Size-Related Effects of Predation on Habitat Use and Behavior of Porcupines (Erethizon Dorsatum)

Richard Alan Sweitzer, Joel Berger

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SIZE-RELATED EFFECTS OF PREDATION ON HABITAT USE AND BEHAVIOR OF PORCUPINES (*ERETHIZON DORSATUM*)[1]

RICHARD ALAN SWEITZER AND JOEL BERGER
Program in Ecology, Evolution, and Conservation Biology, University of Nevada, Reno, Nevada 89557 USA

Abstract. Ecological and behavioral strategies that reduce predation were examined in North American porcupines (*Erethizon dorsatum*) by testing two hypotheses: (1) habitat use varies with activity level and age class of animals, and (2) with increasing nutritional stress, individuals accept increased predation risk to avoid starvation. Observational and experimental data were gathered over a 2-yr period for a Great Basin Desert porcupine population during winter. Field experiments included manipulations of perceived risk using predator urines and simulated predator encounters with a dog (*Canis familiaris*). Compared to foraging animals, sleeping porcupines of all age classes avoided high risk (i.e., open) areas. Mass loss varied by habitat with individuals foraging in open areas (high risk) experiencing less mass loss than those foraging in groves (low risk). Age class also affected habitat use by foraging porcupines. Juveniles invariably remained in low-risk areas, even when more risky habitats contained potentially better quality forage. Two-year-old porcupines shifted to high-risk areas as body condition deteriorated, but condition exerted little influence on habitat use by adults, as this age class utilized habitat similarly throughout winter. These data reveal how a species with formidable antipredator morphology uses habitats in risk-sensitive ways.

Key words: foraging strategies; Great Basin; mammals; nutrition-risk trade-offs; predation; rodents.

INTRODUCTION

Considerable interest has focused on how animals respond ecologically and behaviorally to predation pressure (Cerri and Fraser 1983, Lima and Dill 1990). While animals generally avoid habitats where risk is high, the extent to which age or body size affect habitat use is less clear (Schlosser 1987, Werner and Hall 1988). Nutritional state can also influence foraging decisions because, as the potential for starvation increases, the benefit of energy intake relative to foraging costs such as time expenditure becomes greater (McNamara and Houston 1987). Recent research investigating how animals respond to predation has centered on foraging decisions (Milinski and Heller 1978, Pitcher et al. 1988), but animals may suffer predation during other activities, and habitat use decisions should reflect the perception of risk incurred during those activities as well. Additionally, individuals that vary in age or size and differ in their vulnerability to predation may vary in tactics used to minimize predation (Werner et al. 1983). While size- or age-related differences in habitat use have been linked to predation risk in fishes (Schlosser 1987, Werner and Hall 1988), little is known about such responses in mammals.

Few mammals have evolved morphological defense mechanisms, and in North America only porcupines use quills to deter predators (Vaughan 1978). These animals are especially interesting relative to questions about predation because quills may reduce predation most effectively in larger porcupines (Powell and Brander 1977), making it possible to evaluate age-specific predation in a medium-sized mammal.

Porcupines are herbivores with diverse diets varying seasonally in habitats ranging from open tundra (Payette 1987) to deciduous forests (Dodge 1982) to desert chaparral (Reynolds 1957). Winter diets of porcupines (tree and shrub bark) are of relatively poor quality compared to nutrient-rich spring and summer diets (forbs, grasses, and riparian vegetation; Dodge 1982, Hendricks and Allard 1988). The minimum protein requirement for rodents is ≈15% nitrogen (Wallach and Hoff 1982), and low levels of nitrogen or crude protein in porcupine winter diets (2–6%; Stricklan 1986, Roze 1989) result in mass loss as fat deposits are utilized as a dietary supplement (Oveson 1983). Because of this, porcupines undergo severe nutritional stress in late winter (Roze 1985, Sweitzer and Berger, *in press*).

In late winter, porcupines venture away from dens and trees to feed on protein-rich grasses and riparian vegetation (Woods 1973, Harder 1979, Craig and Keller 1986, Stricklan 1986). Because the tracking of plant phenology may involve shifts to more risky areas, it is possible to investigate how predation risk and nutrition interact to influence habitat shifts. We examined two hypotheses: (1) smaller age classes and/or inactive an-

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imals use habitats relatively high in predation risk less often than less vulnerable larger and/or foraging animals, and (2) under increasing nutritional stress, porcupines tolerate increased predation risk to minimize starvation.

METHODS

Study site

Porcupines were studied in the Granite Range of northwestern Nevada, an insular 2700-m mountain of the Great Basin Desert. We studied the population of porcupines in and around a 20-km^2 enclosed basin (Granite Basin) in the southern portion of the range between 1520 and 1640 m elevation from December 1988 to April 1989, and September 1989 to April 1990. Vegetation in Granite Basin is dominated by sagebrush (*Artemesia tridentata*), saltbush (*Atriplex canescens*), bitterbush (*Purshia tridentata*), and Utah juniper (*Juniperus osteosperma*) (Cronquist et al. 1972). Natural predators in the area included mountain lions (*Felis concolor*), bobcats (*Lynx rufus*), and coyotes (*Canis latrans*). Berger (1986) gave an extensive description of the Granite Range.

Study animals and identification

Porcupines were captured by immobilization with a jab stick using a mixture of ketamine hydrochloride (100 mg/mL, dosage = 100 mg/kg) and xylazine hydrochloride (100 mg/mL, dosage = 40 mg/kg). Upon capture each animal was weighed with a spring scale, sexed, and measured for midsternal chest circumference and middorsal body length from tip of nose to end of tail. Numbered, color-coded plastic tags (Allflex style number C12334–8) were attached to the ears using aluminum self-piercing domestic livestock eartags (National Band and Tag Company, Newport, Kentucky). Lower tails of porcupines were sprayed with two colors of nontoxic enamel spray paint in unique color combinations of red, orange, green, white, and yellow. Eight animals were fitted with radio transmitters (three Telonics implantable transmitters and five Wildlife Materials transmitters affixed to collars). Collars were attached without removing or otherwise impairing quill functions by threading plastic-coated clothes line cord through the quills on the back of the neck.

Capture-recapture techniques were used to monitor changes in nutritional state through the fall and winter seasons for individual porcupines (Sweitzer and Berger, *in press*). Porcupine locations for foraging and behavioral observations were surveyed using a spotting telescope, night vision equipment (moonlit nights only), and radiotelemetry. Early winter (December) body mass was used to assign animals to one of three age classes (Dodge 1982): juvenile <5 kg; 2 yr old = 5.75–7.0 kg; adult >7.0 kg. Animals reweighed the second winter (1989–1990) indicated that these mass classifications reliably indexed age.

Observational data

As many as 33 porcupines were located daily; during winter animals congregated in small riparian areas, primarily occupying nearly impenetrable buffalo-berry (*Shepardia argentia*) and willow (*Salix* spp.) groves. For animals located in buffalo-berry and willow groves we recorded activity (foraging or sleeping), estimates of height in trees, potential height that animals could have climbed to in the immediate area, and linear distance into groves (cover). For those in open grassland areas or in open grove areas, we estimated distances to potential refuge (e.g., rock outcroppings, juniper trees, groves). These areas provided shelter as porcupines were able to hide their quill-free faces, exposing only heavily quilled rump and tail areas. Though we occasionally noted two observations of an individual on one day, individual locations were primarily recorded only once a day. We assumed that observations were relatively independent when separated by ≥12 h, and included only one observation per individual per day in analyses. For 1988–1989 surveys from January to early April, we included an average of 7.3 locations/individual (range = 1–19, N = 44) in analyses. Similarly, for 1989–1990 surveys from mid-October to late March, we utilized 9.8 locations/individual (range = 1–44, N = 38). For analyzing these locations, habitat areas were categorized into different levels of risk according to behavioral data.

The distribution of porcupines in different habitats was also investigated relative to thermal conditions. Porcupines alter patterns of microhabitat use to conserve energy when exposed to temperatures of −4° to −12° C (Irving et al. 1955, Clarke and Brander 1973), and it is possible that these shifts may confound analyses of shifts in response to predation risk. We used −4° C as a conservative measure of the lower critical temperature for porcupines. Temperature was measured and wind speeds estimated using a Beaufort's equivalent wind speed table (Schaefer and Day 1981), and relative temperatures experienced by porcupines were estimated from a windchill chart.

Weather conditions provided an opportunity to examine habitat use relative to predation risk and nutritional status during winter 1989–1990. Snow cover was virtually absent that winter with continuous availability of open grassland areas providing a potential trade-off of risk for access to presumably higher quality food in grassland areas.

Experimental data

Porcupines have poor vision, relying on olfaction to locate sources of danger (Dodge 1982), and since several orders of mammals recognize and respond to predator orders when feeding (Melchiors and Leslie 1985, Sullivan 1986, Jedrzejewski and Jedrzejewska 1990), we manipulated perceived risk of predation by exposing porcupines to predator scents. Specifically, we measured breathing and foraging rates of porcupines in the presence and absence of (1) undiluted bobcat and coyote urine from a trapping supply company, and (2) combinations of predator urine and simulated predator encounters using a trained dog (*Canis familiaris*; dog+urine encounters).

For urine experiments, we quietly approached to within 5–10 m of an animal's location and sprayed urine from a plastic spray bottle to the base of trees occupied by animals in groves, and upwind of animals in open areas (five squirts/experiment ≈5 mL of urine). For dog+urine encounters, the trained dog was released immediately after urine was sprayed and encouraged to approach to within 1 m of porcupines on the ground or low in trees, and as close as possible to an animal's location otherwise. Durations of dog+urine encounters were 30–45 s (included in standard 120-s treatment). Porcupine responses were classified as (1) no apparent response (behaviors before and after treatments were the same), (2) vigilance (remained relatively immobile while sniffing and listening intently) or (3) movement to new location (changed location in trees, or moved to cover from open areas). Preliminary analyses of porcupine responses to predator approaches revealed that no response and vigilance occurred in similar frequencies relative to height in trees or distance into cover. These two response categories were subsequently pooled as "no movement response." Data were collected for 120-s periods both before (control) and after (treatment) each experiment and included: (1) a simple measure of foraging rate noting the proportion of time that an animal fed or walked with head oriented to the ground (Berger 1991), (2) total number of steps taken in open areas, and (3) breathing rates in groves. It was possible to count number of breaths for immobile animals during nonwindy daylight conditions by observing hair and quill movement in the chest and stomach region. Animals that changed location during experiments were excluded from breathing rate analyses. Because porcupines may habituate when repeatedly exposed to predator odors, we limited urine experiments to a maximum of four treatments per individual.

Statistical analyses

Location data for simulated predator approaches were evaluated using one-way ANOVA. Differences between means were tested by two-tailed *t* tests or analysis of variance (ANOVA). Foraging and stepping rates were analyzed using Friedman matched-pairs ANOVA (Siegel 1956). Breathing rates were examined by repeated-measures ANOVA (Sokal and Rohlf 1981). Multiway contingency table analysis followed by *G* tests of significant interactions was used to evaluate porcupine location frequencies in different habitat areas (Sokal and Rohlf 1981).

RESULTS

Experimental data

In groves, a porcupine's perceived risk of predation may decrease with increasing height in trees and distance into cover. Porcupines were more likely to move in response to the potential predator when they were lower in trees and closer to the edge of cover (Table 1; $F_{1,273} = 213.5$, $P < .001$, and $F_{1,273} = 32.7$, $P < .001$, respectively). Juveniles were higher in trees and farther into cover than 2 yr olds when exhibiting no movement responses (Table 1; $t = 5.06$, $P < .001$, and $t = 2.05$, $P = 0.04$, respectively). Additionally, juveniles were higher in trees for no movement responses than adults (Table 1; $t = 3.59$, $P < .001$). Other response comparisons did not differ between age classes (*t* tests, $P > .05$). Breathing rates of porcupines in groves did not differ between urine ($N = 7$) and dog+urine ($N = 11$) manipulations ($F_{1,17} = 1.41$, $P = .24$) so these data were pooled. Breathing rates nearly doubled in response to treatments (Table 1; $F_{1,17} = 50.08$, $P < .001$), implying porcupines perceived increased risk from both olfactory and visual cues. Furthermore, because porcupines erect their quills when alarmed (pilo-erection), it was possible to determine a level of excitement after each encounter. We discriminated between half and full pilo-erections; porcupines exhibited more full erections when exposed to dog+urine treatments ($N = 11$) than to urine treatments alone ($N = 7$; Fisher's exact test; $P = .047$).

Assuming open habitats are riskier than groves, porcupines in these areas should move to cover more often when a predator is encountered. Comparisons of movement to cover responses between grove and open areas were restricted to foraging animals since no sleeping porcupines were observed in open areas. Additionally, although all grove animals could move farther into cover, data on potential heights indicated that some were unable to climb higher, and we removed from consideration all locations for which the ratio of a porcupine's height to potential height was >90%. One-hundred percent ($N = 77$) of encounters in open areas resulted in animals moving to cover, whereas only 57% ($N = 45$) of encounters in groves resulted in porcupines moving higher and/or further into cover ($G = 55.6$, df = 1, $P < .001$). In open areas, porcupines responded to predator urine and dog+urine by vigilance or running. Because neither foraging rates nor stepping rates differed between urine and dog+urine treatments (Mann-Whitney *U*: $Z = 66$, df = 1, $P = .35$, and $Z = 94$, df = 1, $P = .48$, respectively) data were pooled. When porcupines responded with vigilance ($N = 17$), foraging rates decreased threefold (Table 1; Friedman matched-pairs ANOVA: $X_r = 17.0$, df = 1, $P < .001$). In cases where porcupines ran, stepping rates increased by a factor of 10 (Table 1; Friedman matched-pairs ANOVA: $X_r = 11.0$, df = 1, $P < .001$). Frequencies of vigilance and running responses for urine and dog+urine manipulations were similar (Fisher's exact test, $P = .67$).

These data were used to categorize habitat areas into different levels of risk to facilitate analyses of location data. On average, animals did not move in response to predator encounters when they were ≥ 2.2 m high in trees, and/or ≥1.8 m into cover (Table 1), so these locations in groves were considered safe (grove low risk). Grove locations outside this area were considered risky (grove high risk). Finally, open area locations were considered highest in risk (open high risk) since porcupines responded more vigorously when approached by predators there, and because both literature reports and our data suggest porcupines suffer increased mortality in open areas.

Habitat use in relation to activity

The simplest multiway contingency model that fit the data included the interactions of age × sex, sex × activity, activity × risk, and age × risk ($G = 21.35$, df = 14, $P = .09$). For the age × sex interaction, juvenile males and 2-yr-old and adult females were located more often than juvenile females and 2-yr-old and adult males. For the sex × activity interaction, males were active more than females. As no sex differences in habitat use were apparent for sleeping or foraging porcupines ($G = 1.97$, df = 2, $P = .37$, and $G = 0.46$, df = 1, $P = .49$, respectively), these biases should not confound analyses.

Porcupines used different areas for sleeping and foraging ($G = 250.3$, df = 2, $P < .001$; Fig. 1). Sleeping animals of all age classes used grove areas similarly, occurring primarily in safe grove locations ($G = 1.40$, df = 2, $P = .49$; Fig. 1). Foraging individuals utilized habitat areas differently ($G = 48.74$, df = 4, $P < .001$; Fig. 1). Juveniles primarily occupied relatively safe grove areas, 2 yr olds used risky areas more often, and adults occurred in open habitats most frequently (Fig. 1).

Predator-inflicted mortalities for porcupines were in accord with experimental and observational data as 10 of 11 predator-killed porcupines were located in open areas. These mortality data were available for a combined 5-yr period at the study site, during a horse study from 1979 to 1983 (Berger 1986), and from 1988 to 1990 (this study). Mortality data for known-aged individuals from 1988 to 1990 suggested that small porcupines were more vulnerable, with two juveniles and one 2-yr-old predator-killed porcupine located.

The data presented so far suggest that predation risk influences habitat use by porcupines. Alternatively, habitat use may function to minimize heat loss. No differences in habitat use were apparent for sleeping animals at temperatures $> -4°$ C, compared to temperatures $< -4°$ C ($G = 2.11$, df = 1, $P > .14$). However, porcupines slept more often than they foraged ($G = 17.96$, df = 1, $P < .001$), and foraging animals used different habitats when temperatures were $< -4°$ C ($G = 5.08$, df = 2, $P = .079$). Examination of residuals revealed that porcupines foraged less in open areas during cold periods; however, cold temperatures usually followed storms, and the few open area observations probably reflected forage being obscured by snow.

Habitat shifts, nutritional state, and food quality

If changes in nutritional state influence foraging patterns, animals should move to better foraging areas when nutritionally stressed. In addition, if animals shift to more risky areas when in poorer condition, they should benefit by gaining access to higher quality food. Winter mass loss and condition index evaluations for Granite Range porcupines during the period of this study have been described elsewhere (Sweitzer and Berger, *in press*), but briefly, these data indicate that individuals of all sex and age classes experienced nutritional stress, especially in late winter (after 1 February). Because some porcupines foraged primarily in groves while others foraged in open areas, we were able to compare mass changes between groups of foragers that utilized qualitatively different habitats in early and late winter (15 October–31 January and 1 February–15 March, respectively) 1989–1990. Animals that foraged in groves did so almost exclusively in early winter while in late winter they used both grove and open areas. Sufficient data were available for comparisons between adults of both sexes and 2-yr males. No early winter differences in body mass were apparent between groups of porcupines foraging in open vs. grove areas (adult males, $t = 0.25$, NS; adult females, $t = 1.01$, NS;

TABLE 1. Summary of porcupine responses to experimental manipulations, data from winters 1988–1989 and 1989–1990, Granite Range, Nevada. Measurements are given as means ± 1 SE.

	Response to simulated predator					
	No movement			Move to new location		
Age class	Height in canopy (m)	Distance into cover (m)	*N*	Height in canopy (m)	Distance into cover (m)	*N*
Juvenile	2.5 ± 0.1	1.9 ± 0.2	59	1.2 ± 0.1	1.0 ± 0.2	41
Two-year	2.0 ± 0.1	1.5 ± 0.2	48	1.1 ± 0.2	0.5 ± 0.2	11
Adult	2.1 ± 0.1	1.7 ± 0.1	81	0.9 ± 0.1	0.8 ± 0.2	35
Overall	2.2 ± 0.05	1.7 ± 0.1	188	1.1 ± 0.1	0.9 ± 0.1	87

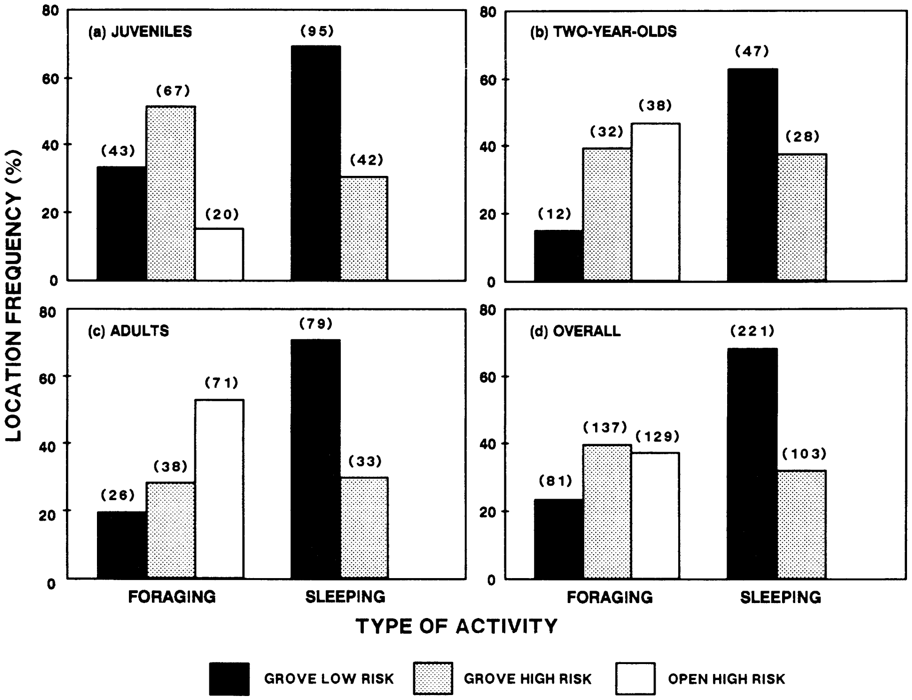

FIG. 1. Comparisons of locations used by foraging and sleeping porcupines of three age classes during two winters (1988–1989 and 1989–1990) in the Granite Range, Nevada. Sample sizes are given in parentheses above each bar.

2-yr males, $t = 0.89$, NS). In late winter, however, open-area adults of both sexes had lost less mass and were heavier than their grove counterparts (Table 2; $t = 2.88$, $P = .045$ and $t = 3.16$, $P = .016$, respectively). Although late winter open- and grove-area foraging 2-yr males were similar in body mass ($t = 1.79$, $P = .13$), open-area 2-yr males lost less mass relative to their early winter masses than did grove 2-yr males (Table 2).

We compared foraging areas used in early winter (15 October–31 January) with those used in late winter (1 February–31 March) to examine the prediction that porcupines in poor condition would trade access to presumed higher quality food in open areas for increased risk. Porcupines foraged more often in open areas during late winter ($G = 16.29$, df = 2, $P < .001$; Fig. 2d). These foraging shifts were also analyzed by age class. Among juveniles, locations in grove risky and open high risk categories were pooled because of sparse cell counts (Sokal and Rohlf 1981). Similarly, among 2 yr olds, locations in grove low-risk and grove high-risk categories were pooled. Juveniles shifted to forage primarily in grove risky areas ($G = 6.85$, df = 1, $P = .009$; Fig. 2a), 2 yr olds occurred more commonly in high-risk open areas ($G = 6.95$, df = 2, $P = .008$; Fig. 2b), and a trend was noted for adults to frequent open foraging areas more often in late winter ($G = 4.76$, df = 2, $P = .09$; Fig. 2c).

DISCUSSION

We assumed a priori that open areas were more risky than groves since fishers (*Martes pennanti*), mountain lions, bobcats, and coyotes are all reported to hunt and kill porcupines most effectively in open habitats (Keller

TABLE 1. Continued.

Response to urine and dog+urine treatments			
	Experimental period		
Type of rate	Control	Treatment	*N*
Breathing (no. breaths/120 s)	44.8 ± 4.1	86.0 ± 8.4	18
Stepping (no. steps/120 s)	15.4 ± 6.5	136.3 ± 21.4	11
Foraging (% of time during 120-s observation)	99 ± 0.001	22 ± 0.09	17

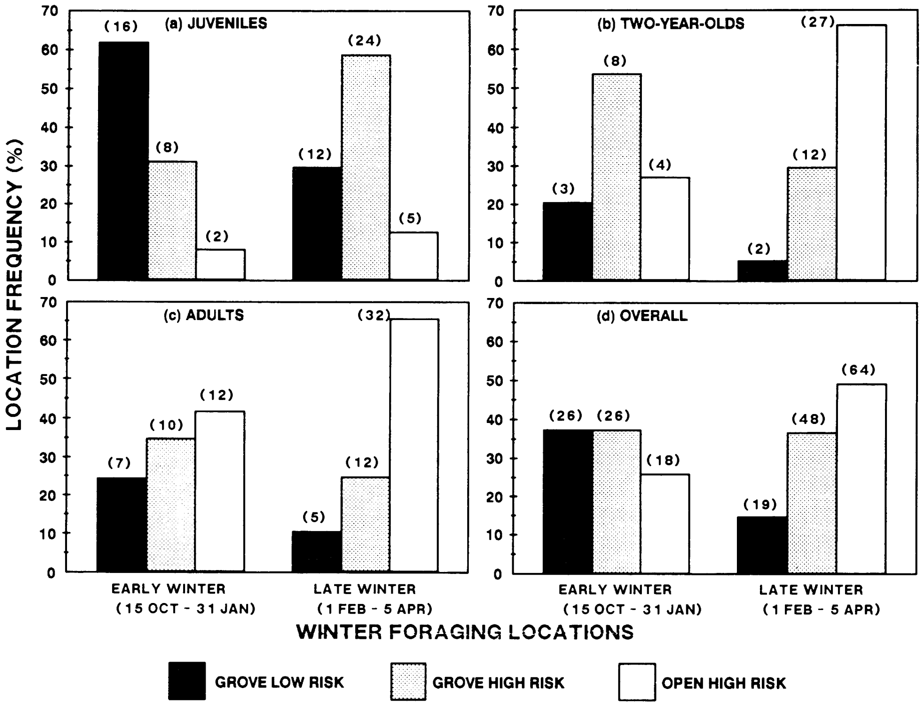

FIG. 2. Early and late winter porcupine foraging locations during winter 1989–1990, Granite Range, Nevada.

1935, Connolly 1949, Robinette et al. 1959, Powell and Brander 1977, Stricklan 1986). Data on staged predator encounters suggested that porcupines perceived habitat areas to differ in degree of safety. Open areas were apparently perceived as highest in risk since 100% of encounters resulted in retreat to shelter. When exposed to predator odors, porcupines in open areas either ran for the nearest cover or ceased foraging to maintain vigilance. These results were consistent with data on locations of predator-induced porcupine mortalities; 90% of predated porcupines were found in open areas. A potential bias here is that our mortality data consists of information from two different studies and search effort probably varied by habitat type between the two study periods. During 1988–1990, groves and open areas were consistently surveyed, while searches for horses from 1979 to 1983 concentrated in open habitats. We mapped mortalities from 1979 to 1983, and all were located in areas used by porcupines in 1988 to 1990.

Within groves, porcupines showed decreasing movement responses to predator encounters with increases in both height in trees and distance into cover. Additionally, when exposed to predator scents, porcupine breathing rates increased by nearly 100% regardless of location in groves. Intuitively, risk of predation should decrease with increasing height in a tree because an animal may become inaccessible to a predator. Literature reports indicate that porcupines may be vulnerable to fishers and mountain lions in trees (Connolly 1949, Powell and Brander 1977), and it is not clear how increased height may provide security from these predators. Thick vegetation between predator and prey may serve as an important predator deterrent (Geist

TABLE 2. Body masses (in kilograms) of grove- and open-area foraging porcupines during early winter (15 October–31 January) and late winter (1 February–15 March) in the Granite Range, Nevada.

	Grove porcupines*				Open-area porcupines†			
	Early winter		Late winter		Early winter		Late winter	
Age/sex	$\bar{X} \pm 1$ SE	N	$\bar{X} \pm 1$ SE	N	$\bar{X} \pm 1$ SE	N	$\bar{X} \pm 1$ SE	N
Adult male	9.4 ± 0.6	5	7.6 ± 0.1	4	9.8 ± 0.6	5	8.0 ± 0.1	7
Adult femlae	7.3 ± 0.4	3	6.3 ± 0.1	3	8.1 ± 0.4	7	7.0 ± 0.1	8
Two-year male	7.3 ± 0.4	4	5.7 ± 0.3	5	6.9 ± 0.2	5	6.4 ± 0.2	5

* Grove porcupines foraged primarily on tree bark in early winter and tree bark and emergent new vegetation in late winter.
† Open-area porcupines foraged primarily on shrubs and dormant grasses in early winter and emergent new vegetation in late winter.

1978, Jelinski 1989), and the buffalo-berry groves at the study site may provide a situation that is analogous to cover serving as a refuge from predation for birds, desert rodents, and fish (Kotler 1984, Lima et al. 1987, Werner and Hall 1988).

We considered sleeping porcupines to be more vulnerable because they might detect approaching predators later than foraging animals. For example, sleeping Herring Gulls (*Larus argentatus*) reacted later than resting gulls when approached by a potential predator (Ball et al. 1984). Results indicated that all porcupine age classes altered patterns of habitat use when sleeping compared to when foraging by occurring higher and/or farther into cover (Fig. 1), suggesting all porcupines are vulnerable to predation when sleeping. In contrast, foraging porcupines occurred throughout the grove canopy and in open areas, and patterns of habitat use varied by age class (Fig. 1).

We assumed small porcupines were at greater risk than large ones because predators may be more effective at killing smaller individuals (Keller 1935, Connolly 1949, Westfall 1956, Robinette et al. 1959, Powell and Brander 1977). Habitat use data suggested that small porcupines perceived risk differently than large porcupines. Juveniles occurred primarily in relatively secure groves and intermediate-sized 2 yr olds used high-risk open areas more than juveniles, but less than larger adults (Fig. 1). Thus, it appears that age- or size-dependent habitat use occurs in porcupines despite the use of quills as a predator defense system. Similar patterns of habitat use have been reported in fish where small, vulnerable size classes are known to use habitats differently than larger individuals and to shift to less protected areas with increasing size (Werner et al. 1983, Post and Evans 1989).

Porcupines may alter patterns of microhabitat use and/or behaviors to conserve energy (Clarke and Brander 1973). We found that when temperatures were < −4° C porcupines slept more than in warmer conditions, consistent with reports of porcupines remaining inactive in heat-conserving postures during cold temperatures (Clarke and Brander 1973, Oveson 1983). Because sleeping porcupines used similar areas in different thermal conditions, including these data in analyses should not bias results.

Habitat shifts and the nutrition-risk tradeoff

In addition to eluding predators, animals must avoid starvation. Empirical evidence suggests that animals can control food quality and their risk of predation and that there is a trade-off between these factors (McNamara and Houston 1987, 1990, Morgan 1988). All ages and sexes of Granite Basin porcupines were nutritionally stressed in late winter (Sweitzer and Berger, *in press*), when potential variation in forage quality prompted porcupines to trade increased risk for access to higher quality diets in open areas (Fig. 2). Habitat shifts were age dependent and in accord with predictions of size-related vulnerability to predation. In late winter, juveniles foraged in more risky grove areas but consistently avoided open areas, while 2 yr olds switched from primarily grove to primarily ground foraging (Fig. 2). A trend was noted for increased use of open areas by adults, yet they consistently used these areas more often throughout the winter than the smaller age classes (Fig. 2). While we indicated earlier that some individuals showed habitat preferences, foraging areas used by these animals were not exclusive (see Table 2) and this phenomenon should not bias our results. Additionally, there were no apparent morphological or behavioral differences between grove and open area foragers that might make one group more or less vulnerable to predators.

It is possible that nutritional requirements vary among age classes and influence foraging patterns, particularly for the juvenile age class. While no data are available on dietary requirements for juvenile vs. older aged porcupines, Robbins (1983) notes that during the rapid growth period juvenile animals require more protein than adults. Mass loss data (Table 2) and literature suggest that the crude protein content of dormant and emergent new vegetation in open areas is greater than that of tree bark. Because of their high protein needs, juveniles should benefit more, and forage more in open areas if nutrition alone were an alternative explanation for habitat use, opposite to the pattern we observed.

Observations of predator-induced porcupine mortalities suggest a clear detriment associated with foraging in open areas, but what, if any, benefits accrue to individuals foraging in open areas? Ideally, to decide whether behavioral trade-offs increase fitness, the value of food to individuals must be known in terms of enhanced reproduction (Nonacs and Dill 1990). In the absence of such data, energy reserves provide one measure of fitness because survivability is directly related to fat reserves (McNamara and Houston 1990). Comparisons of winter mass loss of grove- and open-area foraging individuals indicated that open-area porcupines maintained more fat reserves than did grove animals (Table 2), suggesting that porcupines traded increased risk to predation for decreased risk of starvation.

Porcupines and predation

While mammals use a wide variety of tactics to avoid predation, quilled species also show subtle changes in behavior and microgeographical distribution that appear related to predation pressure. In Old World porcupines, for example, complex patterns of moonlight avoidance occur in both Indian-crested (*Hystrix indica*) and African brush-tailed porcupines (*Atherus africanus*; Emmons 1983, Alkon and Saltz 1988). Additionally, Indian-crested porcupines have been found to preferentially forage in areas of cover where their vulnerability to predators is presumably minimized (Brown and Alkon 1990). Prior to this study, assumptions about how potential effects of predation influence habitat use in New World porcupines (Erethizontidae) (Gill and Cordes 1972, Smith 1979) had not been examined rigorously. The data presented here make clear that quills alone may be insufficient deterrents to potential predators, and that large body size in conjunction with quills may confer additional opportunities for feeding in areas that might be prone to predation pressure. It will be interesting to uncover whether these findings apply to other species of mammals with conspicuous morphological structures designed to thwart predators.

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