

Predation-mediated selection on prey morphology: a test using snowshoe hares

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ABSTRACT

Predation has been implicated in the evolution of many prey characteristics. However, few studies have measured the strength and direction of predation-mediated selection on prey morphology. I tested whether predation exerted directional selective pressure on morphometric measures related to skeletal size in snowshoe hares (*Lepus americanus*). Hares were live-trapped at six study sites in Idaho and monitored between 1998 and 2000. Each hare was characterized using hind-foot length, snout-to-vent length and mass. All trapped individuals ($n = 103$) were equipped with mortality-sensitive radio-collars and predation events were identified. The force of selection on morphology was measured using both multiple linear regression and path analysis. Multiple regression furnished directional selection gradients indicating that predation exerted positive directional selection on both hind-foot length and snout-to-vent length; conversely, the path-analytic model implied that predation-mediated selection acted only on size-adjusted snout-to-vent length (i.e. shape rather than size), favouring juveniles with relatively long bodies. Based on the agreement between the two analytic procedures for snout-to-vent length, I concluded that juvenile hares with small size-adjusted snout-to-vent lengths (i.e. newly weaned individuals) were disproportionately vulnerable to predation, perhaps because this measure is positively correlated with escape speed.

Keywords: *Lepus americanus*, morphology, path analysis, selection, snowshoe hare, vulnerability to predation.

INTRODUCTION

In many species, predator-induced mortality rates differ as a function of certain prey traits or character states (Werner and Gilliam, 1984; Wellborn, 1994; Johnson and Belk, 1999). Thus, predation may influence the evolution of a host of prey attributes, including coloration, growth rate, morphology, life-history strategies, foraging and mating behaviour, genetic and phenotypic plasticity, and cognition (Lima and Dill, 1990; Magurran, 1990; Wellborn, 1994; Brain, 1995; Johnson and Belk, 1999). Moreover, if consistent, predation regimes characterized by habitat dependence may even facilitate speciation (Wellborn, 1994). Despite the putative importance of predation-mediated natural selection, however,

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few field studies have addressed the existence, intensity and direction of selection by predation on prey attributes (for a review, see Kingsolver *et al.*, 2001).

Size often has been invoked as a factor influencing predation risk (e.g. Mattingly and Butler, 1994; Blomberg and Shine, 2000). In theory, small prey animals may be particularly vulnerable to predation because they are young and inexperienced, forced into risky habitat as a result of social interactions, and/or less able to escape and repel predators (e.g. Mykityowycz *et al.*, 1959; Lima and Dill, 1990; Curio, 1993; Mesa *et al.*, 1994). Relatively large animals also may be disproportionately susceptible to predation if they are more conspicuous and/or less agile (e.g. Rohner and Krebs, 1996; Grutter, 1997). The evolutionary implications of size-dependent predation depend upon whether predation is focused on small or large individuals (Wellborn, 1994). For example, predation focused primarily on relatively small animals may cause prey individuals to divert energy to growth, thereby sacrificing early reproduction to bypass vulnerable developmental stages (Taylor and Gabriel, 1992; Wellborn, 1994). Conversely, disproportionate predation on large individuals may lead to increased reproductive investment at smaller sizes (Reznick and Endler, 1982; Wellborn, 1994). Thus, analyses of the relationship between predation rate and size should seek to quantify both the intensity and direction of predation-mediated selection on this trait.

Many authors have inferred the existence of morphology-dependent predation based upon observed relationships between morphometric (e.g. skeletal) measurements and predation risk (e.g. Grutter, 1997; Brown and Brown, 1998; Wirsing *et al.*, 2002). Such an inference may be incomplete, however, for morphometric measurements may reflect prey shape (i.e. the size of particular structural components relative to the size of the subject) rather than overall size *per se* (see Crespi and Bookstein, 1989). Thus, analyses of predation-mediated selection on prey morphology also should seek to distinguish between cases where vulnerability to predation is a function of overall prey size and prey shape.

The snowshoe hare (*Lepus americanus*) is an ideal species on which to base an analysis of predation-mediated selection: hares are easy to monitor, subject to heavy predation rates and they exhibit a high degree of morphological variation (Murray, in press). In this species, larger individuals (as indexed by skeletal size measures) are capable of greater escape speeds than their smaller counterparts (Murray, in press). Thus, in theory, relatively small hares should be disproportionately vulnerable to predation. Most studies of hare demography to date have produced results consistent with this hypothesis; namely, small (i.e. juvenile) hares generally suffer higher predation rates than their larger counterparts (i.e. adults) (Murray, in press; Hodges, 2000a,b). However, the few explicit (i.e. age-cohorts separated) tests of the relationship between skeletal size (indexed using hind-foot length) and predation risk in this species conducted thus far have produced contradictory results. For example, Boutin *et al.* (1986) and Murray (2002) failed to detect a size effect in two northern, cyclic hare populations, suggesting that young hares in these populations may have been disproportionately vulnerable to predation because they were inexperienced rather than (or in addition to being) small, or that vulnerability to predation was related to aspects of size or shape not associated with hind-foot length. Conversely, Wirsing *et al.* (2002) found a strong negative relationship between size and vulnerability to predation in a southern, non-cyclic hare population in Idaho, implying that relatively small hares (or hares with relatively small hind-foot lengths) within both juvenile and adult cohorts were disproportionately vulnerable to predators. This apparent geographic disparity warrants

additional tests of the relationship between predation and morphology across the snowshoe hare's range.

The aim of the present study was to test the hypothesis that morphology (i.e. size and/or shape) influences predation risk in southern snowshoe hare populations. Given that measures of selection reflect the extent to which prey animals manifesting certain characteristics are disproportionately vulnerable to predation, I sought to measure the magnitude and direction of selection imposed by predation on morphology in snowshoe hares using: (i) the multiple regression procedure introduced by Lande and Arnold (1983), which provides a statistical estimate of fitness (e.g. predation risk) using a set of measured characters (e.g. skeletal size measures) that are assumed to influence survivorship independently (Crespi and Bookstein, 1989; Mauricio and Mojonner, 1997); and (ii) a path-analytic model (Crespi and Bookstein, 1989) capable of explaining predation risk in terms of unmeasured factors for general size and shape allometry (i.e. size-adjusted variables). This study differed importantly from previous analyses of the relationship between morphology and predation risk in hares (e.g. Boutin *et al.*, 1986; Wirsing *et al.*, 2002) in that it sought to identify the targets of predation-mediated selection rather than the correlates of vulnerability to predation.

MATERIALS AND METHODS

Field protocol

Snowshoe hares were live-trapped seasonally on six 10-ha study sites in the Clearwater National Forest, Idaho (46°N, 114°W), which is located in the southern portion of the species' distribution, between May 1998 and May 2000. The handling procedures were in accord with standard guidelines (Canadian Council on Animal Care, 1984) and were approved by the University of Idaho Animal Care and Use Committee (protocol # 9029). At each capture, individuals were weighed, sexed, aged (juvenile versus adult) and characterized morphometrically using two indices, hind-foot length and snout-to-vent length. Unlike mass, these two indices traditionally have been used to signify skeletal size (i.e. the structural size of an animal, mass and/or fat deposits notwithstanding); however, they may also represent shape (foot and body length relative to overall size or weight). All morphometric measurements were taken by the same person; thus, correlation factors for multiple measurers were not necessary (Brown and Brown, 1998). Hares weighing >500 g were equipped with a mortality-sensitive radio-collar (Telemetry Solutions, Concord, CA, USA). Survival of collared hares was monitored daily; deceased animals were located within 24 h of death using a hand-held antenna and receiver (Advanced Telemetry Systems, Isanti, MN, USA). Predation events were identified based upon evidence left at the kill site (Boutin *et al.*, 1986; Keith *et al.*, 1993; Murray *et al.*, 1997) and, when possible, via carcass necropsy.

Statistical analysis of selection

Deaths not due to predation ($n = 5$, 7% of total mortalities) were excluded from the analysis. Given that collared hares may experience artificially high predation risk during the first few weeks following instrumentation (e.g. Keith *et al.*, 1984; Boutin *et al.*, 1986), hares monitored for < 1 month ($n = 22$) also were purged to remove this potential bias. Skeletal size (indexed using hind-foot length) in hares scales positively with age (Keith *et al.*,

1968); thus, size- and age-dependent trends in predation may be difficult to differentiate. In the present study, adults and juveniles differed significantly with respect to both hind-foot length (ANOVA: $F_{1,101} = 51.38$, $P < 0.001$) and snout-to-vent length (ANOVA: $F_{1,101} = 54.48$, $P < 0.001$). Consequently, I analysed the two age cohorts separately, as well as together, to test for within-cohort trends. Differences between the sexes were not significant for hind-foot length (ANOVA: $F_{1,101} = 2.18$, $P = 0.14$) or for snout-to-vent length (ANOVA: $F_{1,101} = 2.16$, $P = 0.14$). Given that the P -values associated with these two measures were marginally non-significant, I conducted a power analysis (GPOWER; Faul and Erdfelder, 1992). The results of this analysis indicated that effects associated with both hind-foot length (0.70) and snout-to-vent length (0.72) were likely to be detected; thus, males ($n = 55$) and females ($n = 48$) were pooled. Among depredated animals, the most recent morphometric measurements were used in this analysis. For adult survivors, based on the assumption that they had stopped growing, I averaged all morphometric measurements taken during the final 3 months (one monitoring interval) to produce size values. Given that the juveniles I monitored were undergoing a period of rapid growth and shape change, however, I could not use this approach without introducing bias (i.e. the size and shape values of live juveniles would have been greater than those of depredated juveniles merely because they had come of age). Instead, to ensure that the means and variances associated with the sampling ages of live and depredated juveniles were equal, I paired each surviving juvenile with a randomly selected member of the predator-killed cohort. Measurements taken from each live juvenile at the age closest to the age of final measurement for its depredated counterpart were then used for analysis.

Differences in mean values for mass, hind-foot length and snout-to-vent length within overall, adult and juvenile cohorts were evaluated using analysis of variance (ANOVA). Cases in which marginally significant differences were detected (i.e. $P = 0.05$ – 0.10) were evaluated using power analyses. Multiple linear regression (Lande and Arnold, 1983) was used to generate selection gradients (partial regression coefficients, β_i), which estimate the strength of directional selection on measured characters, for mass, hind-foot length and snout-to-vent length. Second-order (i.e. quadratic) coefficients from multiple regression also were calculated as measures of non-linearity in the relationship between selection and each morphological character (this procedure was used only for the overall cohort, as age-related effects were not expected to apply) (Lande and Arnold, 1983). Mass was square root transformed, and all measures were log-transformed before analysis (Lande and Arnold, 1983). Predation-mediated selection on measured characters was considered to exist in cases where regression coefficients were associated with P -values ≤ 0.05 .

Predation-mediated selection on hare morphology also was evaluated using a path-analytic model developed by Crespi and Bookstein (1989). Path analysis (Wright, 1934) is based upon the assumption that an unmeasured general size factor is the only factor in morphometric studies for which there exists an *a priori* biological explanation; thus, selection (i.e. shape) coefficients were computed by adjusting each morphometric character for general size (Crespi and Bookstein, 1989). In accordance with this model, logarithmic values for mass^{1/2}, hind-foot length and snout-to-vent length were entered into a principal components (PC) analysis using a covariance matrix. The principal components analysis on covariance matrix indicated that 88.3% of the variance in these three parameters could be explained in one dimension (PC1). The component loadings associated with PC1 were all large and positive (Table 1); thus, I deemed PC1 to be the general size factor (see Bookstein *et al.*, 1985). An additional 11.1% of the variance could be explained by a second principal

Table 1. Component loadings from a principal components analysis (covariance matrix) involving logarithmic values for mass^{1/2}, hind-foot length (HFL) and snout-to-vent length (SVL)

Component	Loadings	
	PC1	PC2
Mass ^{1/2}	0.71	-0.70
HFL	0.5	0.53
SVL	0.49	0.48

Note: Measurements were taken from radio-collared snowshoe hares ($n = 103$).

component (PC2). The loading pattern associated with this factor indicated that it represented general shape (i.e. high values represented relatively large body and foot length relative to mass and vice versa; see Table 1); thus, I deemed PC2 to be the general shape factor (Bookstein *et al.*, 1985). Mean differences in general size (PC1) and shape (PC2) between live and predator-killed hares were evaluated using ANOVA. Shape coefficients relating survivorship to size-adjusted mass, hind-foot length and snout-to-vent length were expressed as the differences in adjusted mean between depredated and live cohorts in separate analyses of covariance (ANCOVA) (Crespi and Bookstein, 1989). Coefficients associated with P -values ≤ 0.05 were deemed to represent significant directional relationships between predation-mediated selection and a size-adjusted variable; these coefficients only were interpreted if the assumption of equality of regression slopes was met (F -test, $\alpha = 0.05$; Sokal and Rohlf, 2000). In cases where shape coefficients were significant, I estimated the form of predation-mediated selection on the (unadjusted) shape variable using the non-parametric cubic spline procedure (Schluter, 1988) to determine whether the derived relationships were in fact linear. This technique generates a univariate fitness function (e.g. survival versus an independent variable) using the equation:

$$Y = f(z) + e \quad (1)$$

where Y is survival (binomial distribution), z is the independent variable and e is random error. Thus, the spline technique can identify areas of a particular curve (in this case vulnerability to predation versus shape) that are non-linear (e.g. asymptotes, areas where the relationship is particularly strong or weak).

To analyse further the relationship between predation risk and morphology in hares, I used simple linear regression to generate a predictive equation for hind-foot length based on mass using an independent sample of hares ($n = 30$). Observed hind-foot lengths were then divided by expected hind-foot length estimates furnished by this equation for the animals included in the study, yielding length-mass residual indices (i.e. a foot-loading index) measuring the extent to which an individual's hind-foot length deviated from that expected based on its mass (adapted from Green, 2001). Differences in foot-loading values associated with live and depredated animals within overall, adult and juvenile cohorts were assessed using ANOVA.

I employed a similar procedure to generate a body length/mass residuals index (i.e. hind-foot lengths replaced with snout-to-vent lengths). Cohort-specific differences in this index between live and depredated hares also were evaluated using ANOVA.

RESULTS

Full cohort

Morphometric measurements were taken from 103 radio-collared snowshoe hares, 57 (55%) of which fell victim to predation. Mean mass values associated with live and depredated hares were not significantly different (ANOVA: $F_{1,101} = 1.91$, $P = 0.17$; see Table 2). Differences between mean hind-foot lengths were marginally non-significant (ANOVA: $F_{1,101} = 3.47$, $P = 0.07$; Table 2); the relatively low power associated with this test (0.39) suggested that the observed difference would probably have been significant given a larger sample size. Mean snout-to-vent lengths for depredated hares were significantly lower than those for live animals (ANOVA: $F_{1,101} = 6.36$, $P = 0.01$). All three morphometric characters were highly correlated with one another (Table 3).

Multiple linear regression produced significant positive selection gradients for both hind-foot length and snout-to-vent length but not for mass (Table 3), suggesting that predation-mediated selection favoured hares characterized by relatively large hind-foot and body lengths. Furthermore, quadratic regression yielded significant coefficients for hind-foot length and snout-to-vent length as well (Table 3), indicating that the relationship between these two variables and vulnerability to predation was non-linear over the range of measurements used in this analysis. Live and depredated hares did not differ significantly according to general size (PC1) ($F_{1,101} = 3.63$, $P = 0.06$), although the relatively low power associated with this test (0.48) implies that a significant difference may have been revealed given a larger sample size. The general shape factor (PC2) also failed to differ significantly between these two cohorts ($F_{1,101} = 1.12$, $P = 0.29$). The shape coefficients for mass^{1/2} and hind-foot length were not significant (Table 3), suggesting that, after accounting for size, predation did not impose selective pressure on these two parameters. By contrast, the shape coefficient for snout-to-vent length was significant and positive (Table 3), implying that hares with small body lengths relative to their general body size were disproportionately vulnerable to predation (i.e. vulnerability to predation decreased with increasing snout-to-vent length; see Fig. 1).

Table 2. Summary of analyses of snowshoe hares

Cohort	Live				Depredated			
	<i>n</i>	Mass	HFL	SVL	<i>n</i>	Mass	HFL	SVL
Overall	46	1126.59	131.00	42.01	57	1068.70	127.73	40.66
Adults	33	1211.38	133.85	42.91	29	1193.45	132.73	42.24
Juveniles	13	921.38	123.62	39.74	28	939.50	122.55	39.03

Note: Mass was measured in grams; hind-foot length (HFL) and snout-to-vent length (SVL) were measured in millimetres and centimetres, respectively. Logarithmic values were used for statistical analysis.

Table 3. Multiple regression and path analysis of a morphological character set for snowshoe hares ($n = 103$)

Statistic	All hares ($n = 103$)			Adults ($n = 62$)			Juveniles ($n = 41$)		
	Mass ^{1/2}	HFL	SVL	Mass ^{1/2}	HFL	SVL	Mass ^{1/2}	HFL	SVL
Mean	32.93	129.17	41.27	34.59	133.33	45.6	30.42	122.89	39.25
Standard error	0.32	0.87	0.27	0.33	0.88	0.27	0.36	1.21	0.38
Correlations									
Mass ^{1/2}	–	–	–	–	–	–	–	–	–
HFL	0.75	–	–	0.48	–	–	0.80	–	–
SVL	0.77	0.98	–	0.52	0.97	–	0.80	0.96	–
Mean difference, live minus depredated	0.87	3.23	1.35*	0.27	1.12	0.67	–0.46	1.06	0.71
Multiple regression gradient (β)	1.43	19.95*	25.46*	1.26	29.91*	34.46*	7.15	16.82*	19.56*
Quadratic regression coefficient (γ)	–0.72	–397.90*	198.72*	–3.71	–79.71*	50.84*	–1.11	1575.53*	108.52*
Adjusted mean difference (shape coefficient)	–0.05	–0.08	9.51*	0.03	0.17	6.54	0.19	–7.34	20.89*

Note: Mass was measured in grams and then square-root transformed; hind-foot length (HFL) and snout-to-vent length (SVL) were measured in millimetres and centimetres, respectively. All measured variables were log-transformed before analysis.

* $P \leq 0.05$

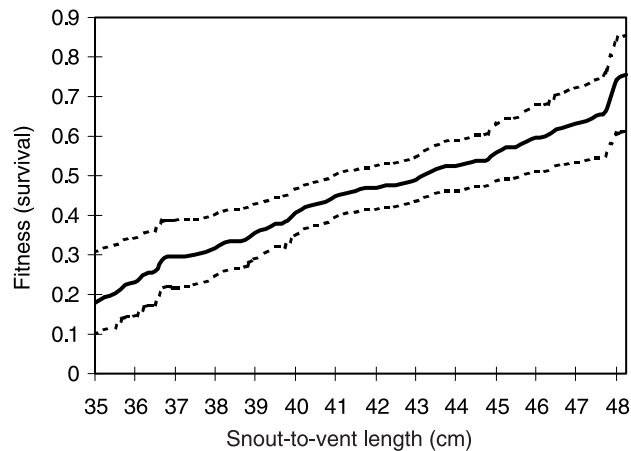


Fig. 1. Relationship between fitness (i.e. survival, expressed as a binomial) and snout-to-vent length in radio-collared snowshoe hares ($n = 103$). The fitness function (solid line) and bootstrapped standard error (dashed lines, 5000 replicates) were estimated using the cubic spline procedure (Schluter, 1988). Increases in snout-to-vent length led to a linear and significant increase in fitness.

Foot-loading residual values did not differ significantly between live and depredated cohorts ($F_{1,101} = 0.62$, $P = 0.43$). There were also no differences in the body length/mass residual between live and predator-killed hares ($F_{1,101} = 3.19$, $P = 0.08$); however, the low power associated with this test suggests that a significant difference may have existed.

Adult cohort

In total, 62 radio-collared adults were subjected to morphometric analysis; 29 (47%) adults fell to predators during the course of the study. The mean values associated with depredated hares were not significantly lower than those characterizing live individuals for mass (ANOVA: $F_{1,60} = 0.17$, $P = 0.68$), hind-foot length (ANOVA: $F_{1,60} = 0.41$, $P = 0.53$) or snout-to-vent length (ANOVA: $F_{1,60} = 1.53$, $P = 0.22$) (Table 2). All three morphometric characters were well correlated with each other (Table 3).

Multiple linear regression produced significant positive selection gradients for both hind-foot length and snout-to-vent length but not for mass (Table 3), suggesting that predation-mediated selection favoured adult hares characterized by relatively large hind-foot and body lengths. Live and depredated adults manifested similar values for both general size (PC1) ($F_{1,60} = 0.61$, $P = 0.44$) and general shape (PC2) ($F_{1,60} = 0.20$, $P = 0.65$). The shape coefficients for mass^{1/2}, hind-foot length and snout-to-vent length were not significant (Table 3), implying that, after size-adjustment, these factors were not subject to directional selective pressure imposed by predation.

Foot-loading residual values did not differ significantly between live and depredated adults ($F_{1,60} = 0.04$, $P = 0.84$). Similarly, live and predator-killed adults were characterized by similar body length/mass residuals ($F_{1,60} = 1.14$, $P = 0.29$).

Juvenile cohort

Morphometric measurements were taken from 41 radio-collared juveniles, 28 (68%) of which died as a result of predation. Live and depredated juveniles did not differ significantly in terms of mass (ANOVA: $F_{1,39} = 0.36$, $P = 0.55$), hind-foot length (ANOVA: $F_{1,39} = 0.16$, $P = 0.69$) or snout-to-vent length (ANOVA: $F_{1,39} = 0.77$, $P = 0.38$) (Table 2). All three morphometric characters were highly correlated with one another (Table 3).

The selection gradients furnished by multiple linear regression were significant and positive for hind-foot length and snout-to-vent length but not for mass (Table 3), implying that predation-mediated selection favoured juveniles characterized by large hind-foot and body lengths. Live and depredated juveniles did not differ significantly according to either general size (PC1) ($F_{1,39} = 0.01$, $P = 0.91$) or general shape (PC2) ($F_{1,39} = 3.38$, $P = 0.07$; power associated with test = 0.81). The shape coefficients for mass^{1/2} and hind-foot length were not significant (Table 3), suggesting that, after accounting for size, predation did not exert selective pressure on these parameters in juvenile hares. However, the shape coefficient for snout-to-vent length was highly significant ($P < 0.01$) and positive (Table 3), implying that juveniles with small body lengths relative to their general body size were disproportionately vulnerable to predation (i.e. vulnerability to predation decreased with increasing snout-to-vent length within the juvenile cohort; see Fig. 2).

Foot-loading residual values did not differ significantly between live and depredated juveniles ($F_{1,39} = 1.43$, $P = 0.24$). A similar trend characterized the body length/mass residual index ($F_{1,39} = 3.04$, $P = 0.09$); however, the low power associated with this test suggests that live and depredated may in fact differ with respect to this index.

DISCUSSION

The results of the present study generally are consistent with the hypothesis that susceptibility to predation in snowshoe hares along the southern periphery of the species'

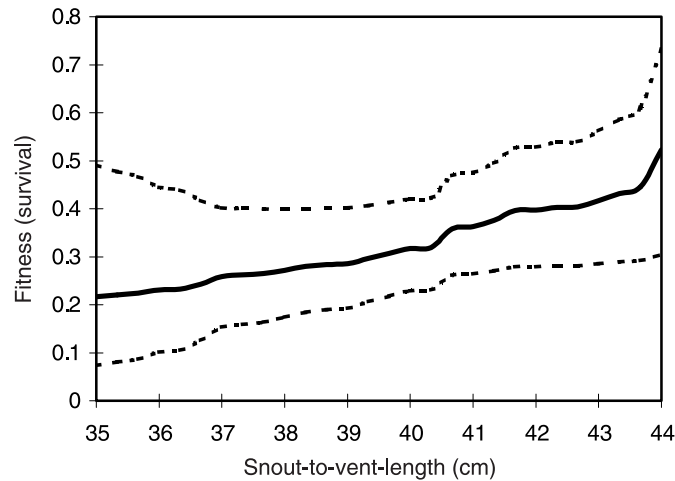


Fig. 2. Relationship between fitness (i.e. survival, expressed as a binomial) and snout-to-vent length in radio-collared juvenile snowshoe hares ($n = 41$). The fitness function (solid line) and bootstrapped standard error (dashed lines, 5000 replicates) were estimated using the cubic spline procedure (Schluter, 1988). Increases in snout-to-vent length led to a linear and significant increase in fitness.

distribution is influenced by morphology. For example, predator-killed hares differed from live individuals with respect to snout-to-vent length and perhaps hind-foot length (Table 2). More importantly, both the multiple linear regression approach introduced by Lande and Arnold (1983) and the path-analytic model used by Crespi and Bookstein (1989) yielded significant predation-mediated selection coefficients for at least one morphometric measure (hind-foot length and/or snout-to-vent length), implying that predation exerted positive directional selection on these measures and, by extension, that hares with small hind-foot and body lengths were disproportionately vulnerable to predators. However, the results also reveal that the implications of selection studies may vary based on the analytical technique used.

Multiple regression produced strong positive selection gradients for both hind-foot length and snout-to-vent length (Table 3), implying that predation exerted directional selection for large hind-foot and body length in the hares analysed. This trend was consistent across both age classes (juvenile and adult), despite the fact that mean hind-foot lengths and snout-to-vent lengths did not differ significantly among live and depredated animals when the age classes were analysed separately. Thus, vulnerability to predation apparently declined with increasing hind-foot length and snout-to-vent length irrespective of age. Moreover, this decline appears to have been non-linear, as significant second-order coefficients were produced for hind-foot length and snout-to-vent length regardless of the cohort being analysed (Table 3). In so far as hind-foot length and snout-to-vent length represent overall body (skeletal) size, the multiple regression model may also suggest that predation risk was highest among relatively small hares. Finally, the selection gradients associated with snout-to-vent length were consistently larger than those associated with hind-foot length (Table 3). Thus, although both metrics were strong determinants of predation risk, snout-to-vent length may be more closely related to vulnerability to predation.

The results of the path analysis suggest a somewhat different interpretation. The only

size-adjusted path coefficient determined to be significant was that for snout-to-vent length (Table 3); differences in general size (a possible difference in PC1 between live and depredated hares disappeared when the age cohorts were separated), general shape (PC2) and size-adjusted hind-foot length apparently did not influence vulnerability to predation. Thus, according to the path model, only hares with short bodies relative to their overall size were disproportionately vulnerable to predation during the course of this study; that is, predation selected for hares with a particular shape (i.e. large snout-to-vent length relative to general size) rather than large size *per se*. However, this trend did not remain consistent when the two age cohorts were separated (Table 3). Among adults, size-adjusted snout-to-vent length was not related to predation risk, suggesting that, within the adult cohort, relative body length ceased to influence the ability of hares to escape predators (or that insufficient variation in size-adjusted snout-to-vent length existed within the adult cohort to influence prey selection trends; see below). Thus, the significant snout-to-vent length coefficient produced for adults by multiple regression may have been a spurious consequence of the strong correlation between the morphometric measures analysed (a correlation matrix revealed tight relationships between mass, hind-foot length and snout-to-vent length; see Table 3). Among juveniles, the shape coefficient for snout-to-vent length remained significant. Juvenile snowshoe hares manifest rapid growth (Keith *et al.*, 1968). Consequently, differences in body length are probably more profound within juvenile relative to adult hare cohorts. Under the assumption that predators are best able to capture and kill hares with comparatively low body lengths, the large variation in snout-to-vent length among juveniles (relative to adults) may lead to significant differences in vulnerability between juveniles characterized by large and small snout-to-vent lengths (see Fig. 2). This possibility is supported by the fact that the variance with respect to snout-to-vent length was larger for the juvenile cohort (5.78) than for the adult cohort (4.60).

The two residual indices failed to provide additional evidence for size-dependent predation. However, while the relationship between predation and the foot-loading (i.e. hind-foot length-based) index was clearly non-significant, the extent to which the mean snout-to-vent length/mass residual for depredated hares fell below that of live animals was nearly significant for both the overall and juvenile cohorts. Indeed, power analyses revealed that the incorporation of additional samples would probably have yielded significant differences in the body length/mass residual index in both cohorts. This trend is consistent with the results furnished by the path-analytic model.

The four methods I used to examine the relationship between morphology and predation risk in hares produced somewhat disparate results; however, there was general agreement among them that snout-to-vent length was a character on which predation exerted positive directional selection. In particular, this trait appears to have been subject to directional selection in juvenile hares, with individuals characterized by relatively small snout-to-vent lengths suffering the highest predation rates. According to the results of the cubic spline procedure, the positive relationship between fitness (i.e. survival) and snout-to-vent length was approximately linear both when hares were analysed collectively (Fig. 1) and when juveniles were analysed separately (Fig. 2). Traditionally, hind-foot length has been used as the chief metric of skeletal size in hares (Murray, *in press*), leading some authors to infer relationships between skeletal size and vulnerability to predation from observed associations between hind-foot length and predation rates (e.g. Wirsing *et al.*, 2002). The importance of snout-to-vent length in this study suggests that body length may serve as a more

appropriate measure of size *vis-à-vis* predation danger in at least some cases, and that the negative relationship between hind-foot length and predation rate observed by Wirsing *et al.* (2002) may have stemmed from the strong correlation between hind-foot length and snout-to-vent length (Table 3). Alternatively, hind-foot size may be equally appropriate but poorly approximated by hind-foot length, a possibility future studies might address by including additional measures of foot size such as hind-foot width and hind-foot surface area.

Although suggestive, this analysis has revealed little about why animals with relatively short body lengths were especially vulnerable to predators. Slight differences in speed may determine the outcome of predator–prey interactions (van Damme *et al.*, 1998). Thus, one possible explanation rests on the positive relationship between skeletal size and escape speed in hares (Murray, in press). Hares rely on quick bursts of speed when flushed from cover by predators (Murray, in press). Given that top speed is determined in part by stride length and that stride length increases as a function of body length relative to overall size (Alexander, 1992), hares characterized by relatively large snout-to-vent lengths presumably are able to generate more speed during chases than hares with more compact bodies. Variability in sprint speed is probably most pronounced among juveniles, given that this cohort is characterized by increased variance in snout-to-vent length relative to adults. Consequently, among juvenile hares, relative size-adjusted snout-to-vent lengths may help determine the outcome of pursuits to such an extent that predation rates dependent on snout-to-vent length occur. A test of this hypothesis might begin with a captive trial designed to quantify the relationship between sprint speed and size-adjusted snout-to-vent length (as well as other measures that may influence speed, such as relative hind-leg length and hind-foot surface area) in juveniles. If size-adjusted snout-to-vent length is related to quickness, then we would expect escape success to be a function of a juvenile's snout-to-vent length. This question might, in turn, be addressed in a controlled setting (e.g. natural enclosure) by comparing the capture success rates of a model hare predator (e.g. a muzzled coyote, *Canis latrans*) when chasing juvenile hares with various size-adjusted snout-to-vent lengths.

If size-adjusted snout-to-vent length is related to elusiveness in the southern portion of the snowshoe hare's range, leading to strong, directional selection for an elongated body shape, then why have rapid changes in hare morphology not been reported in these regions? The answer to this question is simply that, to my knowledge, the present analysis represents the first attempt to quantify the extent of predation-mediated selection on hare morphology. Aided by the availability of trapping records spanning more than a century and extensive demographic information collected from many portions of the hare's distribution, future studies may identify certain hare populations undergoing morphological change. Alternatively, the morphology of hares along the southern periphery of the species' distribution may in fact be stable despite the selective pressure exerted by predation. Morphological stability in hare body shape could be promoted if: (i) individuals killed for reasons other than predation manifest an elongated body shape, resulting in directional selection diametrically opposite to that exerted by predation; (ii) fecundity is greater in more compact adults, leading to an evolutionary trade-off between survival and reproductive output; and/or (iii) the selective pressure imposed by predation is overwhelmed by the effects of catastrophic events (e.g. extremely harsh or mild winters) or gene flow. These putative stabilizing mechanisms each merit further scrutiny.

ACKNOWLEDGEMENTS

I am grateful to D. Murray, T. Steury, K. Bourke, A. Gaul and P. Cook for their help in the field. I thank D. Elliot and the Powell Ranger Station staff for accommodating me during my field stay, P. Nosil for providing statistical aid and B. Crespi for providing many helpful comments on earlier versions of the manuscript. The manuscript benefited from a review by L. Oksanen. Finally, I am indebted to W. Melquist of the Idaho Department of Fish and Game and D. Davis of the USDA Forest Service for providing the funding for this research.

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