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RELATIONSHIP BETWEEN BODY CONDITION AND VULNERABILITY TO PREDATION IN RED SQUIRRELS AND SNOWSHOE HARES

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We examined the relationship between physical condition and vulnerability to predation in 2 species of mammals having different life history traits. We predicted that predators would be more likely to kill substandard individuals disproportionately in red squirrels (*Tamiasciurus hudsonicus*) than in snowshoe hares (*Lepus americanus*), given that sciurids apparently are less susceptible to predation. We also predicted that differences would exist between patterns of substandard-prey selection among groups of predators of red squirrels but not among predators of snowshoe hares because of differential predator efficiencies in capturing elusive prey. Through radio tracking, we found that substandard squirrels (n = 113) were disproportionately vulnerable to predation, whereas hares (n = 125) were killed irrespective of condition. Although the relationship between condition and vulnerability to predation, relative to predator groups, did not differ significantly for either species of prey, the difference was qualitatively greater in squirrels than in hares. These results support the notion that predators are more likely to kill substandard individuals disproportionately when targeting prey species that are difficult to capture and, moreover, that the tendency for particular species of predators to take substandard prey may be a reflection of the predator's hunting strategy and efficiency.

Key words: condition, *Lepus americanus*, life history, predation, prey, red squirrel, snowshoe hare, *Tamiasciurus hudsonicus*

Predators commonly are assumed to kill disproportionately more individual prey animals that are in substandard physical condition (Curio 1976; Errington 1946; Morse 1980; Slobodkin 1968). In theory, substandard individuals may be particularly susceptible to predators because they are conspicuous, prone to risky decision-making, and less able to evade and repel predators (Curio 1993; Lima and Dill 1990; Mesa et al. 1994; Mykytowycz et al. 1959). Previous efforts to demonstrate this phenomenon in terrestrial vertebrates have been plagued by several important limitations: prey animals in terrestrial systems normally are consumed entirely by their predators, leaving little evidence with which to determine condition (Temple 1987); many studies have used potentially biased prey-sampling techniques (e.g., shot samples, opportunistically located carcasses, vehicle-killed animals—FitzGibbon and Fanshawe 1989; Koivunen et al. 1996; Sinclair and Arcese 1995); and many studies have indexed the condition of prey using analysis of bone-marrow fat, which can only detect severely malnourished individuals (Mech and

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DelGiudice 1985). A more objective method for evaluating the substandard-predation paradigm could entail the surveillance of living prey animals, followed by a post hoc comparison of monitored individuals subject to different fates (Boutin 1995). Such an approach should provide more representative samples for tests of differential prey selection.

Temple (1987) argued that life-history characteristics of prey should influence the degree to which prey vulnerability is associated with substandard condition. According to his model, substandard individuals should be disproportionately vulnerable to predation in species that are normally difficult to capture and subdue (e.g., many K-selected species manifesting high survival); conversely, differences in condition should have a lesser effect on vulnerability to predation in species that are easier to capture (e.g., many r-selected species having low survival—Temple 1987). However, rigorous tests of this hypothesis are lacking, partly because few studies have monitored the survival of multiple prey species subject to the same predation pressure (i.e., species sharing predators and studied synchronously in time and space). Thus, we sought to test Temple's substandard-predation hypothesis using 2 species of prey with different life histories, red squirrels (*Tamiasciurus hudsonicus*) and snowshoe hares (*Lepus americanus*).

Sciurids may be better able to escape and rebuff attacks by predators than are leporids because of their smaller size, use of 3-dimensional space, and tendency to defend themselves once grasped (Stuart-Smith and Boutin 1995; Temple 1987). For example, Temple (1987) reported that red-tailed hawks have success rates of 18% when hunting cottontail rabbits (*Sylvilagus floridanus*) and of 12% when hunting gray squirrels (*Sciurus carolinensis*); selection on the former species was found to be unbiased, whereas that of the latter species focused on substandard individuals. Sciurids are characterized by comparably low birth rates and produce offspring that are relatively slow to develop, whereas leporids produce large litters composed of rapidly developing young that emerge synchronously and as a result swamp predators (Nice et al. 1956; O'Donoghue and Boutin 1995). Given the apparent difference in life history and susceptibility to predation between these 2 taxonomic groups, we predicted that body condition would be a significant predictor of vulnerability to predation in the elusive red squirrel but not in the less elusive snowshoe hare (prediction 1).

A logical corollary to Temple's model is that among species of prey that are subject to disproportionate predation of substandard individuals (i.e., those species that are relatively difficult to capture and subdue), the difference in susceptibility of substandard individuals relative to normal individuals should vary as a function of predator hunting strategy (Estes and Goddard 1967; FitzGibbon and Fanshawe 1989; Kruuk 1972; Schaller 1972; Temple 1987). For example, predators that stalk, ambush, and quickly subdue their prey or otherwise encounter their prey randomly should be less likely to take disproportionately individuals in poor physical condition than predators that course (chase their prey over long distances) or have difficulty subduing their prey (Estes and Goddard 1967; Schaller 1968). In species of prey that are relatively easy to capture, however, various predator hunting techniques should not differ greatly in their tendency to yield substandard (or nonsubstandard) individuals. Accordingly, given the likely difference in susceptibility between red squirrels and snowshoe hares, we predicted that the relative vulnerability of substandard individuals would differ as a function of predator class to a greater degree in squirrels than in hares (prediction 2).

Materials and Methods

Survival and proximate cause of mortality.—This study was conducted in the Clearwater National Forest, Idaho (46°N, 114°W) from May 1998 to May 2000. Squirrels and hares were livetrapped seasonally (four 90-day intervals per year) on six 10-ha study sites. Captured animals were handled using procedures in accord with standard guidelines (Canadian Council on Animal Care 1984) and approved by the University of Idaho Animal Care and Use Committee (protocol number 9029). For our index of body condition, we used body mass divided by hind-foot length. This metric, which should be reflective of protein or fat reserves (or both), has been used widely in small mammals in general (Krebs and Singleton 1993), and in hares (Keith and Windberg 1978; Sievert and Keith 1985) and squirrels (Becker et al. 1998) in particular. When multiple measures existed for an animal over a given 90-day trapping interval (range = 1–7), mean values were used to generate the condition index. All captured individuals were equipped with mortality-sensitive radiocollars (Telemetry Solutions, Concord, California). Survival was monitored daily, and individuals were located within 24 h of death by using a handheld antenna and receiver (Advanced Telemetry Systems, Isanti, Minnesota). Predation events were identified on the basis of evidence left at the kill site (Boutin et al. 1986; Murray et al. 1997; Stuart-Smith and Boutin 1995) and, when possible, by carcass necropsy and laboratory analysis. Kills were assigned to 1 of 4 predator classes (avian, canid, mustelid, or unknown) on the basis of location of carcass remains, tracks, and other distinguishing marks at the kill site as well as carcass necropsy (Boutin et al. 1986; Murray et al. 1997; Stuart-Smith and Boutin 1995).

Statistical analysis.—We tested for significant relationships between the condition index and vulnerability to predation using Poisson regression, a procedure in which the dependent variable is a rate and a Poisson distribution is used to draw statistical inference (Selvin 1995). Given that we used 90-day trapping intervals (January–March, April–June, July–September, and October–December) and that temporal changes in prey condition may have affected vulnerability to predation, our dependent and independent variables (daily predation rate and individual condition indices) were stratified seasonally. Four different predation models were generated for both species of prey: an overall model explaining general patterns in vulnerability to predation irrespective of predator type, a model explaining vulnerability to predation of individuals killed by canid predators (deaths attributed to other predators were right-censored—Lee 1992), a model explaining vulnerability to predation of individuals killed by mustelid predators, and a model explaining vulnerability to predation of individuals killed by avian predators. The 1st model allowed us to assess whether nutritional condition influenced vulnerability to predation in general (the Temple hypothesis; prediction 1), whereas the latter 3 models allowed us to examine the relationship between condition and vulnerability to predation among individuals taken by specific classes of predators (prediction 2). The parameters for each model were estimated using the maximum-likelihood method, whereby the significance of the condition index was assessed using the partial-likelihood ratio test (Hosmer and Lemeshow 1999). For all statistics, tests were considered significant at $\alpha = 0.05$. In all analyses, we generated coefficient estimates and confidence measures even if the condition index was not a significant predictor of vulnerability to predation, so that we could further evaluate the influence of condition on predation both among and within species of prey.

We depicted the influence of nutritional condition on predation rates using rate ratios, where rate ratio equals e raised to the power of the coefficient estimate (Hosmer and Lemeshow 1999). Rate ratios express the relative vulnerability to predation of prey as a function of selected independent variables. In our case, rate ratios quantified the influence of each unit decrease in condition equal to 20% of the mean condition index on vulnerability to predation (i.e., the increase in vulnerability to predation associated with each 0.99-g/mm decrease in the condition index for squirrels and with each 1.70-g/mm decrease in the condition index for hares). Thus, by comparing rate ratios we were able to assess the importance of condition in relation to vulnerability to predation in both species, as well as across predator classes. Standard errors of rate ratios are asymmetrical because of the calculation used to convert coefficient estimates to rate ratios. Thus, rate ratios are presented with both positive and negative standard errors.

In light of the potential that our condition index was biased by cohort-specific (i.e., age, sex, and size) differences within the monitored cohort (Green 2001; Hodges et al. 1999), we conducted a separate analysis in which age, sex, and structural size variables were made available for inclusion in the 4 models for each species. For each model, the results produced for both species by this analysis were qualitatively similar to those characterizing our analysis involving the condition index alone (i.e., no additional variables were significant predictors of vulnerability to predation, and species-specific trends with respect to condition and predation risk did not change); thus, we felt confident that the trends reported herein reflect the influence of condition, rather than those of age and sex, on vulnerability to predation. Also, given that our study animals were trapped concurrently in the same areas, we assumed that they were exposed to the same predator cohort and that observed differences in the importance of body condition to vulnerability to predation were not a function of spatial or temporal variability in predation pressure.

We tested for statistical differences among coefficient estimates (i.e., significant differences in the strength of the relationships between the condition index and vulnerability to predation) within and between the 2 prey species using bootstrapping (Krebs 1999; Mooney 1993). Each time the bootstrapping procedure was used, samples were drawn repeatedly with replacement from the original data set until a new data set of equal size was created (each sample represented one 90-day interval over which survival was monitored; $n = 221$ for squirrels, $n = 179$ for hares). Coefficient estimates of the relationship between the condition index and vulnerability to predation were then generated for the new data set. To compare coefficient estimates between prey species or predator groups, bootstrapped data sets for the cohorts being compared (e.g., squirrels versus hares) were generated simultaneously, and the differences between the coefficient estimates were recorded. A total of 2,000 bootstrapped data sets were generated for each cohort in the comparison such that a distribution of the differences in coefficient estimates was produced that could be evaluated for significance. If 0 was not contained within the middle 95% of this bootstrapped distribution (i.e., the 50th to 1,950th ranked value), the differences in coefficient estimates were deemed significant (2-tailed P-value ≤ 0.05).

Results

We monitored the survival of 113 radio-collared red squirrels and recorded 49 predation events, which yielded an annual predation rate of 72%. We determined that 49% of these deaths were from predation by mustelids, 27% by raptors, and 8% by canids; 16% could not be attributed to a specific class of predator. Given the relative paucity of deaths they caused, canids were excluded from predator-group analysis with respect to squirrels. The mean condition index for red squirrels was 4.97 g/mm (range = 3.89–6.36 g/mm).

We monitored the survival of 125 radio-collared snowshoe hares, recording 70 predation events (annual predation rate = 82%). Among these, we determined that the following proportions were taken by each class of predator: canids, 44%; raptors, 21%; and mustelids, 13%; 21% could not be classified according to type of predator. The mean condition index for hares was 8.51 g/mm (range = 5.43–14.44 g/mm).

Prey species comparison.—A significant negative relationship existed between the condition index and vulnerability to predation in red squirrels ($P = 0.02$). The rate ratio describing the influence of this variable (2.62, −0.89, +1.34) indicated that for every 0.99-g/mm decrease in condition index (equals 20% of the mean condition index in squirrels), a squirrel's vulnerability to predation increased by 162% (Fig. 1). Thus, physically substandard squirrels were disproportionately vulnerable to predation.

By comparison, condition was not a significant predictor of vulnerability to predation in snowshoe hares ($P = 0.15$). The rate ratio describing the influence of condition (1.34, −0.25, +0.30) indicated that for every 1.70-g/mm decrease in condition index (equals 20% of the mean condition index in hares), a hare's vulnerability to predation increased by only 34% (Fig. 1). Thus, physically substandard hares were not disproportionately vulnerable to predation.

Bootstrapping indicated that the influence of condition on vulnerability to predation was significantly greater in squirrels than in hares, with only 6 of the 2,000 (P

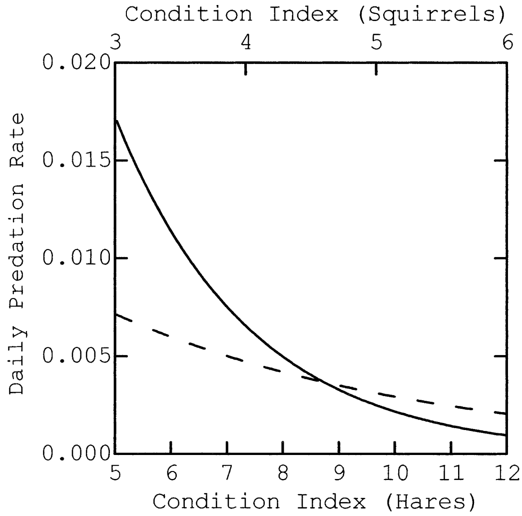

FIG. 1.—Relationships between condition index and daily predation rate in red squirrels and snowshoe hares, generated using Poisson regression. Solid line represents the relationship for squirrels; $P(Y) = e^{-1.15-0.97 \cdot X}$. Dashed line represents the relationship for hares; $P(Y) = e^{-4.05-0.18 \cdot X}$.

= 0.01) bootstrapped differences in coefficient estimates being <0.

Predator class comparison.—Among squirrels depredated by mustelids, condition was a significant predictor of vulnerability to predation ($P = 0.02$). The rate ratio describing the influence of this variable (3.42; Fig. 2) indicated that for every 0.99-g/mm decrease in condition index, a squirrel's vulnerability to predation by mustelids increased by 242%. Condition was not a significant predictor of vulnerability to predation among squirrels depredated by avian predators ($P = 0.27$). The rate ratio describing the influence of this variable (2.35; Fig. 2) indicated that for every 0.99-g/mm decrease in condition index, a squirrel's vulnerability to predation by avian predators increased by 135%. The rate ratios differed by 1.07 across the 2 predator classes.

Condition was not a significant predictor of vulnerability to predation among hares taken by mustelid predators ($P = 0.39$). The rate ratio describing this relationship (1.69; Fig. 2) indicated that for every 1.70-g/mm

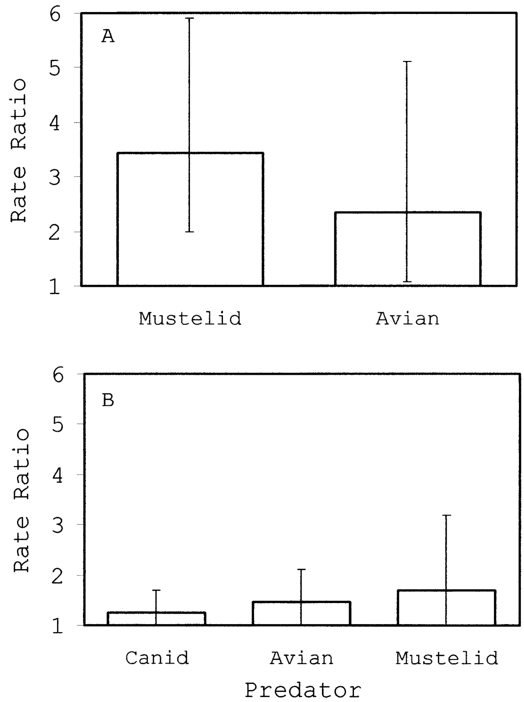

FIG. 2.—Rate ratio describing the effect of condition on vulnerability to predation in A) red squirrels and B) snowshoe hares, stratified across predator classes. Rate ratios indicate the increase in vulnerability to predation for every decrease in the condition index equal to 20% of that prey's mean condition index.

decrease in condition index, a hare's vulnerability to predation by mustelid predators increased by 69%. Furthermore, condition was not a significant predictor of vulnerability to predation among hares killed by avian predators ($P = 0.30$). The rate ratio describing the influence of this variable (1.46; Fig. 2) indicated that for every 1.70-g/mm decrease in condition index, a hare's vulnerability to predation by avian predators increased by 46%. Among hares depredated by canids, condition was not a significant predictor of vulnerability to predation ($P = 0.47$). The rate ratio describing the influence of this parameter (1.24; Fig. 2) indicated that for every 1.70-g/mm decrease in condition index, a hare's vulnerability to predation by canids increased by

24%. Across the 3 predator classes tested, the rate ratios differed by 0.44.

Bootstrapping indicated that the extent to which condition influenced vulnerability to predation in squirrels did not differ significantly according to predator class; 760 of the 2,000 bootstrapped differences in coefficient estimates were <0 ($P = 0.76$). The mean bootstrapped estimate of the difference in coefficient estimates (corrected for bootstrapping bias—see Krebs 1999) was 0.44. Similarly, bootstrapping (comparing the 2 predator groups having the most extreme differences, mustelid and canid predators) indicated that influence of condition on vulnerability to predation in hares did not differ significantly according to predator class; 607 of the 2,000 differences in coefficient estimates were <0 ($P = 0.61$). The mean bootstrapped estimate of the difference in coefficient estimates (corrected for bootstrapping bias) was 0.18.

Discussion

Our results are consistent with Temple's substandard-predation hypothesis (Temple 1987). In accord with our 1st prediction, red squirrels in physically substandard condition (as indexed by a relatively low ratio of body mass to structural size) were significantly more vulnerable to predation than squirrels in superior condition, whereas vulnerability to predation among snowshoe hares was not related to condition. The present analysis served as a rigorous test of Temple's model, given that it was based upon a large sample of hares and squirrels that were monitored simultaneously and intensively in the same areas, rather than on a potentially biased sample of shot animals or carcasses examined postmortem for distinguishing physical characteristics.

Under Temple's model, the relatively greater effect of condition on vulnerability to predation in red squirrels suggests that this species is not particularly susceptible to predation under normal circumstances. Although few studies have addressed the success with which predators hunt red squirrels explicitly, some have shown that annual predation rates on these animals generally are low, relative to those on other small mammals (Kemp and Keith 1970; Rusch and Reeder 1978; Stuart-Smith and Boutin 1995). Predation rates may be influenced by predation pressure rather than by hunting success; however, the fact that red squirrels manifest high survival even when subject to heavy predation pressure (Stuart-Smith and Boutin 1995) suggests that the relatively low predation rates reported in the literature are attributable to the difficulty associated with catching or killing (or both) these animals. Thus, we expected predators to have greater success capturing squirrels in poor condition. Conversely, the lesser effect of condition on vulnerability to predation in hares likely was because of their comparably high susceptibility to predation. Numerous studies have shown that snowshoe hares are subject to heavy predation rates (Keith 1990) and, moreover, that terrestrial predators hunting this species often are successful (≥30%—e.g., Murray et al. 1995; O'Donoghue et al. 1998; Raine 1987). Thus, like other leporids (see Temple 1987), relatively healthy hares may be easy enough to capture; therefore, substandard individuals are not notably more vulnerable.

Biologists typically have addressed questions pertaining to prey selection by categorizing predators according to their size (e.g., small versus large predators—Huggard 1993; Pierce et al. 2000) and hunting techniques (e.g., ambush versus coursing—Caro and FitzGibbon 1992; Gerritsen and Strickler 1977; Greene 1986; Kunkel et al. 1999). This approach potentially is problematic, however, given that it does not take into account the relative difficulties associated with capturing different species of prey (Temple 1987) and that predators may alter their hunting techniques depending on their surroundings and the particular prey animal that they are pursuing (Engelmayer 1992; Guinet 1992; Kullberg 1995). Consequently, the oft-used categorical approach cannot explain why predators using a particular strategy tend to capture substandard animals in 1 species of prey but not in others. An alternative means of explaining selection patterns is to classify predators according to the efficiency with which they capture particular prey species. Although all predators likely are able to capture substandard prey with greater ease than normal prey, Temple's model predicts that only inefficient predators tend to kill substandard prey disproportionately (i.e., the potential for substandard animals to be disproportionately vulnerable to predation is only realized in cases where inefficient predators are involved). By inference, then, prey that are easy to capture should not be subject (or less subject) to substandard predation by any predator class, irrespective of strategy, because most predators should hunt them efficiently enough to produce random (or near random) selection. Conversely, prey animals that are difficult to capture should be subject to substandard predation by some (e.g., those that are inefficient) but perhaps not all predator classes. For example, certain species of predator may hone their hunting techniques through learning or coevolution; these predators should hunt elusive prey with increased efficiency. Therefore, a given predator's efficiency may be inferred from the extent to which it takes substandard individuals from a particular prey population (Temple 1987).

We assumed that snowshoe hares would be captured with greater efficiency by predators than would red squirrels. Thus, we also predicted that the degree to which predator class influenced the relationship between substandard condition and vulnerability to predation would be greater in squirrels. Although the difference between the tendency of mustelid and avian predators to kill substandard squirrels was not significant (rate ratios differed by 1.07), this difference was qualitatively larger than that between the 3 hare predator classes (rate ratios differed by only 0.44). Moreover, with respect to squirrels, the condition parameter was a significant predictor of vulnerability to predation by mustelid predators, but not by avian predators, whereas the condition variable was not a significant predictor of vulnerability to predation for any of the hare predators. This trend supports our 2nd prediction qualitatively because it indicates that the disparity in hunting strategies used by squirrel predators had a larger influence on their tendency to capture substandard individuals than did the varying strategies used by the same predators when hunting hares. Specifically, our results suggest that because hares are relatively easy to capture, the different hunting strategies used by canids (ambush and coursing—Halpin and Bissonette 1988; Murray et al. 1995; Wells and Bekoff 1982), mustelids (coursing—Powell 1978; Raine 1987), and raptors (ambush—Temple 1987; Toland 1986) were roughly equal in efficiency. Conversely, because squirrels are relatively difficult to capture, the different strategies used by their mustelid and avian predators were associated with a wider range of efficiencies. Moreover, given that mustelid predators were more likely to take substandard squirrels than were avian predators, we can surmise that raptors likely hunted squirrels with greater efficiency than did mustelids.

In summary, our results suggest that life-history characteristics affect the relationship between condition of prey and vulnerability to predation, with relatively elusive species of prey being more likely to experience disproportionate predation of substandard individuals than more susceptible species. Furthermore, the outcomes of this analysis suggest that different predator classes may vary in their tendency to take substandard individuals in species of prey that are difficult to capture but not in species of prey that are easy to capture. The logical next step in this field of investigation will be to test this model by monitoring the rates of success in attacks by individual predators on prey for which body condition is known. Under the model discussed here, inefficient predators should experience higher success when pursuing elusive individuals characterized by relatively poor physical condition than when chasing difficult-to-capture prey in relatively good condition. Conversely, the attack-success rates of efficient predators or predators pursuing relatively vulnerable individuals should be similar regardless of condition of prey.

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