Differential body condition and vulnerability to predation in snowshoe hares

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Summary

1. Selection of prey in poor body condition allegedly is a widespread phenomenon in predator–prey systems. Yet, it remains unclear to what extent such selection reflects impeded prey escape ability due to severe malnutrition and/or state-dependent risk taking following lesser changes in prey body condition. In systems where prey food availability is adequate, few individuals should be severely malnourished and thus condition-sensitive predation should be related principally to changes in nutritional status that occur irrespective of an individual's absolute body condition.

2. I studied predation in snowshoe hares (*Lepus americanus*, Erxleben) when food was abundant, to test the prediction that change in body condition would contribute, more than would absolute body condition, to vulnerability to predation. Hares ($n = 618$) were radio-marked and monitored for survival while body condition was indexed during bimonthly livecaptures. A subsample of animals ($n = 36$) was equipped with motion-sensitive transmitters and activity patterns were examined in relation to the body condition index and vulnerability to predation.

3. Manipulation of hare nutritional status via food supplementation improved hare body condition but did not affect vulnerability to predation; reduction of nematode parasite numbers did not improve hare condition but reduced predation among female hares. Reproductive status affected predation in both sexes, with recently pregnant females and non-scrotal males being less vulnerable to predation. Heavier males also tended to experience lower predation rates.

4. Predation rates for both female and male hares were higher among individuals having recently experienced condition deterioration but not among animals considered to be in poor absolute condition. Yet, the parameter representing change in condition was the last to enter survival models, indicating a relatively modest effect of this factor on hare vulnerability to predation. Mammalian but not avian predators tended to kill hares in declining condition, and hare activity patterns were not correlated either to change in condition or to survival.

5. These findings indicate that nutritional status may influence vulnerability to predation even when food is abundant, but that such effects occur indirectly through changing body condition. This implies that hares are likely to forage in a risk-prone manner when subject to worsening condition.

Key-words: body condition, *Lepus americanus*, nutrition, predator–prey interactions, predation, prey selection, snowshoe hare.

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Introduction

Predators often are considered as preying upon disadvantaged individuals disproportionately from the prey population (Errington 1946; Curio 1976). While empirical support for this idea consists largely of *post-hoc* studies showing basic physical or demographic

differences between predator-killed and living prey, identifying the functional mechanisms behind prey selection patterns can be problematic in the absence of a priori information on either prey condition and behaviour, or predator encounter and capture rates (see Temple 1987; Nishimura & Abe 1988; Juanes 1994). Moreover, the attributes of predator-killed prey often are inconsistent across species or populations (e.g. Sinclair & Arcese 1995; Koivunen *et al.* 1996), implying that the determinants of prey selection patterns are complex and possibly multifactorial. It follows that the development of general models of patterns of prey selection will remain challenging in the absence of more detailed empirical work examining specific factors promoting prey vulnerability to predation.

Prey nutritional status is known to impact vulnerability to predation, with individuals in poor body condition having been shown to be killed disproportionately by predators (e.g. Keith *et al.* 1984; FitzGibbon & Fanshawe 1989; Sinclair & Arcese 1995). In theory, the effects of poor condition on prey survival may be direct, with severe malnutrition eliciting physical debilitation and altered predator detection or evasion abilities (Mesa *et al.* 1994). Nutritional status may also affect prey susceptibility indirectly, if changes in prey body condition initiate compensatory foraging or other risk-prone behaviours (i.e. state-dependent risk taking; McNamara & Houston 1987, 1990; Lima 1998). In the former case, a direct increase in predation risk should occur with declines in absolute body condition that fall below a threshold of severe malnutrition and thus prompt physical debilitation of prey. In the latter case, predators should select individuals expressing reduced predation risk sensitivity, which should be associated with change in condition (i.e. relative condition) if alteration of nutritional status correlates inversely with risk sensitivity. It follows that the effects of relative condition on risk sensitivity could be proportional to the rate of condition decline, with individuals experiencing rapid or aggravated declines in condition potentially being most risk-insensitive. While changes in predation-risk perception may occur irrespective of an individual's absolute body condition, such changes may also be aggravated when absolute condition is poor, thereby leading to interactive effects of absolute and relative condition on prey survival.

Previous field studies have focused almost exclusively upon assessing the direct effects of absolute body condition on prey selection by predators, probably because of difficulties associated with documenting changing condition in free-ranging prey (i.e. requires repeated capture and handling of often elusive animals). Therefore, for most systems the extent to which absolute and relative body condition contribute to vulnerability to predation remains unclear. However, it seems reasonable that both direct and indirect effects of condition may impact predation in many food-limited prey populations through the effects of food shortage on both prey physical state (i.e. direct effects due to poor

absolute condition) and risk-taking behaviour (i.e. indirect effects due to changing condition). In contrast, if prey-food availability is not limited and most/all prey are in adequate nutritional status, then condition-sensitive predation should operate principally upon individuals that are in good absolute condition but risk-insensitive, due perhaps to their changing condition (indirect effects only). The important distinction here is that when food is abundant condition should augment predation risk only indirectly, while when food is limited both direct and indirect effects of condition on predation risk may be implicated. Because the majority of prey populations are held at levels below those where food is limiting (see Krebs *et al.* 1997), in most systems condition-sensitive predation probably acts indirectly upon animals otherwise considered to be nourished adequately.

One final point in the discussion of nutritional influences on predation involves the role of predator-hunting strategy on prey selection. Predators employing a coursing rather than an ambush-hunting behaviour may kill substandard individuals because selection and testing of prey take place during a predator chase, but not during an ambush (see FitzGibbon & Fanshawe 1989). Alternatively, ambush predators may more likely kill substandard individuals if visual cues are responsible for eliciting predator chases (see Greene 1986). These two contrasting models may be relevant in that condition-sensitive predation should occur among coursing predators mainly if absolute condition affects predation (i.e. physical debilitation inhibits prey escape when coursed by a predator), while ambush predators may kill undernourished prey disproportionately if relative condition is the principal determinant of risk sensitivity (i.e. deteriorating condition begets increased prey visibility through reduced risk sensitivity).

This paper examines the relationship between condition and predation among snowshoe hares (*Lepus americanus*, Erxleben) from Manitoba, Canada, during a period of hare-food abundance. Across most of their geographical range, snowshoe hare populations experience 8–11 year numerical cycles with populations typically being subject to heavy predation (Boutin *et al.* 1986; Krebs *et al.* 1995). Cyclic populations are also subject to food limitation and starvation during peaks/declines (Keith *et al.* 1984; Boutin *et al.* 1986), whereas during numerical lows food availability does not appear to be limited (Boonstra, Krebs & Stenseth 1998b). During the present study, hare populations were characterized by heavy predation and low starvation, while natural food was deemed to be superabundant on the site (Murray, Cary, & Keith 1997; Murray, Keith & Cary 1998; Murray 1999). Yet, while predation and nutritional status are recognized as interacting to affect hare survival and population dynamics (Keith *et al.* 1984; Hik 1995; Boonstra *et al.* 1998a), the specific nature of the condition–predation interaction remains to be elucidated fully (Keith 1990; Murray 2003).

Because of the apparent food abundance and heavy predation pressure during the present study, I predicted that (i) depredated animals should be in adequate absolute nutritional state, with little/no reduction in predation rates following experimental attempts to improve absolute condition. However, despite food abundance on the site some prey should still be more vulnerable to predation through state-dependent risk taking, implying that (ii) depredated hares should be those experiencing declining condition, irrespective of their absolute condition. In addition, condition-sensitive predation should be observed principally among (iii) prey killed by ambush rather than coursing predators because of their likely augmented risk-insensitivity and higher visibility. Finally, the presumed increased risk insensitivity among hares in declining condition should be (iv) manifested through increased activity.

Materials and methods

STUDY SITE

The study was conducted in Manitoba, Canada (51°N, 98°W), in an aspen (*Populus tremuloides*, Michx.) forest with an understorey comprised of a variety of deciduous browse species (Murray 1999). Hares were studied on six 25-ha areas that were stratified initially into three groups of two based on the relative size of the resident hare population (see Murray *et al.* 1998; Murray 1999). All study areas were separated by > 500 m, with little/no movement of hares between areas.

FIELD PROCEDURES

Hares on each study area were live-trapped (Tomahawk Live Trap Co., Tomah, WI, USA) bimonthly during April 1991–June 1993, with all trapping/handling procedures conforming to standard guidelines (Canadian Council on Animal Care 1984). Hares were weighed, aged (adult or juvenile) and sex was determined. Structural size was indexed via measurement of hind foot length (HFL; Bailey 1968) and individuals were identified by numbered web tags. Approximately 20 hares in each area were equipped with mortality-sensitive radio-transmitters (transmitters weighed 3–4% of body mass of adults). Transmitters were deployed mainly on animals weighing > 900 g but occasionally upon individuals weighing 700–900 g; previous studies have suggested that radio-collars increase hare vulnerability to predation of hares for a period of about 7 days post-collaring (Keith *et al.* 1984; Boutin *et al.* 1986). When collared hares died or their radio-signal was lost, they were replaced during subsequent trapping sessions. Survival of radio-collared hares was monitored daily and dead animals were retrieved promptly; proximate cause of death was assessed from evidence left at the kill site and carcass necropsy (Boutin *et al.* 1986; Murray *et al.* 1997). Hare kills made by mammalian vs. avian predators were

differentiated by tracks in the snow, location of carcass remains (i.e. at a den site or plucking post), puncture wounds on the carcass, or from predator faeces found near the carcass; the major predators in this study included coyote (*Canis latrans*, Say), great-horned owl (*Bubo virginianus*, Gmelin) and red-tailed hawk (*Buteo jamaicensis*, Gmelin). Birds of prey usually capture prey by surprise in the absence of a chase, whereas mammalian carnivores typically chase prey before they are subdued (Curio 1976), implying that mammalian predators may test prey absolute condition more than raptors. Thus, I considered hares killed by mammalian predators as being 'coursed' and those killed by raptors as being 'ambushed'. Hares not dying of predation were distinguished easily from predation-induced mortalities (Boutin *et al.* 1986), and because scavenging occurred only rarely (Murray *et al.* 1997) my diagnosis of proximate cause of hare deaths was probably correct.

A subsample of hares (*n* = 36) in two study areas were equipped with motion-sensitive radio-transmitters whose pulse rate increased when the collar was tilted. I confirmed, using visual observations of captive hares (*n* = 3), that transmitters emitted a variable pulse rate (i.e. collar shifted between fast and slow mode) during normal feeding or grooming, as well as during most movement activities. Hare activity was monitored continuously between April 1992 and May 1993 using an automated data logger, by scanning through transmitter frequencies at an interval of 5 min per transmitter. Percentage of time spent active was averaged across 24-h periods, and activity was defined as the standard deviation (SD) of transmitter pulse rate exceeding 0·10 during the 5-min interval. The data logger was moved between study areas every 7–10 days.

Hare body condition was considered to represent nutritional status and was manipulated experimentally through two means: During November–April 1991–92 and 1992–93, one study area at each hare-density stratum received 3 kg/ha of supplemental food (i.e. commercial rabbit chow, 17% protein) every 3–5 days (Murray 1999). During each bimonthly trapping session, half the animals on each study area were administered an anthelmintic treatment (Ivermectin, Merck-Agvet, Rahway, NJ, USA) whereas the other half received a placebo; parasite-reduction reduced the burdens of four of five nematode species effectively for 20–50 + days post-treatment (Murray, Keith & Cary 1996). Both food and parasite treatments were shown previously to elicit small and short-term effects on survival or production (Murray *et al.* 1997; Murray *et al.* 1998); the present analysis expands upon my previous work specifically to relate body condition of individual animals to their vulnerability to predation.

DETERMINATION OF CONDITION INDEX

A sample of hares was captured and euthanized to develop an index of body condition that could be

applied to free-ranging live hares. Carcasses were weighed and HFL was measured; because multiple measures of HFL were taken and averaged for each carcass, little error existed in the structural size index. Bone-marrow fat (BMF), the last fat depot to be mobilized before starvation in ungulates (Mech & DelGiudice 1985), may decline more gradually with body condition deterioration in lagomorphs (D.L. Murray, unpublished data). BMF was removed from tibial bones and calculated as percentage of dry mass (oven-dried at 70 °C for 24 h) from fresh mass (Keith *et al*. 1984). Recognizing the difficulty associated with obtaining unbiased and precise indices of condition in live animals (e.g. see Cone 1989; Kotiaho 1999; Green 2001), I explored the relationship between body mass of carcasses vs. several indices of structural size (HFL, HFL^2, and HFL^3; see Cone 1989). The stepwise Model I regression of carcass BMF against the three body mass–structural size relationships and dummy variables representing sex and age class, indicated that both mass/HFL ($t_{1,271} = 7.032$, $P < 0.001$) and sex ($t_{1,271} = 3.957$, $P < 0.001$) were correlated significantly to BMF (all remaining $P > 0.32$). This implied that mass/HFL was the metric that was the most closely related to BMF but that it scaled differently between sexes. Mass/HFL also was tested against two alternate condition indices [mass/HFL^z, where Z = slope of the line generated by the Model I regression of body mass vs. HFL for each sex (Jakob *et al*. 1996), and residuals for the line generated by Model I regression of body mass vs. HFL for each sex (Green 2001)]. For carcasses of both male and female hares ($n = 290$), all condition indices were highly correlated (all $r > 0.85$; $P < 0.001$); stepwise regressions of bone-marrow fat (BMF) against the three condition indices (mass/HFL, mass/HFL^z, and residual) revealed that the residual index was the only index to be retained in the models (female: $t_{1,124} = 4.089$, $P < 0.001$; male: $t_{1,148} = 5.755$, $P < 0.001$; all other $P > 0.08$). Accordingly, this index constituted the superior correlate to an independent measure of carcass body condition (BMF) and therefore was applied to obtain an index of condition among live hares.

Because 60–100% of the live radio-collared cohort on each study area was recaptured, weighed and hind-foot length was measured during bimonthly trapping periods, it was possible to monitor short-term (i.e. 50–70 day) changes in hare condition closely and evaluate these in the context of vulnerability to predation. While hares may lose mass when captured in live traps due to gastrointestinal tract evacuation, such losses are apparently modest (i.e. < 10% body mass, D.L. Murray, unpublished data) and should have been constant among captured individuals due to the consistent timing of daily trap checking (i.e. 07.00–09.00 a.m.). However, it remains possible that the condition index may cause bias in favour of pregnant females (i.e. heavy mass) or against juveniles (i.e. small structural size); accordingly, a suite of complementary variables was

also made available for inclusion in survival models (see below).

ANALYSIS OF DATA AND MODEL FITTING

Temporal, spatial and cohort-specific differences in body condition of live and depredated hares were examined using ANOVA, by blocking across bimonthly time periods, sex/age groups, and parasite and food treatments. A single condition measurement was selected randomly for each individual animal and used in analyses. Selection of hares by different predator groups and hare activity patterns were analysed using linear and logistic regression and ANOVA, with all proportions being arcsin-square root-transformed before analysis (Krebs 1999). For the analysis of hare activity, the observed temporal variability in activity patterns necessitated blocking by bimonthly time periods. Due to the relatively short duration of individual telemetry-monitoring periods and the small sample of animals monitored for activity, I was unable to employ a repeated measures approach and instead used the mean activity level for an individual during a given time period as the experimental unit. In all analyses of condition, activity and predator selection, probability values between 0·05 and 0·10 were considered to be marginally significant.

Predation rate, rather than mortality rate, was used as the dependent variable for survival analysis, with all hares that died from non-predation causes ($n = 16.5\%$ of the radio-marked population whose natural cause of death was ascertained) being right-censored (Lee 1992). Potential temporal variability in predation rate was examined by using each bimonthly time period separately (e.g. March–April 1992) as well as by pooling bimonthly time periods from multiple years (e.g. March–April). The former measure is most sensitive to bimonthly changes in mortality that do not follow an annual pattern, whereas the latter measure is sensitive to changes in mortality rate that are repeated annually. Temporal variables were made available for inclusion in survival models both as a single categorical variable as well as a set of dummy variables (entered into the model as a group) representing each time period individually. To maintain model parsimony, only the temporal variables showing significant correlation were retained, and individual time periods within a set of significant dummy variables were removed by backwards selection if non-significant. The following attributes of individual hares were tested for association with predation rate: sex, age (adult or juvenile, juveniles were considered adults on March 1 of the year following birth), study area, structural size (HFL), and parasite-reduction and food supplementation treatments. Because there may have been a time delay before hares experienced the survival benefits of parasite-reduction or food supplementation, parameters were also created representing 60-day delays in parasite-reduction and exposure to food supplementation

during the previous winter (for the following summer time periods). Log-transformed values for hare body mass and the condition index were included; these indices differ in that the former is not scaled to structural size and thus should be sensitive to absolute changes in mass only. The body condition index should be retained in models only if absolute condition had a continuous effect on vulnerability to predation. A second index of absolute condition consisted of partitioning the population into adequately fed vs. severely malnourished cohorts based on the regression of carcass BMF vs. the condition index; animals predicted to have BMF < 28% were considered to be severely malnourished (see Keith *et al*. 1984). Changes in body condition between bimonthly trapping periods (i.e. current value minus value obtained during previous trapping period) measured potential indirect effects of condition on predation, while bimonthly changes in mass or HFL determined effects of changing size on predation. Variables representing mass, size and condition also were analysed using a 60-day time delay. Finally, variables representing hare reproductive status (females pregnant, males scrotal) as well as 60-day delays in reproductive status were made available in models. All 2-way interactions between significant variables (excluding individual temporal variables) were examined for statistical significance (see Hosmer & Lemeshow 1999).

Stepwise Poisson regression (Selvin 1995) was used to evaluate the effect of independent variables on predation rate, with sexes analysed separately. In Poisson regression, the dependent variable is a rate (i.e. dead/alive offset by the no. of radio days). Poisson distribution provides the basis for statistical inference. Poisson regression is particularly useful for analysis of category-specific rates in a *post-hoc* manner and can be used to evaluate differences among cohorts that are subject to disparate occupational or environmental hazards (Selvin 1995). Because of the large number of parameters considered for retention in survival models, I did not select models using Aikike's Information Criterion (AIC) weights (see Anderson, Burnham & Thompson 2000). Rather, models were built via manual forward selection procedures, and variables reducing the model's AIC by > 2·0 were considered to be significant (Anderson *et al*. 2000). Some parameters were not complete for all samples (e.g. missing body mass or body condition measurements) and inclusion of others (i.e. reproductive information) necessarily restricted time periods under consideration in the model to reproductive seasons (March–October for females, January–October for males; includes 60-day time delays). Following such changes in model structure, all parameters found previously to be significant were re-tested for retention via backwards selection. I used the odds-ratio for the coefficient ($e^{coefficient}$ = odds-ratio), specifically at time of initial entry into the model, to describe parameter effects on survival (see Hosmer & Lemeshow 1999).
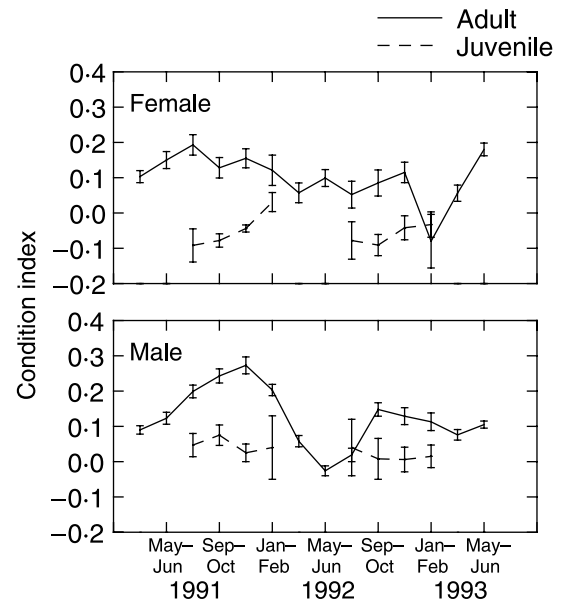
Fig. 1. Temporal changes (mean ± SE) in the body condition index for 978 free-ranging snowshoe hares in Manitoba. Juveniles were considered as adults on 1 March of the year following their birth.

Results

HARE BODY CONDITION

A total of 978 hares were marked during the study and the condition index differed among sexes ($F_{1,860}$ = 6·984, P = 0·008), and bimonthly time periods ($F_{13,860}$ = 10·549, P < 0·001). The mean value for the condition index was higher among live animals than that for necropsied carcasses, as indicated by the positive residuals for each sex (i.e. mean condition index; adult females: 0·110 ± 0·008, n = 322; adult males: 0·089 ± 0·008 (mean ± SE), n = 300). According to the condition index, juveniles were in poorer nutritional state than were adults ($F_{1,860}$ = 73·283, P < 0·001), and condition of juvenile females appeared to be poorer than that of juvenile males (Fig. 1). For both adults and juveniles, condition seemed to be worse during 1992–93 than during 1991–92 (Fig. 1). Overall, hare condition was influenced positively by food supplementation ($F_{1,860}$ = 16·738, P < 0·001); improvements in condition following supplementation were apparent for adult females (mean condition index for supplemented was 33·3% higher, n = 222), juvenile females (37·8% higher, n = 82) and juvenile males (33·3% higher, n = 66). Condition improvement for adult males was biased slightly against supplementation (7·7% lower, n = 300). The parasite-reduction treatment failed to affect hare body condition ($F_{1,860}$ = 0·883, P = 0·35).

FEMALE PREDATION RATES

Predation rates of radio-collared hares were monitored during 26 consecutive months; the average duration
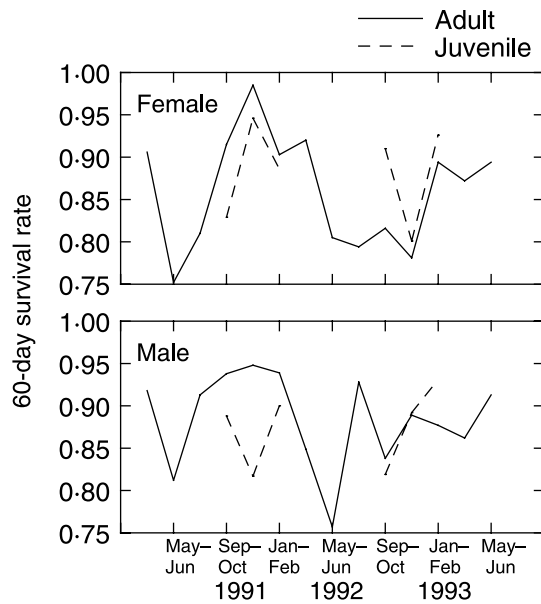
Fig. 2. Temporal changes in 60-day survival rates ((1-predation deaths/radio days)^{60}) for free-ranging snowshoe hares in Manitoba. Temporal changes were significant for both sexes; for females bimonthly survival patterns differed between years; for males, patterns repeated annually (see text). Juveniles were considered as adults on 1 March of the year following their birth. Error bars are not included for figure clarity.

of monitoring per individual was 144·6 ± 6·4 days (*n* = 612). For females, the first variable to be retained in the survival model was the set of dummy variables representing individual bimonthly time periods (ΔAIC = 11·721), indicating that there was limited seasonal repeatability to patterns of female survival (Fig. 2). Female survival tended to be highest in November–December 1991 and lowest in May–June 1991. The parameter representing parasite-reduction treatment was next retained in the model (ΔAIC = 18·052), with a coefficient (−0·845±0·20) that indicated that daily predation rate of parasite-reduced females was lower than that of parasite normals by a factor of 43% ($e^{-0.845}$ = 0·43). Next, the analysis revealed that animals known to have been palpably pregnant during the previous capture period had a higher survival probability than animals that were not palpably pregnant (ΔAIC = 11·604). The coefficient for this parameter (−1·43 ± 0·45) indicated that female predation rate declined by a factor of about 24% for animals that were found to be pregnant in the past 60 days. Retention of the time-delayed pregnancy status variable in the model necessarily restricted subsequent model iterations to the time-delayed breeding season only (May–October).

The next and final parameter to be retained in the female survival model was the index of change in condition (ΔAIC = 4·486). The coefficient associated with change in condition (−6·56 ± 2·74) yielded a mean odds-ratio indicating that for each single increment increase in the change in condition index, female
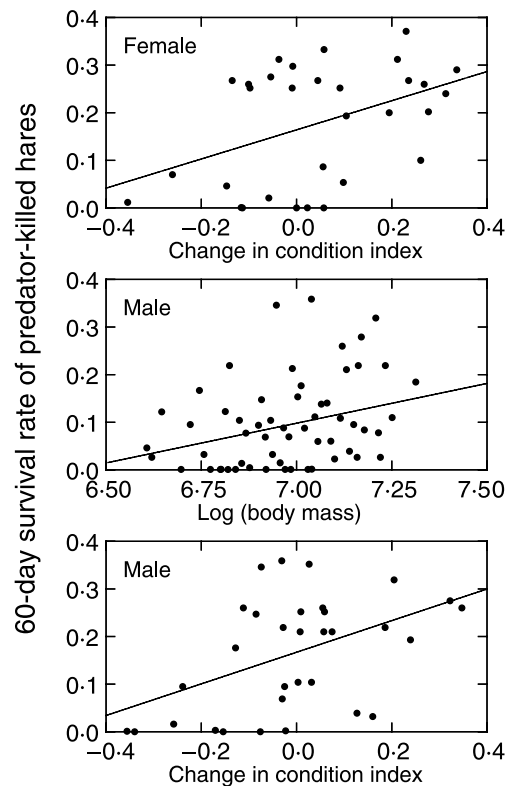
Fig. 3. Correlation between change in the body condition index (females), log-transformed body mass (males) and change in the body condition index (males) of hares that were killed by predators within a 60-day time interval, vs. survival rate. Positive values for the change in condition index are indicative of animals having experienced an improvement in condition in the last 60 days; negative values indicate a deterioration in condition. Hares surviving the 60-day time period were excluded from the analysis.

predation rate declined by a factor of 0·14%. Restricting the analysis to 60-day periods when females had been killed and change in condition was measured (i.e. surviving animals not included), females with the largest gains in condition exhibited a higher survival rate (t_{29} = 2·521, *P* = 0·017, *r* = 0·42; Fig. 3). Neither the condition index itself (ΔAIC = 1·237) nor the index of severe malnutrition (ΔAIC = −1·996) were retained in the model, indicating that direct effects of absolute condition on female hare survival were absent. None of the other remaining variables or interaction terms between significant parameters were included in later model iterations (all ΔAIC < 0·766), and no retained parameters could be removed by backward selection from the final model (all ΔAIC < 0·127).

To evaluate further the temporal strength of changing condition on survival, the parameter representing time-delayed pregnancy was removed and I re-ran the model for the entire study period (rather than simply for the time-delayed breeding season). Subsequent removal of the change in condition term failed to provide a better model fit (ΔAIC = −1·116), implying that the effects of changing condition on female hare predation occurred year-round and were not an artefact of reproductive status.

Survival of juvenile female hares differed qualitatively from that of adult females (Fig. 2), and the effect of age on female hare predation was explored by restricting the survival analysis to September–February. It was found that inclusion of age in this restricted survival model failed to provide significant explanatory power ($\Delta AIC = -0.985$), implying that adult and juvenile female survival rates did not differ.

MALE PREDATION RATES

For males, survival was more strongly related to annual time periods rather than to individual bimonthly periods ($\Delta AIC = 11.356$), suggesting that male predation rates underwent a repeatable annual cycle during the study. Survival was particularly low during May–June of 1991 and 1992 (Fig. 2). Predation rates differed significantly across time periods and therefore all dummy variables representing bimonthly time periods were retained in the model. The next parameter to enter the model was that representing log-transformed body mass ($\Delta AIC = 3.110$); the model coefficient for this parameter (-1.692 ± 0.694) indicated that on average, for every 1 unit increase in the natural log of hare mass, hare daily predation rate decreased by a factor of about 18%. When the analysis was restricted to males having been killed by predators during a 60-day interval, it was found that animals with heavier mass tended to survive longer than did lighter animals ($t_{93} = 2.254$, $P = 0.027$, $r = 0.23$; Fig. 3). The next parameter to be retained was the variable representing whether males were scrotal during January–August ($\Delta AIC = 3.056$). The coefficient for this parameter (-1.140 ± 0.694) indicated that during the reproductive season male predation rate decreased by a factor of 32% for scrotal vs. non-scrotal males.

The next and final parameter to enter the model was change in male condition ($\Delta AIC = 3.741$). The coefficient for this parameter (-4.52 ± 1.96) translated to a mean odds ratio which implied that for each increment increase in the change in the condition index, male predation rate declined by a factor of 0.11%. When the analysis was restricted to males that died during the 60-day interval for which change in condition index was measured, it was found that increases in the change in condition index correlated with improved survival ($t_{31} = 2.927$, $P = 0.006$, $r = 0.47$; Fig. 3). Neither the condition parameter itself ($\Delta AIC = -1.970$) nor that representing severe malnutrition ($\Delta AIC = -1.966$) were retained in the model, indicating that the direct effects of absolute condition on predation risk were non-significant. Neither additional independent variables nor interaction terms were retained during subsequent model iterations (all $\Delta AIC < 1.836$), and no parameters could be removed from the final model via backwards selection (all $\Delta AIC < -4.761$). However, because the final model was restricted to the male reproductive season, the parameter representing male reproductive status was

removed manually; it was determined that subsequent removal of the parameter representing change in condition was not significant for this newer model ($\Delta AIC = 1.432$), indicating that change in condition affected male predation rates principally during the reproductive season.

I examined the qualitative differences in survival rate between adult and juvenile males (Fig. 3), by restricting the analysis to September–February. I found that while age made modest improvements in the fit of the model ($\Delta AIC = 1.136$), such gains were eliminated when body mass was first included in this latter model ($\Delta AIC = -1.677$). Because body mass was the first parameter relevant to animal physical state to be retained in the original male survival model, the significant role of body mass on male vulnerability to predation was probably not an artefact of age-specific differences in mass.

SIZE AND CONDITION OF DEPREDATED HARES

The physical attributes of animals dying of predation within a given time interval were compared to a single size and condition measurement taken from individuals ($n = 503$) that were not known to have been killed by predators (i.e. did not die during the study, trapping-related death, never radio-collared, etc.). When I blocked for bimonthly time period and age, female mass ($F_{1,422} = 0.217$, $P = 0.64$) and condition ($F_{1,418} = 0.119$, $P = 0.73$) did not differ between predator-killed and live animals (Table 1). However, 60-day change in mass and condition indicated that the depredated cohort tended to have gained less mass ($F_{1,207} = 10.174$, $P = 0.002$) and experienced less of an improvement in condition ($F_{1,194} = 4.543$, $P = 0.034$) compared to live prey (Table 1). The proportion of live vs. predator-killed females predicted to be severely malnourished was similar ($\Delta AIC = -0.446$; Table 1), implying that absolute condition failed to influence female predation risk.

For males, when blocked for time period and age, it was found that the predator-killed cohort was lighter ($F_{1,347} = 9.321$, $P = 0.002$) and in marginally poorer condition ($F_{1,344} = 2.773$, $P = 0.097$; Table 1) than surviving animals. Predator-killed male hares also had a smaller change in mass ($F_{1,186} = 11.048$, $P = 0.001$), but change in condition was similar between groups ($F_{1,171} = 0.063$, $P = 0.80$; Table 1). Similar proportions of severely malnourished males were found in the live vs. predator-killed cohorts ($\Delta AIC = -2.00$; Table 1), again suggesting that effects of absolute condition were modest/absent. Thus, these results confirmed that the role of condition on predation in female hares was related largely to deteriorating nutritional state, whereas for males low mass (i.e. smaller size), and to a lesser extent deteriorating condition during the reproductive season, were principally associated with predation.

Table 1. Comparison of attributes (mean ± SE) of predator-killed hares to that of animals not known to have been killed by predators (live population). Severely malnourished refers to the percent of hares predicted to have bone marrow fat < 28% given their body condition index. Data were back-transformed for display in the table and sample sizes are in parentheses

	Female		Male	
	Live population	Predator-killed	Live population	Predator-killed
Body mass (g)	1254 ± 15 (272)	1225 ± 18 (166)	1120 ± 11 (231)	1110 ± 14 (132)*
Body condition index	0·07 ± 0·03 (271)	0·05 ± 0·02 (153)	0·10 ± 0·04 (231)	0·08 ± 0·02 (129)**
Change in body mass (g)	10·0 ± 1·9 (134)	7·5 ± 1·7 (89)*	17·8 ± 1·6 (123)	3·3 ± 2·2 (79)*
Change in condition index	0·04 ± 0·01 (124)	0·02 ± 0·02 (86)*	0·02 ± 0·01 (111)	−0·02 ± 0·02 (76)
Severely malnourished (%)	55·8 (271)	61·9 (153)	15·5 (231)	13·5 (133)

*Significant ($P < 0.05$) differences between live and predator-killed cohorts. **Marginally significant ($0.05 < P < 0.10$) differences between live and predator-killed cohorts.

Table 2. Comparison of attributes (mean ± SE) of hares killed by known avian and mammalian predators. Severely malnourished refers to the percent of carcasses with bone-marrow fat < 28%. Data were back-transformed for display in the table and sample sizes are in parentheses

	Avian	Mammalian
Sex (% female)	50·4 (103)	51·9 (108)
Age (% adult)	53·3 (103)	42·6 (108)
Body mass (g)	1184 ± 18 (102)	1148 ± 20 (108)
Body condition index	0·06 ± 0·02 (100)	0·08 ± 0·01 (106)
Change in body mass (g)	11·4 ± 1·7 (60)	7·4 ± 1·3 (61)
Change in condition index	0·02 ± 0·02 (58)	−0·03 ± 0·02 (58)*
Bone-marrow fat (%)	35·6 ± 1·2 (53)	37·3 ± 4·2 (17)
Severely malnourished (%)	38·8 (103)	43·5 (108)

*Significant ($P < 0.05$) differences between prey killed by avian and mammalian predators.

HARES KILLED BY AVIAN AND MAMMALIAN PREDATORS

Of the 302 predator-implicated deaths, avian predators, known mammalian predators and suspected mammalian predators killed 34%, 36% and 30% of the sample, respectively. The proportion of hares killed by known avian and mammalian predators was similar across bimonthly time periods ($\Delta AIC = −1.902$), sex ratios ($\Delta AIC = −1.960$), and age ratios ($\Delta AIC = 0.472$; Table 2). The size and condition of the predator-killed cohort also was largely similar across predator taxa; when blocking for sex and age, it was found that body mass ($F_{1,198} = 1.958$, $P = 0.16$), and the condition index ($F_{1,190} = 0.709$, $P = 0.40$) measured during the final live capture were similar between hares killed by known avian and mammalian predators (Table 2), as was the change in body mass ($F_{1,104} = 0.007$, $P = 0.94$). However, the change in condition index differed between avian and mammalian predators ($F_{1,100} = 4.111$, $P = 0.045$) with animals killed by avian predators tending to have experienced slight improvement in condition, compared to the slight worsening of condition observed in mammal-killed hares (Table 2). Because on average the live prey cohort also tended to experience improving condition during the study (Table 1), these results suggest that mammalian predators selected hares in declining condition, rather than avian predators selecting hares in improving condition.

Bone-marrow fat levels of depredated hares failed to differ among predator groups ($F_{1,54} = 0.188$, $P = 0.67$; Table 2). Using the proportion of live animals that were predicted to be severely malnourished (i.e. < 28% BMF), it was estimated that similarly low proportions of avian and mammalian kills were severely malnourished ($\Delta AIC = −1.316$, $P = 0.44$; Table 2). Average BMF in predator-killed hares was relatively high ($36.1 ± 1.8\%$, $n = 70$), confirming that comparatively few predator-killed animals were in poor absolute condition.

HARE ACTIVITY PATTERNS

Analysis of activity patterns among hares equipped with motion-sensitive transmitters revealed that activity differed seasonally ($F_{5,71} = 6.744$, $P < 0.001$), yet overall was similar between sexes ($F_{1,71} = 0.150$, $P = 0.70$). On average, males and females were active $34.2 ± 2.7\%$ ($n = 31$) and $35.4 ± 2.3\%$ ($n = 52$) of the time, respectively. However, males were more active during the early phase of the reproductive season (March–April), whereas females increased activity later in the season (May–June) (sex–time interaction: $F_{5,71} = 2.637$, $P = 0.030$; Fig. 4). Using a stepwise procedure, it was found that female activity patterns were correlated positively to body condition ($F_{1,36} = 2.15$, $P = 0.038$) but not to body mass ($P = 0.59$), whereas for males neither mass nor condition were related to activity
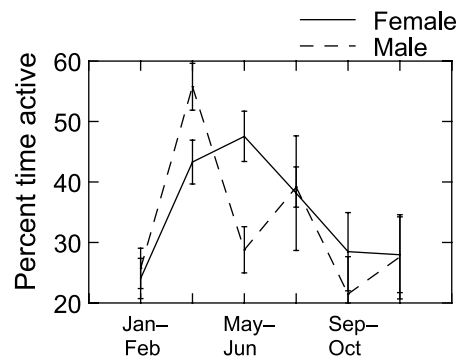
Fig. 4. Seasonal activity patterns of hares equipped with mortality-sensitive radio-transmitters. Data were back-transformed for display in the figure.

($P > 0.36$). Both change in mass and change in condition failed to correlate to activity for hares of either sex (all $P > 0.63$). Activity patterns were similar between individuals that were depredated during a 60-day interval vs. those known to have survived (females: $F_{1,45} = 0.063$, $P = 0.80$; males: $F_{1,24} = 0.901$, $P = 0.35$).

Discussion

Risk-sensitive foraging and starvation-predation trade-offs have been implied extensively from both the theoretical (e.g. Fraser & Huntingford 1986; McNamara & Houston 1987, 1990, 1999; Ludwig & Rowe 1990) and empirical (e.g. Milinski & Heller 1978; Sullivan 1989; Sinclair & Arcese 1995) perspectives. However, there remains a clear need to show in the field that relative condition of prey and vulnerability to predation are linked. Results from the present analysis support the general premise that when food is abundant nutritional status plays only an indirect role in determining prey vulnerability to predation. In support of my first prediction (i.e. no direct effects of absolute condition on predation), most hares were found to be in adequate condition during the study and predators did not select severely malnourished individuals disproportionately from the population. A survival advantage was not gained by improvements in hare condition elicited by food supplementation, implying that condition in unmanipulated controls for the most part was above any threshold where direct predation risk augmentation could act through physical debilitation. This result contrasts with other studies showing direct effects of nutritional status on hare predation either during periods of food limitation and population decline (Keith *et al.* 1984), or in marginal habitat probably characterized by poor food abundance (Sievert & Keith 1985; but see Wirsing, Steury & Murray, in press). While in the present study female hares clearly benefited from a survival perspective following parasite-reduction, this treatment failed to elicit detectable changes in body condition. This supports the contention that the advantage gained from parasite reduction was

ultimately not manifest through energy intake maintenance but rather via reduced foraging activity (Murray *et al.* 1997; see also Milinski 1984). This point also is consistent with the alleged tendency for hares to trade-off energy gain for risk minimization, when predation pressure is high (Hik 1995; Boonstra *et al.* 1998a). However, given that most hare populations are characterized by high productivity and low survival rates (see reviews by Hodges 2000; Murray 2003), energy gains and investment into production, in theory, should be maximized at the expense of predation risk avoidance (Magnhagen 1991; Sih 1994; Oksanen & Lundberg 1995; see also Belovsky 1984). Thus, relatively modest changes in hare condition should elicit reduced predation risk sensitivity under most circumstances.

The second prediction (i.e. indirect effects of relative condition on predation) was supported by results suggesting that the role of nutrition on hare vulnerability to predation was a function of the interaction between changing condition and increased predation risk. Recall that the index of change in condition represented a continuous metric, so that retention of this parameter in survival models indicated that both female and male hares were disadvantaged when body condition was deteriorating most dramatically, irrespective of their absolute condition. This is an important point illustrating the linkage between potential fitness and survival-production trade-offs, even when prey are not faced with absolute food shortage. However, hares have scant fat reserves (Litvaitis & Mautz 1980; Whittaker & Thomas 1983), meaning that even modest fluctuations in body condition are probably protein-based and ultimately may elicit physical deterioration and reduced fecundity and productivity. Unless met by compensatory foraging that inevitably would be associated with increased predation risk, such body-condition fluctuations may me significant to hares faced with a volatile fitness potential. Similar justification has been offered to explain riskier foraging among prey following periods of food limitation (e.g. Pettersson & Brönmark 1993; Damsgård & Dill 1998) and/or body condition deterioration (e.g. Sweitzer & Berger 1992). Note, however, that the change in condition index was the last parameter to be retained in survival models and that the overall effects of relative condition on predation risk were modest. Thus, the predation costs associated with observed changes in condition were mild in comparison to other factors contributing to hare mortality.

Further evidence for this latter point can be derived from the minor physical differences between 'live' vs. predator-killed female hares. Mean gains in condition were less for the depredated than the live female cohort, which is generally consistent with results from the present survival analysis. However, the absolute condition of females was similar between live and depredated groups, indicating that their overall physical state was also similar. In contrast, for males both absolute

and relative body mass, and not condition, were the principal features differentiating live and depredated groups. For male hares, reproductive opportunities favouring larger (i.e. heavier) individuals could exist and thus lead to increased risk insensitivity among smaller animals. However, the higher predation rate among scrotal males is difficult to reconcile in this context, presuming that such animals also are larger and in better condition. Typically, the onset of reproductive condition precedes increased mobility in small mammals (e.g. Behrends, Daly & Wilson 1986; Magnhagen 1991), and such increases in mobility may in turn augment predation rates (Norrdahl & Korpimäki 1998). The failure for the fourth prediction (increased activity following condition change) to be upheld by study results supports further the idea that the effect of changing condition on activity and predation risk of hares was subtle. Indeed, the observed increases in male activity patterns early in spring corresponded with possible increases in mate-searching behaviour at the onset of the reproductive season; females increased their activity levels later in spring during pregnancy and weaning time periods. These increases corresponded loosely with seasonal increases in male and female predation rates. It is notable, however, that no measure of relative condition was related to observed behavioural changes of activity-monitored hares, suggesting that the implied linkage between condition change and behavioural alteration remains tentative. Indeed, condition-sensitive changes in predation risk were probably modest compared to those elicited directly by reproductive activities.

Models describing patterns of prey selection suggest that prey vulnerability is determined by the product of predator encounter and capture rates (Gerritsen & Strickler 1977; Sih & Moore 1990), and that disadvantaged individuals are selected disproportionately by predators when capture success is low (e.g. Temple 1987; Juanes 1994). Encounter and capture probabilities should be closely related to predator hunting behaviour, and thus be largely specific to particular predator species. For snowshoe hares, reported capture success by mammalian predators (see Murray *et al.* 1995; O'Donoghue *et al.* 1998) is high relative to that observed for other predator and prey taxa, implying that animals killed by such predators should not be characterized by specific physical attributes (Wirsing *et al.* in press). My third prediction (i.e. ambush predators kill prey in declining condition) was not borne out by the present analysis, and in fact it was found that hares experiencing condition declines were killed principally by predators (i.e. coyotes) that were considered to hunt by coursing rather than by ambush. This observation goes contrary to both the prevailing thought regarding predator hunting strategy and prey selection patterns (see Greene 1986; FitzGibbon & Fanshawe 1989), and the observation that overnourished hares are killed disproportionately by ambush (i.e.

great-horned owl) predators (Rohner & Krebs 1996). However, coyotes may actually employ an ambush rather than a coursing hunting strategy to capture hares (Murray *et al.* 1995; O'Donoghue *et al.* 1998). It follows that if hare deaths from coyote predation occurred principally through ambush rather than coursing, then the generalization regarding patterns of prey selection relative to predator hunting strategy, may in fact be correct. Clearly, at this juncture the relationship between absolute vs. relative condition of prey, predator hunting strategy, and patterns of prey selection requires further investigation.

Previous studies on prey nutritional status and vulnerability to predation have been limited in their assessment of the condition–predation link because of a reliance upon single-sample indices that are restricted to the effects of absolute condition on predation. Some measures (e.g. BMF measurement) may also only differentiate between starving and non-starving individuals (see Mech & DelGiudice 1985), and thus be of limited utility. Most previous studies showing condition-sensitive predation probably were undertaken when food availability was limited, yet because the majority of prey populations probably are held below levels of food limitation (Krebs *et al.* 1997) the widespread recognition of direct effects of condition on prey selection may be overestimated. Results from this study show that the occurrence of relative condition effects need not be linked to absolute condition, and that populations not subject to food shortage could be influenced by an indirect nutrition–predation association. For hares, this relationship may be temporally and spatially variable, such that across the species' range differences in food availability, predator species and predator abundance may alter substantially patterns of prey selectivity and the role of relative condition on hare predation risk. More generally, the critical enigma remains the nature of the linkage between condition and predation through behavioural change of the prey, and how this linkage may vary according to an individual prey's fitness potential. Accordingly, the role of prey condition on vulnerability to predation needs to be examined more closely across a range of predator–prey systems and environmental conditions, using sensitive and relevant measures of both prey condition and behaviour.

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