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Overwinter mass loss of snowshoe hares in the Yukon: starvation, stress, adaptation or artefact?

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Summary

1. Overwinter mass loss can reduce energetic requirements in mammals (Dehnel's phenomenon). Alternatively, mass loss can result from food limitation or high predation risk.

2. We use data from fertilizer, food-supplementation and predator-exclusion experiments in the Yukon during a population cycle from 1986 to 1996 to test the causes of overwinter mass loss by snowshoe hares (*Lepus americanus*). In all years, some hares on control sites gained mass overwinter. During the increase phase the majority gained mass, but in all other phases the majority lost mass.

3. Snowshoe hares weighing < 1000 g in autumn always gained mass overwinter, as did the majority that weighed 1000–1400 g. Hares weighing > 1800 g in autumn usually lost mass.

4. Snowshoe hares on the predator-exclosure + food site gained mass overwinter in all years. Hares on the food-supplementation sites lost mass during the decline but gained mass in all other phases. Fertilization had little effect on mass dynamics.

5. Snowshoe hares were more likely to lose mass during winters with low survival rates. Snowshoe hares on the predator-exclosure treatments were more likely to gain mass than were hares on control sites.

6. Overwinter mass loss was correlated with maximum snow depth. At equivalent snow depths, hares on food-supplemented areas lost 98 g (± 14·6 SE) less on average than hares on the controls and predator-exclosure treatment.

7. Bone-marrow fat was related to body mass and cause of death. Small hares had the lowest marrow fat. Hares killed by humans had higher marrow fat than those killed by predators; hares that simply died had the lowest marrow fat. Hares on food-supplemented sites had the highest kidney and marrow fat.

8. Overwinter-mass loss for snowshoe hares is explained interactively by winter conditions, food supply, predation risk and autumn mass. Some snowshoe hares lost mass overwinter in all years and on all treatments, suggesting that reducing body mass may facilitate survival, especially in cases where foraging costs are high energetically or increase predation risk.

Key-words: body mass, Dehnel's phenomenon, energetics, food-supplementation, predation risk.

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Introduction

Surviving overwinter in northern areas is challenging for vertebrate herbivores (Boonstra 2004). Winter combines the challenges of cold temperatures, snow, food scarcity and, often, high predation. Winter thus provides a template against which strong natural selection may occur, with only those individuals best able to obtain and to allocate resources surviving to the subsequent breeding season.

Strategies for surviving winter vary with an organism's body size and physiological flexibility. For mammals that weigh < 1 kg, strategies include food caching (e.g. red squirrels, *Tamiasciuris hudsonicus*, pikas, *Ochotona*

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princeps), alteration of fur to obtain greater insulation (Chappell 1980; Steudel, Porter & Sher 1994), and use of microclimate refugia such as subnivean spaces and dens, which are warmer than the ambient temperatures (e.g. lemmings, pikas, weasels) (Chappell 1980). Body-mass changes, with concomitant changes in energetic requirements, are also common. In ground-dwelling sciurids that hibernate, intense hyperphagy to increase body mass is essential for survival. For animals that stay active throughout winter, such as shrews and microtine rodents, reducing body mass to reduce energy requirements and foraging time is a common strategy termed Dehnel's phenomenon (Brown 1973; Iverson & Turner 1974; Heldmaier & Steinlechner 1981; Hansson 1990). For some small mammals, reductions in body mass are linked to photoperiod; they occur even when temperatures are maintained and animals are allowed *ad libitum* food [e.g. hamsters *Phodopus sungorus*, Heldmaier & Steinlechner (1981); meadow voles *Microtus pennsylvanicus*, Dark & Zucker (1986)].

For medium-sized mammals, such as snowshoe hares (*Lepus americanus*, Erxleben, ~1·5 kg), it is not clear whether the mass loss is the adaptive Dehnel's phenomenon or a consequence of environmental conditions. The body-mass dynamics of hares are fundamentally different from those of voles (Aars & Ims 2002): juvenile hares do not stop growing before winter, and when mass loss occurs it is gradual and occurs throughout the winter. Presumably these differences between hares and voles are related to fat storage and metabolism. Snowshoe hares do not undertake hyperphagy, and their fat stores provide only a few days of support prior to starvation (Whittaker & Thomas 1983), so mass loss is likely to involve more than fat stores. Some researchers suggest that mass loss derives from direct food limitation, especially when hare populations are at cyclic peaks or declining (Keith & Windberg 1978; Vaughan & Keith 1981). This pattern would be akin to the mass dynamics of ungulates, which commonly experience food stress overwinter (DelGiudice, Peterson & Samuel 1997; DelGiudice *et al*. 2000) but also undergo seasonal mass fluctuations in the presence of superabundant food (Cowan, Wood & Kitts 1957). Alternatively, predation risk may affect foraging behaviour (Hik 1995; but see Hodges 1999; Hodges & Sinclair 2003) and stress physiology (Boonstra *et al*. 1998), and either of these responses could cause mass loss even in the presence of an adequate food supply. Overwinter mass loss in snowshoe hares is not affected by reproduction, because weaning occurs by the end of September and pregnancies are initiated typically in April in our Yukon study area.

In this paper, we use data from a snowshoe hare cycle in south-western Yukon (see Krebs, Boutin & Boonstra 2001a for a full description of this long-term study and its results), with experimental treatments of fertilization, food-supplementation, terrestrial predator-exclosure and food-supplementation plus predator-exclosure to test the following hypotheses about snowshoe hare mass loss overwinter. (1) Mass loss is an adaptive overwinter strategy to minimize energy needs, irrespective of food supply. In this case, snowshoe hares on all treatments should lose mass overwinter. The amount might be correlated with winter severity. (2) Mass loss results from food limitation. If so, then mass loss should be more prevalent during peak and decline years. Snowshoe hares on fertilized or food-supplemented areas are more likely to maintain mass. Body-fat stores should reflect food availability. (3) Mass loss results from behavioural and physiological responses to predation risk. Mass loss should be most pronounced during periods of highest predation. Hares inside the predator-exclosures should maintain their mass. Body fat should be reduced in animals exposed to higher predation risk. (4) Mass loss is an artefact of measuring mass loss based on populations (mean spring mass – mean autumn mass), which could be affected by differential survival of animals overwinter. Some previous studies have used this metric rather than an analysis of individuals caught both in autumn and in spring.

Methods and materials

STUDY AREA, EXPERIMENTAL TREATMENTS AND SNOWSHOE HARE TRAPPING

We worked on nine study sites near Kluane Lake, south-western Yukon (Krebs *et al*. 2001a). The boreal forest in this region consists of white spruce (*Picea glauca* (Moench) Voss), balsam poplar (*Populus balsamifera* L.) and trembling aspen (*Populus tremuloides* Michx.). To address the influence of winter severity on mass loss of snowshoe hares, we used weather data collected by Environment Canada at the Burwash Airport, about 40 km north of our study sites. Weather variables measured at Burwash are correlated highly with those measured at Haines Junction, 40 km to the south of our study sites. The climate is cold continental, with snow cover from October to late April with depths up to a metre, and with temperatures during February averaging −18 °C (20 years average, 1973–92).

As part of the Kluane Boreal Forest Ecosystem Project (Krebs *et al*. 1995, 2001a), four large-scale experimental treatments were established (Boutin *et al*. 2001). Three control sites were not manipulated. Two 1-km^2 fertilizer sites had 35 : 10 : 5 NPK applied aerially during 1988–94 (fertilizer). Fertilization strongly affected herbaceous vegetation (Turkington *et al*. 2002) and increased the growth rates of shrubs (Krebs *et al*. 2001b). Most herbaceous plants were buried by snow in the winter, and fertilization did not alter substantially the overwinter food supply of hares. Two 35-ha areas had *ad libitum* commercial rabbit chow (16% protein) added to them year-round from 1988 to 1996 (food). Because the chow was broadcast with a fertilizer spreader along 570-m-long feeder rows, all hares on each food-supplemented site had access and interference from black bears (*Ursus americanus* Pallas), grizzly bears (*U. arctos* L.) and moose (*Alces alces* L.) was minimal.

Our final two treatments increased hare survival by excluding predators. One 1-km^2 area was enclosed by chicken-wire and electrical fencing (predator-exclosure) from 1987 to 1996 to exclude terrestrial predators, primarily lynx (*Lynx canadensis* Kerr) and coyotes (*Canis latrans* Say). One 1-km^2 area was fenced from 1988 to 1996 and provided with supplemental rabbit chow (predator-exclosure + food). The fences allowed hares to move in and out. The predator-exclosure + food manipulation was disrupted during winter 1995–96, because a coyote got inside the fence during November 1995 and we stopped food addition in January 1996, as the coyote was still inside.

The fences did not exclude the primary avian predators on hares, great horned owls (*Bubo virginianus* Gmelin) and goshawks (*Accipiter gentilis* L.). Throughout the cycle, more than 85% of hares on all sites were killed by predators, primarily terrestrial predators; hares on the fenced sites had substantially higher survival than hares on unfenced sites (Krebs *et al.* 1995; Hodges, Krebs & Sinclair 1999; Hodges *et al.* 2001). Furthermore, territoriality prevented high raptor densities on the fenced sites (Rohner & Krebs 1998), so fenced and unfenced hares faced similar raptor predation. The fences also excluded bears and moose, but these species had low densities in the study area so this potential reduction in competition for browse was negligible (Krebs *et al.* 2001a).

Complete details of the impacts of these treatments on snowshoe hare demography and on other species are in Krebs *et al.* (2001a). All treatments resulted in increased hare densities, but this difference from controls was slight on the fertilizer treatments (Hodges *et al.* 2001). There was a 30-fold variation in autumn hare densities among study sites and years (< 0·3–8·0 hares/ha), but there is no evidence of negative density dependence and there was no effect of density on mass change ($r^2 = 0{\cdot}01$). Study sites differed in the availability of the main overwinter foods, white spruce, bog birch (*Betula glandulosa* Michx.) and grey willow (*Salix glauca* L.), but the supply of birch and willow alone was amply sufficient for snowshoe hares in all winters on all sites (Krebs *et al.* 2001b).

The predator-exclosure and predator-exclosure + food sites were not replicated, owing to the high costs of maintaining 8 km of electric fencing on a nearly daily basis for a decade (Boutin *et al.* 2001). Ecologists are caught increasingly in the tension between the manipulations necessary to understand large-scale ecological processes and the impossibility of replicating large manipulations (Carpenter *et al.* 1995; Oksanen 2001, 2004). Our control sites sampled a wide range of natural variation within our study area, increasing the likelihood that differences on the treatments were due to our manipulations rather than to underlying natural variation.

Snowshoe hares were live-trapped during autumn (primarily October) and spring (primarily March) from 1986 to 1996, encompassing one population cycle (Fig. 1). The 40-ha trapping sites contained 86 Tomahawk live traps baited with alfalfa cubes; rabbit chow was also used on food-supplemented sites. Trapping was conducted with the approval of the University of British Columbia's Animal Care Committee. Hares increased from 1986 to 1988, were at peak densities in 1989 and 1990, and declined from 1991 to 1993. They remained at low numbers from 1993 to 1995 and then began another increase phase.

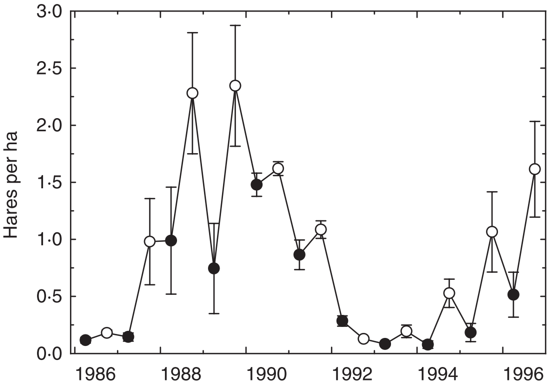

Fig. 1. Average density of snowshoe hares from three control sites during a population cycle in south-western Yukon 1986–96. Autumn ○, spring ●. Values are means ± 1 SE.

Individual snowshoe hares were ear-tagged and weighed to the nearest 10 g with a Pesola spring scale. Snowshoe hares often lose some mass during trapping, especially over multiple nights (DeGroot 1996). To minimize this problem, we used masses from the first capture of each hare in each session. We examined mass change based on individuals that were trapped both in autumn and in the subsequent spring. We compared these values to mass change estimated at the population level, i.e. by calculating mass of all hares caught in autumn vs. all hares caught in spring (Keith & Windberg 1978). Many hares caught in autumn were not recaptured in the spring; our telemetry records suggest that predation rather than emigration is the major cause of this disappearance (Hodges *et al.* 2001). The information we have on dispersal does not indicate that dispersers are a biased subset of the hare population. Radio-collared hares might have been somewhat affected by the 30–40 g mass of their collars, but the majority of the hares used in our mass change analyses were not collared.

Adult snowshoe hares lose mass overwinter in a gradual manner from November onwards, reaching a minimum overwinter mass in late March to mid-April (Krebs, unpublished data, 1977–84). This pattern makes it possible to judge overwinter changes in mass by weighing hares in early winter and again in late winter. There are, however, measurement errors in obtaining hare weights. Our spring scales were checked continuously for accuracy and we are confident that weights obtained were within 10 g. A more serious error arises from stomach contents. Hares trapped on two successive nights differed in mass by 54 g on average ($n = 835$,

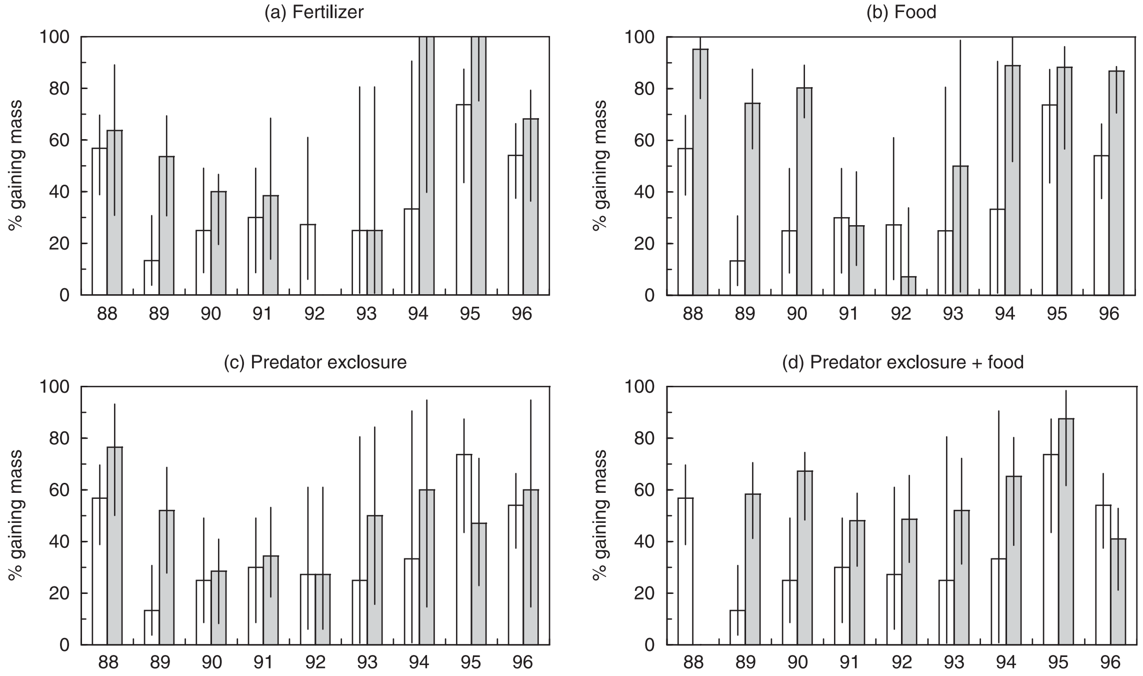

Fig. 2. The percentage of snowshoe hares gaining mass overwinter. The years on the *x*-axis represent spring (e.g. 89 indicates overwinter mass change from 1988 to 1989). Sample sizes per winter are control: 44, 50, 20, 20, 11, 4, 3, 19, 50; fertilizer: 11, 28, 50, 13, 3, 4, 4, 20, 22; food: 21, 35, 66, 26, 14, 2, 9, 17, 83; predator-exclosure: 17, 25, 28, 32, 11, 8, 5, 17, 5; predator-exclosure + food: 0 (treatment not started yet), 48, 58, 52, 37, 25, 23, 16, 19. The clear bars are repeated in each panel to show the control percentages and 95% binomial confidence limits, and shaded bars show the treatment values. The patterns are significant: $\chi^2 = 60{\cdot}6$, $P < 0{\cdot}01$; the same result was obtained with logistic regression.

SD = 44·8), and 41% of these individuals gained mass and 59% lost mass between the captures. Because the majority of hares are captured only once in a trapping session, this variation could introduce a bias into our analysis (Blomqvist 1977). We checked for the bias inherent in consecutive measurements of body mass of hares in autumn and spring, data that are used to estimate the regression of overwinter mass change on initial autumn mass (Blomqvist 1977). Because we captured and weighed many hares twice within a single week's capture session, we were able to estimate independently the variance in initial mass owing to changes in stomach contents. In autumn, this variance within individuals (SD = 45) was much less than the variance among individuals (SD = 227), giving a variance ratio of 0·039 and a negligible 1·7% bias in the estimation of the regression of mass change on autumn body mass.

ANALYSIS OF FAT STORES IN SNOWSHOE HARE CARCASSES

We collected all carcasses of snowshoe hares that died in live-traps, were killed by vehicles on the Alaska Highway, were collected specifically for necropsy, or were found dead. We also collected remains at predator kill-sites. Carcasses were stored at −20 °C until necropsy. We present necropsy data for hares dying between 1 October and 30 April to match our data on overwinter mass change. We used two indices to assess condition. First, we weighed the fat from around both kidneys. The bodies of many hares were partially eaten, so we considered kidney fat without reference to total body mass.

Second, we used the techniques of Brooks, Hanks & Ludbrook (1977) to estimate how much of the marrow of the long bones (femur or tibia) was fat. The marrow was dissected out of the bone, oven-dried at 70 °C for 24 h and the amount of fat expressed as a percentage of the fresh weight. These measurements tend to be high because of non-fat residue (Brooks *et al.* 1977 subtracted 7% from their estimates for ungulates to account for this residue), but uncorrected results indicate relative body condition. Several authors have used this technique, without correction, for snowshoe hare condition (Keith *et al.* 1984; Murray, Cary & Keith 1997; Murray 2002), so we also do not adjust the values. Wirsing, Steury & Murray (2002) showed that this index of marrow fat is correlated strongly with whole body fat (obtained by complete extraction) in snowshoe hares and is a good reflection of body condition.

We considered hares dying within 100 m of the predator-exclosure fences to be from those treatments, as hares moved frequently in and out of the fenced areas. Snowshoe hares were grouped into four fate categories to explore how condition interacted with cause of death. First, human-killed hares were killed on the Alaska Highway, shot for physiological research (Boonstra & Singleton 1993; Boonstra *et al.* 1998) or trapped specifically for necropsy. Second, predator-killed hares were collected along predator tracks (O'Donoghue *et al.* 1998) or located via radio-collars with mortality sensors (Lotek, Newmarket, Ontario). Hares could be assigned to the predator-killed category with certainty, as predators leave distinct signs such as scat, tracks, feathers and pellets (Krebs *et al.* 2001a). Third, natural non-predation deaths were radio-collared hares that were found dead in their resting places with no evidence of predation. Fourth, trap deaths were hares that died in the traps during the census periods. Traps were set typically at dusk and checked at dawn, and thus hares could be in the traps up to 12–14 h.

STATISTICAL ANALYSIS

We used ANOVA and ANCOVA to compare winters and treatments, and there was no need to transform data to meet the assumptions of these tests. We explored curvilinear fits to the data, but we found that these did not provide improvement over linear fits. We analysed the data both in absolute terms (spring mass – autumn mass) and by the proportional change [(spring mass – autumn mass)/autumn mass]; the patterns were identical, so we present absolute change in this paper. We found no significant differences in overwinter mass change by males and females, so we present data with the sexes combined. With the exception of asking how initial mass affected overwinter mass change, analyses are based on animals that weighed ≥ 1000 g in autumn, because animals weighing < 1000 g had not finished growing. We used χ^2 analyses and logistic regression to address the proportions of animals gaining and losing mass overwinter.

Analyses were conducted in STATISTICA (StatSoft 1995) and STATVIEW (Caldarola *et al.* 1998). To normalize the marrow-fat data, the arcsine transform was used. However, as the transformed and untransformed analysis were similar (most values between 30% and 70%), we present untransformed means and standard errors, rather than back-transformed values. We used the Tukey–Kramer multiple comparison *post-hoc* test to address the main effects.

Results

OVERWINTER MASS CHANGE PATTERNS

In all winters, some control snowshoe hares lost mass and some gained mass (Fig. 2). The proportion of individuals gaining mass was highest during years of early population increase (1987–88, 1994–95, 1995–96), with 58% (95% CI: 49–68%) gaining mass. The late increase winter of 1988–89 had the lowest percentage of control snowshoe hares gaining mass, at only 13% (95% CI: 4–31%). During the peak, decline and low phases, the overwhelming majority of control snowshoe hares lost mass overwinter.

Snowshoe hares on fertilizer sites (Fig. 2) showed very similar patterns to control hares for the proportion losing or gaining mass each winter. The major exception is that during two winters of the low phase, 1993–94 and 1994–95, a higher proportion of snowshoe hares on fertilizer sites gained mass overwinter. Unfortunately, sample sizes during the low phase were often < 10 individuals per treatment per year, so inferences about the low phase are not strong. Snowshoe hares on food-addition sites were much more likely to gain mass than were control hares, except during the population decline. Snowshoe hares on the predator-exclosure treatment were similar to control hares in their overwinter mass change. A higher percentage of snowshoe hares on the predator-exclosure + food treatment

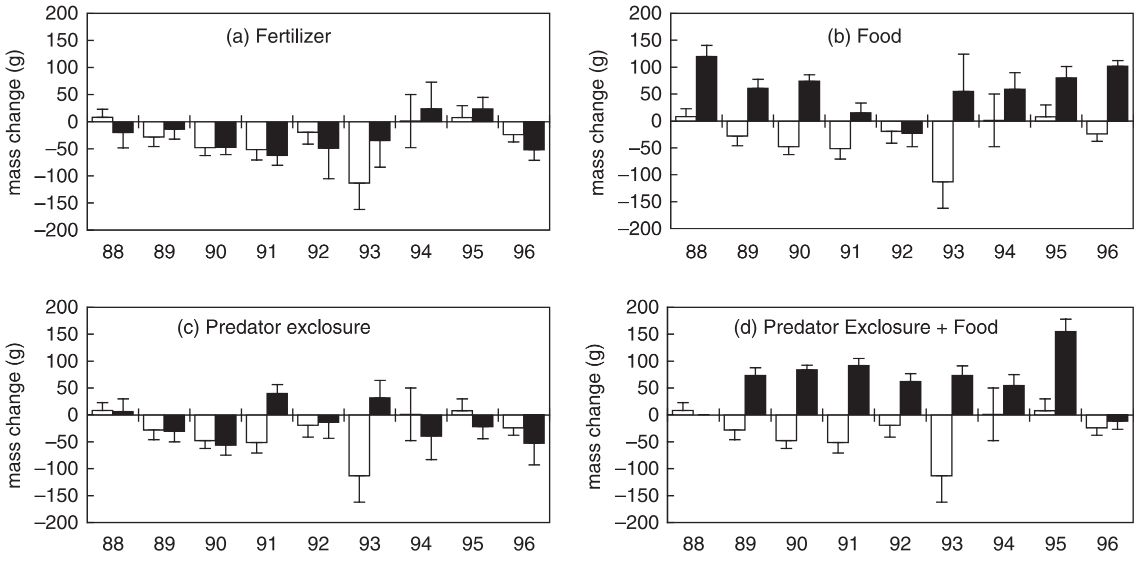

Fig. 3. Mean mass change of individual snowshoe hares overwinter. Positive values indicate mass gain, and negative values indicate mass loss. Values are means and standard errors for individuals caught in both seasons, adjusted by the analysis of covariance to a standard hare of 1464 g. The missing bar for predator-exclosure + food in 1988 is because the treatment had not yet started. The years on the *x*-axis represent spring (e.g. 89 indicates mass change from 1988 to 1989). Sample sizes are as in Fig. 2. The clear bars are repeated in each panel to show the control values, and black bars show the treatment values.

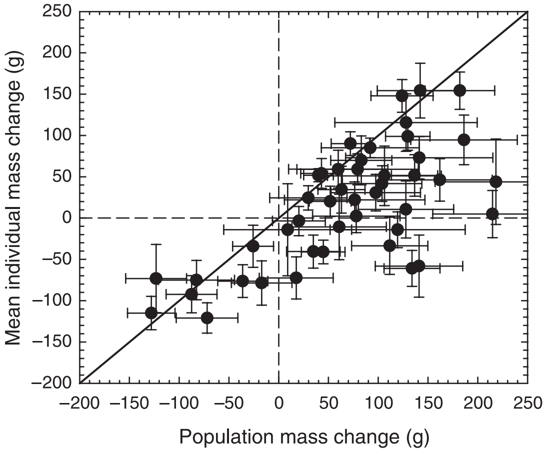

Fig. 4. Population- vs. individual-based estimates of overwinter mass change of snowshoe hares. Population estimates are (mean spring mass – mean autumn mass), and may sample different individuals. Individual estimates are the means of (spring mass–autumn mass) for individuals caught in both seasons. Each point represents one overwinter period on one of the nine control or treatment sites (± 1 SE), for which the number of individual hares caught was ≥ 5. The solid diagonal line indicates a 1 : 1 correspondence, and the dashed lines indicate no mass change. The regression of the individual-based estimate on the population-based estimate (not shown) was significantly different than a slope of 1 ($y = -24{\cdot}7 + 0{\cdot}58x$, $r^2 = 0{\cdot}47$, $P < 0{\cdot}001$).

gained mass relative to hares on control sites in every year except 1995–96, when the coyote disrupted this treatment. We found highly significant differences among treatments in the proportions of hares gaining or losing mass. Across all years (but excluding 1995–96 on predator-exclosure + food), animals on food or predator-exclosure + food sites were most likely to gain mass overwinter and control and predator-exclosure animals were most likely to lose mass.

We quantified these differences more precisely with an analysis of covariance of mass change overwinter for the five treatments and 9 years, using autumn mass as a covariate (Fig. 3). Three patterns occurred (treatment $F_{4,941} = 22{\cdot}54$, $P < 0{\cdot}001$, year $F_{7,941} = 2{\cdot}5$, $P = 0{\cdot}015$, interaction $F_{28,941} = 4{\cdot}1$, $P < 0{\cdot}001$). Hares on the control and fertilizer treatment areas gained mass in increase phase winters, but lost mass in the other phases. In contrast, hares on the food and the predator-exclosure + food areas gained mass in almost all winters. The predator-exclosure hares were intermediate in response. The most substantive mass loss for control snowshoe hares occurred during the peak and early decline winters of 1989–90 and 1990–91, when the average hare lost 51 ± 19 g (mean ± SE). During the same years on the three areas provided with supplemental food, hares on average gained 61 ± 12 to 84 ± 8·5 g overwinter.

Previous studies have addressed overwinter mass loss by comparing the difference between the average mass of individuals in spring and the average mass of individuals in autumn. This methodology often samples different individuals in the two seasons. Figure 4 shows that there is poor concordance between population-based estimates and records for individual mass change. Although the two metrics are correlated, of particular concern is that in 24% of cases, the population-based estimate indicated mass gain overwinter, whereas the individual-based estimate showed mass loss. This result means that incorrect annual and cyclic patterns of individuals would be inferred from the population-based estimates.

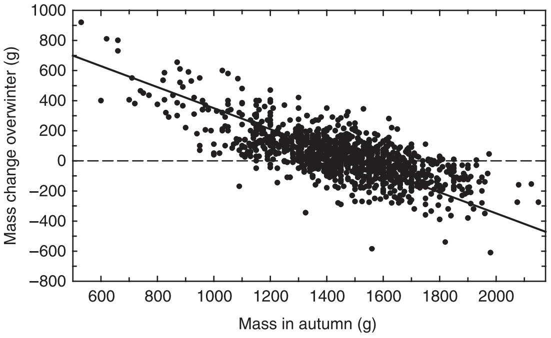

Fig. 5. Overwinter mass change of snowshoe hares relative to autumn mass. Each point represents an individual snowshoe hare. The solid line is the functional regression ($y = 1049 - 0{\cdot}70x$, $r^2 = 0{\cdot}52$, $P < 0{\cdot}001$, $n = 1138$; intercept SE 21·1, slope SE 0·014), and the dashed line indicates no mass change. Snowshoe hares that were < 1100 g in autumn gained mass overwinter, whereas animals > 1800 g in autumn usually lost mass. There was no significant effect of treatment on the slope of this regression.

CORRELATES OF OVERWINTER MASS CHANGE

There was a strong inverse relationship between a snowshoe hare's mass in autumn and its subsequent mass change (Fig. 5). We tested this regression with analysis of covariance, and both treatment and year significantly affected the position of the linear regression models, although the slope of the line was equal for all combinations of factors ($P_{\text{treatments}} = 0{\cdot}01$, $P_{\text{years}} = 0{\cdot}005$, $r^2 = 0{\cdot}52$, $P < 0{\cdot}001$). In particular, snowshoe hares weighing less than ~1100 g in autumn always gained mass overwinter. The smaller the animal in autumn, the more mass it gained overwinter; animals that weighed 500–700 g were able to double their mass. In contrast, snowshoe hares that were extremely heavy in autumn (more than ~1800 g) almost all lost mass overwinter, and frequently lost significant amounts of mass (35% of animals lost > 180 g, or > 10% of their autumn mass). These high autumn masses are not associated with reproduction, because the live-trapping occurred after the end of the breeding season. For snowshoe hares weighing between 1100 and 1800 g, lighter hares were more likely to gain mass than to lose it overwinter, and heavier hares were more likely to lose mass.

Overwinter survival rates, an indicator of predation risk because the high majority of dying hares were depredated, only weakly predicted overwinter-mass change (Fig. 6, $r^2 = 0{\cdot}15$, $P < 0{\cdot}01$). Largely, this weak prediction reflected an inability to predict the mean

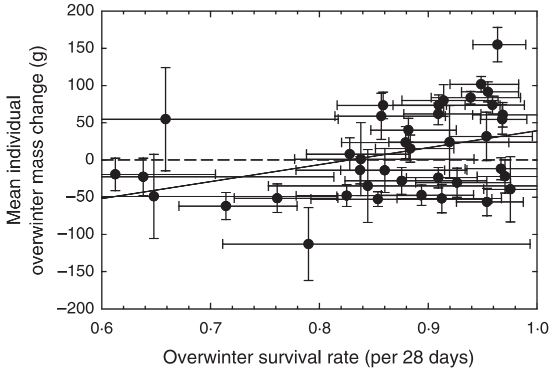

Fig. 6. Overwinter survival rate as a predictor of mass change in individual snowshoe hares. The overwhelming majority of hares that died were killed by predators. By definition, animals contributing to our estimates of mass change survived overwinter, so the survival rates shown here are an indicator of predation risk. Survival rates were estimated from radio-collared snowshoe hares (Krebs *et al.* 2001) and are standardized to 28-day periods for the 6 winter months. Each point represents the mean and 1 SE for one overwinter period. The regression line (dark) is $y = -187 + 227x$ ($r^2 = 0·15$, $P < 0·01$), and the dashed line indicates no mass change.

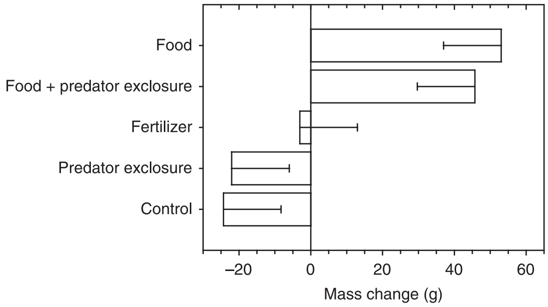

Fig. 8. Mean mass change overwinter adjusted to a maximum snow depth of 19 cm, 1986–96, for five treatments, Kluane, Yukon. The treatments shown in Fig. 7b are adjusted via the common regression slope to the average winter snow depth for these years as measured at Burwash Airport and plotted with one SE (16·0 g). The control and predator-exclosure differ significantly from the food and predator-exclosure + food treatments.

amount of mass change. Looking only at the directionality of mass change, survival was a much better predictor: for 4-week survival rates during winter that were < 0·90, mean mass loss occurred 76% of the time, whereas when survival was > 0·90, mean mass loss occurred only 21% of the time ($\chi^2 = 10·0$, $P < 0·01$).

Mass change overwinter was related strongly to maximum winter snow depth on all treatments (Fig. 7a,b, ANCOVA, $P < 0·001$). We tested for non-linear effects but could find no regression model significantly superior to a linear relationship. On average, an increase of 10 cm in snow depth was associated with a loss of 69 g (95% CI: 49–89 g) overwinter. The changes in mass shown in Fig. 7 were affected strongly by treatments (Fig. 8, ANCOVA, $P < 0·002$). Hares on food-supplemented sites gained mass in almost all years except those with the deepest snow. Control hares and those in the predator-exclosure lost mass in almost all years except those with the lowest snowfall. With multiple regression, average overwinter mass loss could be predicted from maximum snow depth and treatments with $r^2 = 0·67$ ($n = 48$). Overwinter mass change was only poorly predicted by any of the temperature measures of winter severity ($r^2 =$ 0·01–0·02). Total snowfall was closely correlated with maximum snow depth during our study ($r^2 = 0·72$, $n = 10$).

MARROW AND KIDNEY FAT STORES

Both kidney fat and marrow fat of snowshoe hares dying overwinter were correlated with body mass (kidney fat $= -2·69 + 0·002 \times$ body mass, $r^2 = 0·14$, $P < 0·001$; marrow fat $= -33·3 + 0·057 \times$ body mass, $r^2 = 0·42$, $P < 0·001$). We also examined marrow fat as a categorical variable following Keith *et al.* (1984), who suggested that < 28% marrow fat was associated with malnourishment. We considered the three mass classes suggested by Fig. 5: < 1100 g (all hares gained mass), 1100–1800 g (hares sometimes gained and sometimes lost mass), and > 1800 g (hares usually lost mass). The pattern was highly

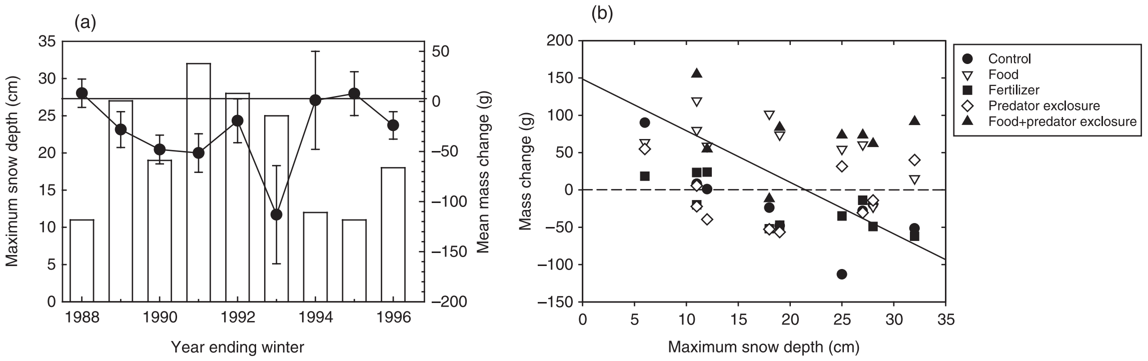

Fig. 7. Mean mass change of snowshoe hares overwinter in relation to snow depth, Kluane, Yukon. (a) Maximum snow depths (bars) and mean mass change (points) during 1986–96; 1990 was the peak of the hare cycle. (b) Mass change on the treatments. Mass change was negatively correlated with maximum winter snow depth on all areas with a common slope but significantly variable intercepts for the treatments, illustrated in Fig. 8. The common slope is −8·23 with SE 1·04. The regression is: $y = -8·23x + 167·6$.

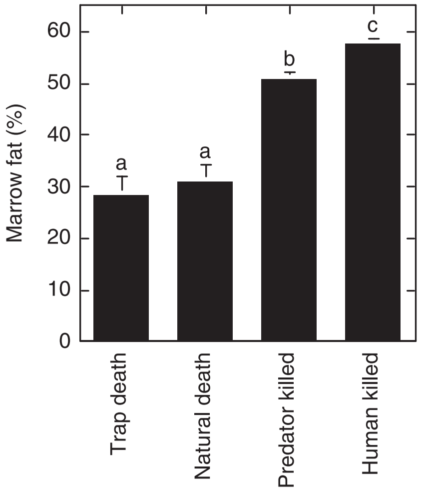

Fig. 9. Marrow fat content of snowshoe hares dying of different causes. Values are means ± 1 SE for 499 carcasses analysed during the 6 winters with sufficient data, 1989–90 to 1995–96. Sample sizes are: trap deaths ($n = 28$), non-predation deaths ($n = 34$), predator-killed ($n = 256$) and human-killed ($n = 181$). Bars with similar letters were not significantly different.

significant: 87% of the small animals had marrow fat < 28%, 23% of the mid-sized animals did, and none of the large animals did ($\chi^2 = 36{\cdot}8$, $P < 0{\cdot}001$, $n = 261$). Thus, even though all the small snowshoe hares gained mass overwinter, their marrow fat stores were low, and the opposite pattern occurred with heavy animals losing mass but having high marrow fat.

The marrow fat of snowshoes hares was related directly to how they died (Fig. 9; $F_{3,495} = 35{\cdot}08$, $P < 0{\cdot}001$). Hares that died in traps or were found dead had 20–29% less marrow fat than those killed by predators or by humans. A similar pattern occurred when we examined cause of death *vis-à-vis* the 28% marrow fat threshold. Hares dying naturally or in traps had low marrow fat in 64% of cases, whereas only 30% of predator-killed hares and 6% of human-killed hares had low marrow fat ($\chi^2 = 74{\cdot}9$, $P < 0{\cdot}001$, $n = 252$). We do not know to what extent human-killed hares represent a biased subsample of the hare population (e.g. more visible or more mobile).

Most of the hares we necropsied came from the three winters 1989–90 to 1991–92, the peak and first 2 years of decline ($n = 499$ of 570 from all winters; cause of death could not be determined in all cases). Because of low sample sizes, we pooled non-predation (natural) death with trap deaths. There was a marginal year effect ($F_{2,457} = 2{\cdot}57$, $P = 0{\cdot}08$), a clear cause of death effect ($F_{2,457} = 16{\cdot}43$, $P < 0{\cdot}001$) and an interaction effect ($F_{2,457} = 3{\cdot}07$, $P < 0{\cdot}02$). The interaction effect was the result of having four hares that died either naturally or in traps in 1991–92, with these animals and human-killed hares having similar marrow fat. Despite this small interaction, the overall pattern in marrow fat was that hares dying naturally or in traps had low marrow fat of 29·5 ± 2·6% ($n = 58$), those killed by predators had 51·0 ± 1·3% ($n = 239$) and those killed by humans had 58·4 ± 1·1% ($n = 169$).

To examine for a treatment effect on marrow fat across the cycle, we pooled all years and excluded all human-killed hares and those whose cause of death could not be identified. There was a significant treatment effect (Fig. 10a, $F_{4,308} = 3{\cdot}39$, $P = 0{\cdot}01$), with hares from controls and the fertilized sites having lower values than those on predator-exclosure + food; those from the food-supplemented sites were not different from either group. Because of small sample sizes, we restrict our treatment and year effect analyses of marrow fat by examining only hares killed by predators in the two decline winters (1990–91 and 1991–92). There was a marginally significant treatment effect ($F_{4,196} = 2{\cdot}02$,

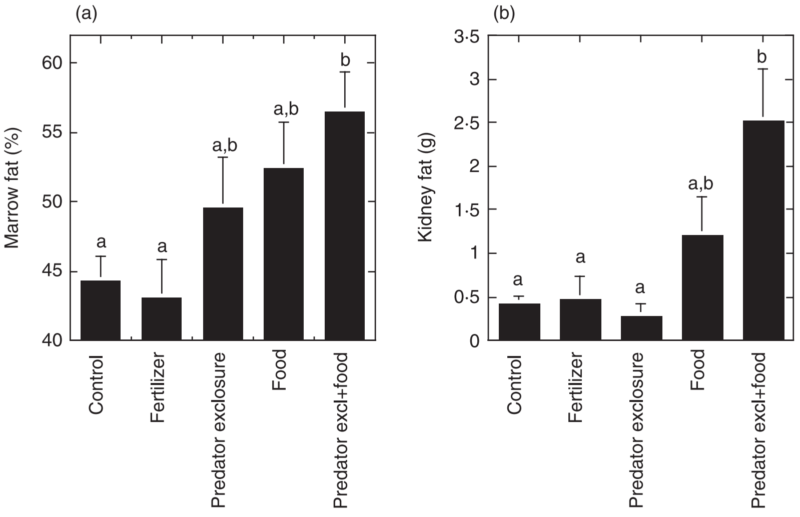

Fig. 10. The impact of the experimental treatments on the percentage of marrow fat in the femur ($n = 313$) and on kidney fat mass ($n = 225$, means ± 1 SE) of hares dying of non-human causes during the population cycle. Sample sizes for the marrow fat samples are: controls 156, fertilizer 57, predator-exclosure 38, food addition 27 and predator-exclosure + food 35; and for the kidney fat samples are: controls 118, fertilizer 34, predator-exclosure 30, food addition 20 and predator-exclosure + food 23. Bars with similar letters were not significantly different.

$P = 0{\cdot}07$), but no year effect ($F_{1,196} = 0{\cdot}17$, $P = 0{\cdot}68$) or interaction effect ($F_{4,196} = 0{\cdot}81$, $P = 0{\cdot}52$). The *post-hoc* multiple comparison test could not discriminate among treatments. To assess further possible treatment impacts, we ran an analysis on three groups: predator-exclosure, pooled food and predator-exclosure + food and pooled fertilization and controls (fertilization had little impact on density, Hodges *et al*. 2001). Treatment group had a clear impact ($F_{2,200} = 4{\cdot}24$, $P = 0{\cdot}016$), but there were no year ($F_{1,200} = 0{\cdot}09$, $P = 0{\cdot}76$) or interaction effects ($F_{2,200} = 1{\cdot}04$, $P = 0{\cdot}35$). In this analysis, control and fertilizer hares had 48·4 ± 1·9% marrow fat, which was significantly less than the food and predator-exclosure + food hares, with 57·0 ± 2·2%. Hares on the predator-exclosure had marrow fat not significantly different from either group, with 53·4 ± 4·2%. Food-supplementation improved marrow fat content, and predator-exclusion had a modest positive impact. The marrow fat on the various fed and protected treatment areas was still slightly less than for human-killed hares in the winters of 1990–91 and 1991–92 (60·0 ± 1·2%, $n = 126$; $F_{1,197} = 3{\cdot}05$, $P = 0{\cdot}08$), suggesting that even small differences in marrow fat increased the chance a hare would be killed by a predator.

Kidney fat was not correlated with how snowshoe hares died ($F_{3,437} = 1{\cdot}12$, $P = 0{\cdot}34$). Sample sizes were small, because kidneys were often eaten by predators. We were able to examine year effects only for the last peak winter (1989–90) and the two decline winters (1990–91 and 1991–92). Kidney fat did not vary with year ($F_{2,358} = 0{\cdot}23$, $P = 0{\cdot}79$), cause of death ($F_{3,358} = 0{\cdot}77$, $P = 0{\cdot}51$), or their interaction ($F_{6,358} = 1{\cdot}41$, $P = 0{\cdot}21$). Experimental treatment significantly affected the kidney fat across all years and condition-related causes of death (i.e. excluding human-killed hares) (Fig. 10b; $F_{4,220} = 11{\cdot}19$, $P < 0{\cdot}001$). Snowshoe hares on non-fed areas had a third to a sixth as much kidney fat as hares on the fed grids.

Discussion

Snowshoe hares clearly had the capacity to maintain or gain mass overwinter in all years of the population cycle. However, the proportion of animals doing so and the amount of mass change varied substantially. This variation in mass-change patterns was affected by a complex interplay of food availability, risk of predation, autumn body mass and snow conditions. These patterns suggest that body mass is a plastic trait that responds as animals balance conflicting demands. Our results do not support the common argument that overwinter mass loss by snowshoe hares is driven primarily by absolute food shortage (Newson & de Vos 1964; Keith & Windberg 1978; Vaughan & Keith 1981; Keith *et al*. 1984). Instead, some hares lost mass even when food was superabundant, some hares gained mass even in severe winters and other factors also influenced overwinter mass dynamics (Table 1).

Snow depths appeared to impose energetic costs on hares, with deeper snow correlated with more mass loss. The decline winters had deeper snows than most other winters during this cycle, thus partly confounding

Table 1. Synopsis of overwinter mass loss hypotheses, predictions and results for snowshoe hares

Hypotheses	Predictions	Results
A priori hypotheses		
(1) Mass loss is an adaptive overwinter strategy to minimize energy needs	Hares on all treatments should exhibit overwinter mass loss	Possibly supported but too simplistic. Some hares on all treatments lost mass, but others gained mass. Mass dynamics were also affected by food supply, predation risk and autumn mass
(2) Mass loss results from food limitation	Hares should lose more mass during peak and decline years	Accept hypothesis with reservations. Mass loss on control areas was most severe during the decline phase but food limitation interacted with predation pressure
(3) Mass loss results from behavioural and physiological responses to predator pressure	Mass loss should be most pronounced during periods of highest mortality and should not occur in predator reduction sites	Accept hypothesis. Predator-exclosures reduced or stopped overwinter mass loss, which was completely eliminated in the predator-exclosure + food treatment
(4) Mass loss is an artefact of measuring mass loss based on populations rather than individuals	Mass loss overwinter will not be found if individuals are followed overwinter	Reject hypothesis. Overwinter mass loss does occur but is poorly predicted by population mean measurements
Additional patterns		
(5) Autumn mass affects overwinter mass dynamics		Small hares gained mass and heavy hares lost mass overwinter, irrespective of food supply and predation risk
(6) Snow depths affect mass loss		Hares lost more mass in winters with deeper snow

cyclic phase and snow depth. However, our primary goal was to explore how the experimental manipulation of food and predators affected hares, and the treatments had clear impacts on mass change within years: when costs of obtaining food declined via either mechanism, snowshoe hares were more likely to maintain or gain mass. Snowshoe hare density had no impact on mass change patterns, indicating that hares were not directly competing for resources. The impacts of food supply and predation risk interacted with autumn mass, because across all treatments light animals were likely to gain mass, and heavy animals to lose it. Although we have insufficient sample sizes to tell conclusively if small animals grew to larger final body sizes on the food addition or predator-exclosure + food treatments, we suspect that this is likely.

Predation risk also influenced overwinter mass dynamics. Low overwinter survival rates corresponded to the most severe mass loss, and virtually all hares that disappeared did so because they were killed by predators, with 80–100% of the deaths of radio-collared hares caused by predators (Krebs *et al*. 1995; Hodges *et al*. 1999). Survival was extremely low during the decline (survival on the control grids was 0·7%/ year, similar on the two food addition sites (3·7%) and much higher in the predator-exclosures (predator-exclosure 9·5%; predator-exclosure + food 20·8%) (Krebs *et al*. 1995; Hodges *et al*. 1999, 2001). Mass loss is affected by high predation risk because of the physiology of the stress response: under conditions of high stress, gluconeogenesis is accelerated, mobilizing body resources and tissues for the formation of glycogen (Boonstra *et al*. 1998). Glycogen can be converted rapidly to glucose to fuel muscles when a predator threatens survival.

Our results also show clearly that population-based analyses of mass change are quite different from individual-based estimates. Annually, snowshoe hare densities are lowest in the spring and highest in the autumn, so sample sizes of hares often differ substantially between these trapping periods (Hodges *et al*. 2001), and small spring sample sizes weaken inferential power and could lead to biases. Additionally, population-based estimates are likely to be affected by sampling different numbers of each cohort in the two seasons. For example, females typically weigh more than males, and if different proportions of males and females were caught in the two seasons, that would affect the estimate of mass change. Similarly, if the autumn trapping session contained a different proportion of young-of-the-year than the spring session, that could lead to faulty conclusions about mass dynamics. Such biases could arise either via biological mechanisms such as differential dispersal or mortality of one sex or age class, or via sampling problems such as different trappabilities.

The energetic costs for snowshoe hares overwinter include thermoregulation, foraging effort, warming and digesting food, and mitigating predation risk through habitat selection and movements away from predators (avoiding areas with predator sign, or being chased by predators). Some energetic costs for snowshoe hares are reduced by changes in morphology of hair (Russell & Tumlison 1996), digestive structure (Smith, Hubbart & Shoemaker 1980) and physiology (Irving *et al*. 1957; Hart, Pohl & Tener 1965; Feist & Rosenmann 1975). Several small mammal species show similar seasonal variation in organ size, lean mass and fat mass (Batzli & Esseks 1992; Virgl & Messier 1992; Piersma & Lindström 1997; Zuercher, Roby & Rexstad 1999; Derting & Hornung 2003). These alterations in proportional mass of different body components facilitate effective digestion of less nutritious foods, minimize the energy expenditures on reproductive organs during nonreproductive times and store energy in different tissue types.

Despite these energy-saving changes, body mass by itself also affects energetic costs. Heavier animals have increased total locomotion costs, especially in deep snow (Buskirk, Ruggiero & Krebs 2001), and higher absolute metabolic rates, thus requiring more food and more foraging time to maintain their mass. Carrying more mass may also impose costs when snowshoe hares try to escape from predators, as has been documented for small birds (Witter & Cuthill 1993; Gosler, Greenwood & Perrins 1995). However, heavier animals also benefit from reduced surface area to volume ratios, which helps to retain heat.

Maintaining an 'optimal mass' is therefore a challenging problem for an overwintering snowshoe hare, both because so many variables contribute to what may be optimal and because substantial mass change by hares is a slow process that cannot respond to small environmental fluctuations. Although small birds can adjust their fat stores on a daily basis by adjusting food intake (Gosler 2002), snowshoe hare fat-store changes respond slowly, in large part because their food is low quality (Hodges & Sinclair 2003). Nor is it clear to what extent body mass and composition changes are adaptive or simply responsive to environmental conditions and behavioural decisions. Body mass or changes in condition have been linked to survival or cause of death (Rohner & Krebs 1996; Murray 2002), which suggests overwinter body-mass dynamics are subject to selection.

Fat stores in bone marrow and around kidneys were related weakly to body mass of snowshoe hares. Kidney fat fluctuates seasonally in *L. europaeus* (European hares, Pepin 1987), and seasonal variation in tissue allocation may prevent a strong relationship between these fat stores and body mass. Marrow fat was associated with the causes of mortality: snowshoe hares that died of non-predation causes had much lower marrow fat than animals killed by predators or humans. Both kidney and marrow fat were higher for animals on the food-supplemented grids, even during winters when the majority of animals on these sites lost mass. These patterns suggest that body mass and internal allocation of energy into different tissues both influence survival overwinter.

Dehnel's phenomenon of overwinter mass loss is at odds with Bergmann's rule of increasing body mass with latitude and winter severity (Ashton, Tracy & de Queiroz 2000; Freckleton, Harvey & Pagel 2003). Explanations for Bergmann's rule have emphasized the thermal advantages of larger bodies: the heat-conservation hypothesis suggests that larger organisms retain heat more efficiently because they have lower surface area to volume ratios (Steudel *et al*. 1994), while the fasting-endurance hypothesis argues that larger-bodied organisms can maintain larger fat stores, thus tolerating cold and food shortage better (Millar & Hickling 1990). Clearly, if overwinter mass loss is an adaptive strategy for surviving winter, then these two patterns need to be reconciled. Although Bergmann's rule has typically been considered from the standpoint of winter energetics, it is possible that summer or reproductive energetics drive the observed cline in body mass (Speakman 1996). Alternatively, different body masses may be ideal at different times of year, leading to seasonal trade-offs (Michener & Locklear 1990; Smith & Charnov 2001).

We suspect that the complex mass dynamics in snowshoe hares are typical of species that are active overwinter, rather than hibernating or migrating. In addition to the small rodents that were initially described by Dehnel's phenomenon, species such as beavers (*Castor canadensis*), muskrats (*Ondatra zibethica*) and porcupines (*Erithizon dorsatum*) also show complicated patterns of mass loss overwinter, with autumn mass and food supply or foraging costs co-implicated in shaping mass dynamics and juveniles frequently not showing the same patterns as adults (Virgl & Messier 1992; Sweitzer & Berger 1993; Smith & Jenkins 1997). Furthermore, body mass is highly variable multi-annually in cyclic species (voles, Boonstra & Krebs 1979; Norrdahl & Korpimäki 2002; Ergon *et al*. 2004; snowshoe hares, Keith & Windberg 1978), which suggests further that body mass is variable and is shaped by the costs and benefits of obtaining and expending resources.

Our results do not support the idea that hares lose mass overwinter as a direct reflection of limited food supply. Nor do our data support the idea that overwinter mass loss is an adaptive strategy that reduces energetic expenditures and boosts survival as suggested by Dehnel's phenomenon. Both are refuted because there is substantial variation in individual mass dynamics overwinter and multiple factors beyond food supply influence mass dynamics. We suspect that overwinter mass dynamics are subject to selection, because body-fat stores and foraging behaviour are linked to the risk of predation, but for some hares the optimal strategy probably involves mass gain rather than mass loss. Clearly, winter is a challenging time that requires hares to make the best of a bad situation, with many environmental factors affecting the changes that occur (Table 1). Foraging costs are affected by snow depths, food availability and predation risk, and these factors influenced body-mass dynamics of snowshoe hares overwinter. Starting body mass also has a large influence: very small hares gained mass and very large hares lost mass no matter what the environmental conditions were. Small hares are challenged by this growth overwinter, because their marrow fat is quite low. In contrast, the heaviest hares were able to lose mass while retaining high marrow fat. The costs and consequences of mass change therefore are quite different for these two groups. As with many ecological problems, the challenge is to quantify the relative impact of these different factors and to determine the consequences particular patterns of mass maintenance or change have on subsequent fitness.

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