that survival of hares was not significantly different compared over all five years (*k*-test,  $P > 0.05$ ); however, there were significant differences between experimental grids within each year (Fig. 4). In 1992, survival on FOOD and CONTROL was lower than that on FENCE and FENCE+FOOD. In 1993, survival on FENCE+FOOD decreased significantly, but was similar to that on the other treatments (about 0.8). Differences between 1990 and each year of the decline are indicated in Table 1.

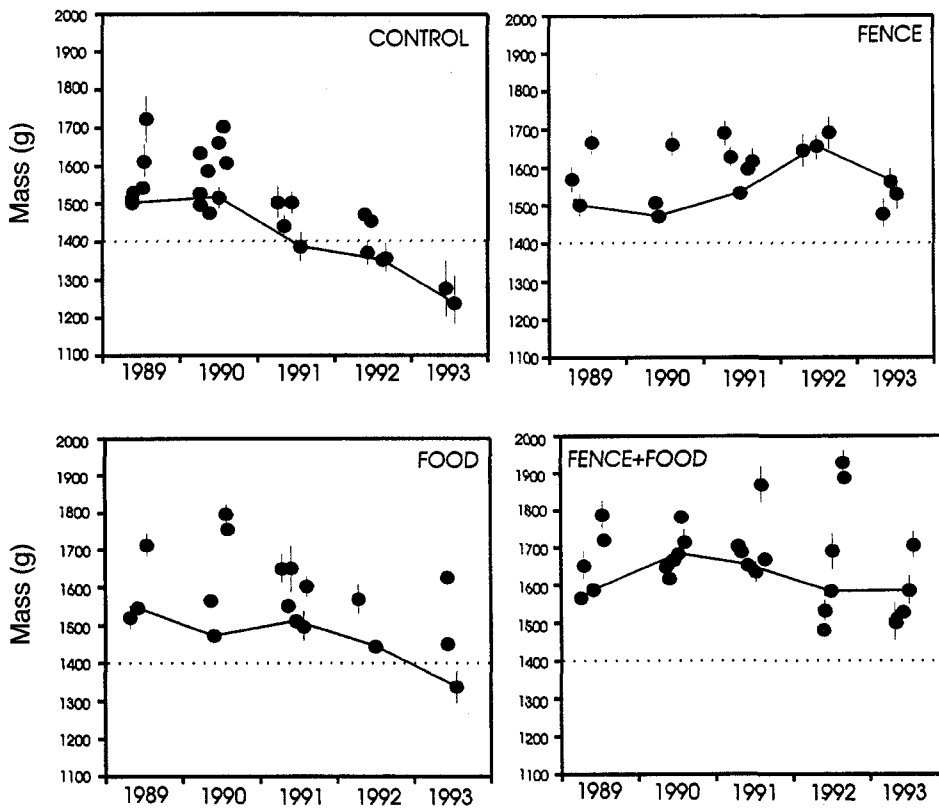


Fig. 3. Mean body mass of female hares during January–May 1989–1993 on CONTROL, FENCE, FOOD and FENCE+FOOD areas at Kluane, Yukon. Sample size for each mean value varied from 3 to 130 individuals depending on the year. Error ( $\pm 1$  s.e.) is less than the size of the symbol unless otherwise indicated. The solid line joins estimates of mean body mass in early April of each year. The dotted line at 1400 g is a reference for comparison between treatments.

*Does the Evidence Support the Predation-sensitive Foraging Hypothesis?*

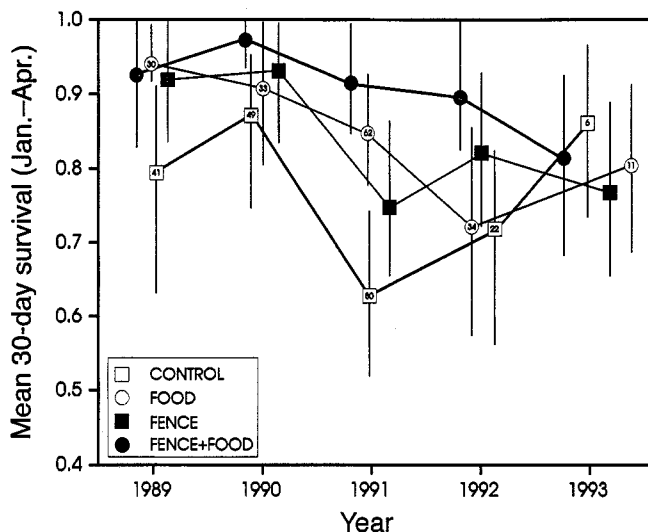
The observed changes in body mass at the end of winter (Fig. 3) and winter survival (Fig. 4) during the hare decline, relative to the population peak, are compared with predictions of the condition constraint (CC), predator-avoidance constraint (PAC) and predation-sensitive foraging (PSF) hypotheses in Table 1. On CONTROL, the reduction in condition and survival during the hare decline supports the PSF hypothesis. However, in 1993, survival improved while body mass continued to decline, a result consistent with the PAC hypothesis. On FOOD grid, the results supported the CC hypothesis in 1992 and the PSF hypothesis in 1993, suggesting that increased predation risk restricted access to food in the third year of the population decline. Even though *ad libitum* supplemental food was available, survival increased and mass declined between 1992 and 1993, suggesting that hares adopted a strategy of minimising predation risk.

On FENCE and FENCE+FOOD treatments, body mass remained high even though survival decreased during the decline. These results supported the CC hypothesis. The observed decrease in survival inside the fenced areas may be due to increased activity of avian predators following the hare decline outside the fences (Hik 1994). Hares may not have adopted predation-sensitive foraging behaviours inside the fences if avian predators are more difficult to detect than

**Table 1. Predictions and hypotheses supported**

Observed changes in condition (body mass) and survival (+, conditions during or similar to the population peak; -, significantly less than at the population peak,  $P < 0.05$ ) on CONTROL, FENCE, FOOD and FENCE+FOOD grids during the snowshoe-hare decline (1991–1993), relative to the last peak year (1990). The hypothesis supported on each experimental grid is indicated: CC, condition constraint hypothesis; PAC, predator avoidance constraint hypothesis; PSF, predation-sensitive foraging hypothesis

Treatment	Year	Condition (body mass)	Survival	Hypothesis supported
CONTROL	1989	+	+	
	1990	+	+	
	1991	-	-	PSF
	1992	-	-	PSF
	1993	-	+	PAC
FENCE	1989	+	+	
	1990	+	+	
	1991	+	-	CC
	1992	+	-	CC
	1993	+	-	CC
FOOD	1989	+	+	
	1990	+	+	
	1991	+	+	
	1992	+	-	CC
	1993	-	-	PSF
FENCE+FOOD	1989	+	+	
	1990	+	+	
	1991	+	+	
	1992	+	+	
	1993	+	-	CC



**Fig. 4.** Mean 30-day survival ( $\pm$  95% confidence interval) in winter (January–April) of hares on CONTROL, FENCE, FOOD and FENCE+FOOD areas at Kluane, Yukon, 1989–1993. The number of radio-collared hares monitored during each sampling period is also indicated.

terrestrial predators, as demonstrated by Jedrzejewski *et al.* (1993) for a population of voles. In addition, hares may have spent more time foraging where supplemental food was not provided. Differences in hare densities among the treatments may have had some influence on the results, but these effects were probably small. Although higher density may result in lower survival and poorer condition because of competition among hares for food or space (Sinclair 1986; Ferron 1993), the observed results were in the opposite direction.

Overall, the results suggest that, where predation risk is reduced (in this case by constructing fences) and whether supplemental food is provided or not, hares adopted a foraging strategy that allowed them to maintain condition (and hence fecundity) even though survivorship may have decreased (i.e. FENCE and FENCE+FOOD). Where predation risk was higher hares initially adopted a strategy to maintain condition (FOOD grid in 1992), but as risk increased both condition and survival declined, a result consistent with the predictions of the PSF hypothesis (CONTROL in 1991–1992, and FOOD in 1993). On CONTROL there was a further indication that high levels of predation risk may lead to a continuing decline in condition even though survival increased (1993), a result consistent with the PAC hypothesis.

## Discussion

### *Consequences of Predator-sensitive Foraging Behaviour*

#### *Decreased body mass*

Behavioural responses of snowshoe hares to increased risk of predation include increased use of safer, closed-forest habitat poor in food resources (Hik 1994). Another possible strategy to increase survival is to reduce time spent foraging. However, snowshoe hares have resting metabolic reserves of only 2–4 days in winter and so must forage repeatedly on a short-term basis in order to maintain body mass (Whittaker and Thomas 1983). In either case, reduced foraging effort in response to increased predation risk will lead to a loss of body mass.

According to several models, the energy reserves available to an individual will influence their foraging decisions (see Ludwig and Rowe 1990; Clark 1993, 1994; Houston *et al.* 1993). Saarikko (1992) observed that the response of shrews (*Sorex araneus*) to the presence of a potential predator (weasel) was positively correlated with body mass. Under risk of predation large shrews were able to decrease foraging activity (at the cost of mass loss), but smaller individuals with lower energy reserves could not. For snowshoe hares, there is a suggestion that provisioning with supplemental food may have allowed hares to maintain condition without



increasing risk of predation: survival and condition of hares on the FOOD grid was higher than that on CONTROL during the first and second years of decline.

The body mass of hares on the CONTROL area decreased during the population decline. Here, hares increased use of closed habitat and the proportion of poor-quality *Picea* browse in their diet (Hik 1994). Increased use of spruce browse may have contributed, in part, to observed declines in body mass: captive hares were unable to maintain mass on a diet of *Picea* twigs, and could just maintain mass on a diet of *Salix* twigs (A. Rogers and A. R. E. Sinclair, unpublished data). In an earlier study, Krebs *et al.* (1986b) found that extra natural food supplied to snowshoe hares during a population decline prevented loss of body mass, but did not lead to increased survival. This is similar to the pattern observed on the FOOD grid in the present study. Similarly, on FENCE grid, where predation risk was reduced and adequate food was available (but no supplemental food provided), body mass did not decline, suggesting that lower risk of predation allowed hares to forage for longer, or to continue to use higher-quality, but riskier, open habitats.

The effects of predators on body mass of snowshoe hares are different from those reported by Desy and Batzli (1989) for prairie voles (*Microtus ochrogaster*). They did not observe any differences in body mass of voles protected from predators in small field enclosures compared with animals where predators were present; however, adult survival did increase significantly in the absence of predators. The absence of any effect of predators on body mass of voles may be due to the smaller scale and shorter period over which these experiments were conducted. It is also possible that predation risk was not sufficiently high to have a significant effect on foraging behaviour of voles. However, even if predators do not influence body mass of prey species, they may still have a negative effect on other demographic characters.

#### *Decreased female reproduction*

Keith and Windberg (1978) and Cary and Keith (1979) showed that changes in body weight of female snowshoe hares during winter are positively correlated with litter size and pregnancy rate in summer: when winter loss of body mass is high, fecundity is low. They observed that reproduction remained low for at least three years following a hare peak. Their interpretation of these results is that poor winter nutrition during the population decline caused a reproductive decline. Body mass at the end of winter was lowest during the population decline, and this reduction may result in smaller litters. These results are not unexpected because, in general, ovulation in mammals is regulated indirectly by female energy reserves (Bronson and Manning 1991). However, poor female condition does not appear to affect all litter groups equally since the size of the first litter remains fairly constant, but the size of subsequent litters declines significantly (Keith and Windberg 1978; Keith 1990; Royama 1992).

Similarly, hares in poor condition at Kluane appeared unable to maintain reproductive output during the cyclic decline. The mean total number of leverets born to hares on CONTROL in 1989, 1990, 1991 and 1992 was 13.7, 13.7, 7.8 and 3.3, respectively (see Fig. 1f). On FENCE+FOOD the mean total number of leverets born in those same years was 14.0, 15.1, 16.3 and 17.1. These litter sizes are pooled means of each of the three litters from pregnant females placed in maternity cages 2–3 days prior to parturition (see O'Donoghue and Krebs 1992 for description of methods), on CONTROL grid and adjacent areas (1989–1992), FOOD (1989–1990) and FENCE+FOOD (1991–1992) grids (O'Donoghue and Krebs 1992; C. J. Krebs *et al.*, unpublished data). I am assuming that reproduction on FENCE+FOOD was similar to that on FOOD in 1989 and 1990 (litter size was not measured on FENCE or FOOD during the population decline). On CONTROL, the size of the first litter was similar in all four years in 1989 and 1990, but no third litter was produced in 1991. In 1992 neither second nor third litters were produced. Three litters were produced in all years on FENCE+FOOD.

Since winter food does not appear to be absolutely limiting for snowshoe hares at Kluane (Smith *et al.* 1988; Hik 1994), reduced fecundity observed during the population decline may be a consequence of foraging under high risk of predation. The mechanisms by which increased

predation risk may lead to decreased reproduction have not been studied in detail, but behavioural responses to increased risk of predation result in reduced growth and reproduction in grey treefrogs (Skelly 1992), mayflies (Peckarsky *et al.* 1993) and bluegill sunfish (Werner and Hall 1988). There is also direct evidence for the effects of predation risk on reproduction in voles. Ylönen *et al.* (1992) found that the odour of small mustelids delayed sexual maturation of young voles (*Clethrionomys* spp.) and suppressed female reproduction under laboratory conditions. More recently, Ronkainen and Ylönen (1994) showed that female bank voles (*C. glareolus*) exposed to mustelid odours decreased their activity and actively avoided copulations. Korpimäki *et al.* (1994) and Norrdahl and Korpimäki (1995) conducted a field experiment where reproduction of voles was measured at different weasel densities, and their results suggest that the presence or scent of small mustelids decreases the reproductive rate of voles. In contrast, Desy and Batzli (1989) found that protection from predators did not affect reproduction of *Microtus ochrogaster* in small field enclosures.

#### *Increased physiological stress*

Poor body condition is often associated with increased physiological stress (Christian 1980). 'Stress' is difficult to measure in the field, but several studies have attempted to do this for snowshoe hares. Studies in Alaska and Alberta (Feist 1980; Keith 1990) found that adrenal gland weight (a rough index of adrenocortical hypertrophy and cortical hormone production) and adrenal activity was not significantly related to population density or levels of nutrition. The results of recent experiments to examine the ability of hares to recover from short-term stress in winter suggested that the pituitary–adrenocortical feedback system in hares from a declining population in 1991 was operating normally, but also that hares in poorer condition had higher levels of free-cortisol (Boonstra and Singleton 1993). In 1992, when hares on the CONTROL area were in even poorer condition, the deleterious effects of experimentally imposed short-term stress were even more pronounced (R. Boonstra, D. Hik and G. Singleton, unpublished data). However, by spring 1994 hares appeared to be able to cope with this experimental challenge to their endocrine system again. It remains to be seen whether the cumulative effects of higher stress (chronic exposure to high levels of free-cortisol) have long-term effects on the behaviour, growth and reproductive performance of hares (Boonstra and Singleton 1993; Hik 1994).

#### *Maternal effects*

Periodic, multi-annual fluctuations (cycles) in abundance are characteristic of a number of small boreal mammals including voles and snowshoe hares (Elton 1924; Finerty 1980; Hansson 1984; Keith 1990; Batzli 1992). Population declines are characterised by low body weights and reduced reproductive effort (e.g. shortened breeding season), which have been attributed to food limitation, predation, changes in spacing behaviour and a variety of 'multi-factor' interactions. However, no common cause for these cycles has yet been discovered. Several lines of evidence suggest that the sublethal effects of predation risk on behaviour and physiology may play a large role in determining the decline and eventual recovery of cyclic populations.

Oksanen and Lundberg (1995) have shown that, theoretically, as predation risk increases, animals may still be able to maximise their fitness by opting for submaximal reproductive effort and adopting behaviour intermediate between time minimisation and energy maximisation. Small changes in the availability of food or cover, or in the density of predators, may result in a shift from one strategy to another (Oksanen and Lundberg 1995). Nonetheless, adaptive changes in foraging behaviour and reproductive effort in response to increased risk of predation do not necessarily imply that populations will be able to increase rapidly once predation risk is reduced. The cumulative effects of behavioural and physiological adaptations to avoid predators may not be easily reversible, and there is mounting evidence that long-term detrimental maternal effects may actually prolong the cyclic low-phase.

Elevated endocrine stress may lead to suppression of hare reproduction over several years through maternal effects. Maternal effects refer to the influence of environmental conditions experienced by mothers on the growth, survival and fitness of offspring. The importance of maternal effects in regulating populations has recently been considered for insect (Rossiter 1991; Peckarsky *et al.* 1993) and mammal (Hansson 1984; Albon *et al.* 1987; Mech *et al.* 1991; Mihok and Boonstra 1992) populations. Christian (1980) reviewed the evidence that the environment of cyclic species at peak densities may have long-term negative consequences on demography through impaired reproduction mediated by endocrine responses to elevated stress. Several recent experimental results are consistent with this hypothesis. Under laboratory conditions, Mihok and Boonstra (1992) showed that the prior experience of decline-phase female meadow voles (*Microtus pennsylvanicus*) had long-term detrimental consequences for the performance of the next two generations. Laboratory studies have shown that a variety of pre- and postnatal stresses can have long-lasting effects and impair reproductive performance for one or two generations (Pollard 1986; Boonstra 1994). Similarly, in a field study, Mech *et al.* (1991) showed that the mass and survival of fawns of white-tailed deer (*Odocoileus virginianus*) were directly correlated with maternal nutrition during gestation.

In several cases these maternal effects can be attributed to increased risk of predation. Ylönen *et al.* (1992) reported that female red-backed voles (*Clethrionomys rutilus*) exposed to predator odour at the beginning of pregnancy had foetuses that were about 25% lighter than those of control females, suggesting that stress associated with high predation risk may influence the survival of offspring, and that the consequences of poor condition in one breeding season may carry over to the next generation. Heikkilä *et al.* (1993) demonstrated that predation risk from mustelids resulted in reduced growth and lowered rate of maturation of juvenile *C. rutilus*.

## Conclusions

The proximate cause of mortality of snowshoe hares is predation, and this mortality may be sufficient to generate the population decline. However, sublethal effects associated with predation-sensitive foraging appear to initiate a cascade of behavioural and physiological responses that may lead to a further decline during the low-phase of the cycle. Hares that survive the initial decline or are born and recruited during this time live in an environment of high predation risk. If they adopt anti-predator behaviours that reduce foraging success, this may lead to decreased body mass and fecundity even though food is abundant. The adverse consequences of poor condition may persist for more than one year or generation. May (1974, 1981) predicted that a lag-time of 2–3 years for population recovery of hare populations could generate the observed 8–11-year cycle. Maternal effects lasting one generation (thereby causing a reproductive lag) could potentially complement the delayed density-dependent predation response demonstrated by Trostel *et al.* (1987).

The results of experiments reported here suggest that, as predation risk increased, hares attempted to maintain condition (thus maximising reproduction) rather than maximising survivorship. There is clearly a balance between these two behaviours as implied by the PSF hypothesis. The results on the CONTROL grid also suggest that under very high levels of predation risk (i.e. 1993), hares favoured survival over condition, a result consistent with the predictions of the PAC hypothesis. Future modelling and field studies should investigate whether maternal condition has an influence on the behaviour, survival and reproductive success of hares in order to establish the impact of predation risk and associated behavioural and physiological responses on the population dynamics of hares.

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## References

- Abrams, P. A. (1989). Decreasing functional responses as a result of adaptive consumer behavior. *Evolutionary Ecology* **3**, 95–114.
- Abrams, P. A. (1990). The evolution of anti-predator traits in response to evolutionary change in predators. *Oikos* **59**, 147–56.
- Abrams, P. A. (1992a). Adaptive foraging by predators as a cause of predator-prey cycles. *Evolutionary Ecology* **6**, 56–72.
- Abrams, P. A. (1992b). Why don't predators have positive effects on prey populations? *Evolutionary Ecology* **6**, 449–57.
- Abrams, P. A. (1992c). Predators that benefit prey and prey that harm predators: unusual effects of interacting foraging adaptations. *American Naturalist* **140**, 573–600.
- Abrams, P. A. (1993). Why predation rate should not be proportional to predator density. *Ecology* **74**, 726–33.
- Albon, S. D., Clutton-Brock, T. H., and Guinness, F. E. (1987). Early development and population dynamics in red deer. II. Density-independent effects and cohort variation. *Journal of Animal Ecology* **56**, 69–81.
- Anderson, P. K. (1986). Foraging range in mice and voles: the role of risk. *Canadian Journal of Zoology* **64**, 2645–53.
- Batzli, G. O. (1992). Dynamics of small mammal populations: a review. In 'Wildlife 2001: Populations'. (Eds D. R. McCullough and R. E. Barrett.) pp. 831–50. (Elsevier: London.)
- Boonstra, R. (1994). Population cycles in microtines: the senescence hypothesis. *Evolutionary Ecology* **8**, 196–219.
- Boonstra, R., and Singleton, G. R. (1993). Population declines in the snowshoe hare and the role of stress. *General and Comparative Endocrinology* **91**, 126–43.
- Boulanger, J. (1993). Evaluation of capture–recapture estimators using a cyclic snowshoe hare population. M.Sc. Thesis, University of British Columbia, Vancouver.
- Boutin, S. (1995). Testing predator–prey theory by studying fluctuating populations of small mammals. *Wildlife Research*, **22**, 89–100.
- Boutin, S., Krebs, C. J., Sinclair, A. R. E., and Smith, J. N. M. (1986). Proximate causes of losses in a snowshoe hare population. *Canadian Journal of Zoology* **64**, 606–10.
- 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. S., 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*, in press.
- Bronson, F. H., and Manning, J. M. (1991). The energetic regulation of ovulation: a realistic role for body fat? *Biology of Reproduction* **44**, 945–50.
- Brown, J. S. (1989). Desert rodent community structure: a test of four mechanisms of coexistence. *Ecological Monographs* **59**, 1–20.
- Brown, J. S. (1992). Patch use under predation risk: I. Models and predictions. *Annales Zoologici Fennici* **29**, 301–9.

- Brown, J. S., Morgan, R. A., and Dow, B. D. (1992). Patch use under predation risk: II. A test with fox squirrels, *Sciurus niger*. *Annales Zoologici Fennici* **29**, 311–18.
- Cary, J. R., and Keith, L. B. (1979). Reproductive change in the 10-year cycle of snowshoe hares. *Canadian Journal of Zoology* **57**, 375–90.
- Cassini, M. H., and Galante, M. L. (1992). Foraging under predation risk in the wild guinea pig: the effect of vegetation height on habitat utilization. *Annales Zoologici Fennici* **29**, 285–90.
- Christian, J. J. (1980). Endocrine factors in population regulation. In 'Biosocial Mechanisms of Population Regulation'. (Eds M. N. Cohen, R. S. Malpass and H. G. Klein.) pp. 55–115. (Yale University Press: New Haven, Connecticut.)
- Clark, C. W. (1993). Dynamic models of behaviour: an extension of life history theory. *Trends in Ecology and Evolution* **8**, 205–9.
- Clark, C. W. (1994). Flexible antipredation strategies. *Behavioral Ecology* **5**, 159–70.
- Desy, D. A., and Batzli, G. O. (1989). Effects of food availability and predation on prairie vole demography: a field experiment. *Ecology* **70**, 411–21.
- Dickman, C. R. (1992). Predation and habitat shifts in the house mouse, *Mus domesticus*. *Ecology* **73**, 313–22.
- Elton, C. S. (1924). Periodic fluctuations in the numbers of animals: their causes and effects. *Journal of Experimental Biology* **2**, 119–63.
- Feist, D. D. (1980). Corticosteroid release by adrenal tissue of Alaska snowshoe hares in a year of population decline. *Journal of Mammalogy* **61**, 134–6.
- Ferron, J. (1993). How do population density and food supply influence social behaviour in the snowshoe hare (*Lepus americanus*)? *Canadian Journal of Zoology* **71**, 1084–9.
- Finerty, J. P. (1980). 'The Population Ecology of Cycles in Small Mammals.' (Yale University Press: New Haven, Connecticut.)
- FitzGibbon, C. D., and Lazarus, J. (1995). Anti-predator behaviour of Serengeti ungulates: individual differences and population consequences. In 'Serengeti II: Research, Management and Conservation of an Ecosystem'. (Eds A. R. E. Sinclair and P. Arcese.) (University of Chicago Press: Chicago.) (In press.)
- Gilliam, J. F., and Fraser, D. F. (1987). Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology* **68**, 1856–62.
- Hansson, L. (1984). Composition of cyclic and non-cyclic vole populations: on causes of variation in individual quality among *Clethrionomys glareolus* in Sweden. *Oecologia* **63**, 199–206.
- Hassell, M. P., and May, R. M. (1985). From individual behaviour to population dynamics. In 'Behavioural Ecology: Ecological Consequences of Adaptive Behaviour'. (Eds R. M. Sibly and R. H. Smith.) pp. 3–32. (Blackwell: Oxford.)
- Heikkilä, J., Kaarsalo, K., Mustonen, O., and Pekkarinen, P. (1993). Influence of predation risk on early development and maturation in three species of *Clethrionomys* voles. *Annales Zoologici Fennici* **30**, 153–61.
- Hik, D. S. (1994). Predation risk and the snowshoe hare cycle. Ph.D. Thesis, University of British Columbia, Vancouver.
- Holmes, W. G. (1984). Predation risk and foraging behavior of the hoary marmot in Alaska. *Behavioral Ecology and Sociobiology* **15**, 293–301.
- Houston, A. I., McNamara, J. M., and Hutchinson, J. M. C. (1993). General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society of London, Series B* **341**, 375–97.
- Hughes, J. J., Ward, D., and Perrin, M. R. (1994). The effects of predation risk and competition on habitat selection and activity of gerbils in the Namib Desert. *Ecology* **75**, 1397–405.
- Ives, A. R., and Dobson, A. P. (1987). Antipredator behaviour and the population dynamics of simple predator-prey systems. *American Naturalist* **130**, 431–47.
- Jedrzejewski, W., Leszek, R., and Jedrzejewski, B. (1993). Responses of bank voles to odours of seven species of predators: experimental data and their relevance to natural predator-vole relationships. *Oikos* **68**, 251–7.
- Keith, L. B. (1990). Dynamics of snowshoe hare populations. In 'Current Mammalogy'. (Ed. H. H. Genoways.) pp. 119–95. (Plenum Press: New York.)
- Keith, L. B., and Windberg, L. A. (1978). A demographic analysis of the snowshoe hare cycle. *Wildlife Monographs* **58**, 1–70.
- Keith, L. B., Cary, J. R., Rongstad, O. J., and Brittingham, M. C. (1984). Demography and ecology of a declining snowshoe hare population. *Wildlife Monographs* **90**, 1–43.

- Kotler, B. P. (1984). Risk of predation and the structure of desert rodent communities. *Ecology* **65**, 689–701.
- Kotler, B. P., Blaustein, L., and Brown, J. S. (1992). Predation facilitation: the combined effects of snakes and owls on the foraging behavior of gerbils. *Annales Zoologici Fennici* **29**, 199–206.
- Korpimäki, E., Norrdahl, K., and Valkama, J. (1994). Reproductive investment under fluctuating predation risk: microtine rodents and small mustelids. *Evolutionary Ecology* **8**, 357–68.
- Krebs, C. J., Gilbert, B. S., Boutin, S., Sinclair, A. R. E., and Smith, J. N. M. (1986a). Population biology of snowshoe hares. I. Demography of food-supplemented populations in the southern Yukon, 1976–1984. *Journal of Animal Ecology* **55**, 963–82.
- Krebs, C. J., Boutin, S., and Gilbert, B. S. (1986b). A natural feeding experiment on a declining snowshoe hare population. *Oecologia* **70**, 194–7.
- Krebs, C. J., Boonstra, R., Boutin, S., Dale, M. R. T., Hannon, S., Martin, K., Sinclair, A. R. E., Smith, J. N. M., and Turkington, R. (1992). What drives the snowshoe hare cycle in Canada's Yukon? In 'Wildlife 2001: Populations'. (Eds D. R. McCullough and R. E. Barrett.) pp. 886–96. (Elsevier: London.)
- Lee, E. T. (1992). 'Statistical Methods for Survival Data Analysis.' (Wiley and Sons: New York.)
- Lima, S. L., and Dill, L. M. (1990). Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**, 619–40.
- Ludwig, D., and Rowe, L. (1990). Life-history strategies for energy gain and predator avoidance under time constraints. *American Naturalist* **135**, 686–707.
- Matsuda, H., and Abrams, P. A. (1994). Timid consumers: self-extinction due to adaptive change in foraging and anti-predator effort. *Theoretical Population Biology* **45**, 76–91.
- May, R. M. (1974). 'Stability and Complexity in Model Ecosystems.' (Princeton University Press: Princeton, New Jersey.)
- May, R. M. (1981). Models for single populations. In 'Theoretical Ecology: Principles and Applications'. 2nd Edn. (Ed. R. M. May.) pp. 5–29. (Blackwell: London.)
- McNamara, J. M., and Houston, A. I. (1987). Starvation and predation as factors limiting population size. *Ecology* **68**, 1515–19.
- McNamara, J. M., and Houston, A. I. (1990). Starvation and predation in a patchy environment. In 'Living in a Patchy Environment'. (Eds B. Shorrocks and I. Swingland.) pp. 23–43. (Oxford University Press: Oxford.)
- Mech, L. D., Nelson, M. E., and McRoberts, R. E. (1991). Effects of maternal and grandmaternal nutrition on deer mass and vulnerability to wolf predation. *Journal of Mammalogy* **72**, 146–51.
- Mihok, S., and Boonstra, R. (1992). Breeding performance in captivity of meadow voles (*Microtus pennsylvanicus*) from decline and increase-phase populations. *Canadian Journal of Zoology* **70**, 1561–6.
- Norrdahl, K., and Korpimäki, E. (1995). Does predation risk constrain maturation in cyclic vole populations? *Oikos*, in press.
- O'Donoghue, M., and Krebs, C. J. (1992). Effects of supplemental food on snowshoe hare reproduction and juvenile growth at a cyclic population peak. *Journal of Animal Ecology* **61**, 631–41.
- Oksanen, L., and Lundberg, P. (1995). Optimization of reproductive effort and foraging time in mammals: the influence of resource level and predation risk. *Evolutionary Ecology* **9**, 45–56.
- Peckarsky, B. L., Cowan, C. A., Penton, M. A., and Anderson, C. (1993). Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. *Ecology* **74**, 1836–46.
- Pollard, I. (1986). Prenatal stress effects over two generations in rats. *Journal of Endocrinology* **109**, 239–44.
- Pollock, K. H., Winterstein, S. R., Bunck, C. M., and Curtis, P. D. (1989a). Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management* **53**, 7–15.
- Pollock, K. H., Winterstein, S. R., and Conroy, M. J. (1989b). Estimation and analysis of survival distributions for radio-tagged animals. *Biometrics* **45**, 99–109.
- Ronkainen, H., and Ylönen, H. (1994). Behaviour of cyclic bank voles under risk of mustelid predation: do females avoid copulations? *Oecologia* **97**, 377–81.
- Rossiter, M. C. (1991). Environmentally-based maternal effects: a hidden force in insect population dynamics? *Oecologia* **87**, 288–94.
- Rowe, L., and Ludwig, D. (1991). Size and timing of metamorphosis in complex life cycles: time constraints and variation. *Ecology* **72**, 413–27.
- Royama, T. (1992). 'Analytical Population Dynamics.' (Chapman and Hall: London.)

- Saarikko, J. (1992). Risk of predation and foraging activity in shrews. *Annales Zoologici Fennici* **29**, 291–9.
- Sinclair, A. R. E. (1986). Testing multifactor causes of population limitation: an illustration using snowshoe hares. *Oikos* **47**, 360–4.
- Sinclair, A. R. E., and Smith, J. N. M. (1984). Do plant secondary compounds determine feeding preferences of snowshoe hares? *Oecologia* **61**, 403–10.
- Sinclair, A. R. E., Krebs, C. J., Smith, J. N. M., and Boutin, S. (1988). Population biology of snowshoe hares. III. Nutrition, plant secondary compounds and food limitation. *Journal of Animal Ecology* **57**, 787–806.
- Sinclair, A. R. E., Gosline, J. M., Holdsworth, G., Krebs, C. J., Boutin, S., Smith, J. N. M., Boonstra, R., and Dale, M. (1993). Can the solar cycle and climate synchronize the snowshoe hare cycle in Canada? Evidence from tree rings and ice cores. *American Naturalist* **141**, 173–98.
- Skelly, D. K. (1992). Field evidence for a cost of behavioural antipredator response in a larval amphibian. *Ecology* **73**, 704–8.
- Smith, J. N. M., Krebs, C. J., Sinclair, A. R. E., and Boonstra, R. (1988). Population biology of snowshoe hares. II. Interactions with winter food plants. *Journal of Animal Ecology* **57**, 269–86.
- Trostel, K., Sinclair, A. R. E., Walters, C. J., and Krebs, C. J. (1987). Can predation cause the 10-year hare cycle? *Oecologia* **74**, 185–92.
- Werner, E. E., and Hall, D. J. (1988). Ontogenetic habitat shifts in bluegill: the foraging rate–predation risk trade-off. *Ecology* **69**, 1352–66.
- Whittaker, M. E., and Thomas, V. G. (1983). Seasonal levels of fat and protein reserves of snowshoe hares in Ontario. *Canadian Journal of Zoology* **61**, 1339–45.
- Wolff, J. O. (1980). The role of habitat patchiness in the population dynamics of snowshoe hares. *Ecological Monographs* **50**, 111–30.
- Ylönen, H., Jedrzejewska, B., Jedrzejewski, W., and Heikkilä, J. (1992). Antipredatory behaviour of *Clethrionomys* voles: 'David and Goliath' arms race. *Annales Zoologici Fennici* **29**, 207–16.