

Can shrub cover increase predation risk for a desert rodent?

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Abstract: Previous research indicates that predation risk may influence activity patterns, habitat partitioning, and community structure of nocturnal desert rodents. Shrub microhabitat is typically considered safer than open microhabitat for these small mammals. We investigated predation risk for Townsend's ground squirrels (*Spermophilus townsendii*), which are diurnal desert rodents that detect predators visually and use burrows for refuge. Our results suggested that shrub cover may increase risk for these squirrels by decreasing their ability to escape from predators. Our field experiment indicated that running speeds of juvenile squirrels were lower in shrub (*Ceratoides lanata*) habitat than in open areas. Shrub cover was also associated with shorter predator-detection distances (mammalian and avian) and fewer refuges (burrow entrances per hectare) than in open areas in one year but not in another. Our study demonstrated that the visual and locomotive obstruction of vegetative cover may increase predation risk for diurnal desert rodents and that elements of habitat-dependent risk may be temporally dynamic.

Résumé : Des études antérieures indiquent que les risques de prédation peuvent influencer l'activité, le fractionnement de l'habitat et la structure des communautés chez les rongeurs nocturnes du désert. Les microhabitats reliés aux zones buissonneuses sont généralement considérés plus sécuritaires que les microhabitats des milieux ouverts pour ces petits mammifères. Nous avons mesuré les risques de prédation encourus par le Spermophile de Townsend (*Spermophilus townsendii*), un rongeur diurne du désert qui détecte la présence des prédateurs à vue et qui utilise des terriers comme refuges. Nos résultats indiquent que la couverture de buissons peut augmenter les risques de prédation de ce spermophile en diminuant sa capacité de fuir. Nos expériences sur le terrain ont démontré que la vitesse de course de spermophiles juvéniles est plus lente dans la zone de buissons (*Ceratoides lanata*) que dans les zones ouvertes. Au cours d'une année, la couverture de buissons s'est également avérée associée à des distances de détection des prédateurs plus courtes (mammifères et oiseaux) et à des nombres moins élevés de refuges (entrées de terrier par hectare) que les zones ouvertes, mais cette relation n'a pas été observée au cours d'une autre année. Nos résultats ont démontré que l'obstruction visuelle et locomotrice que représente la végétation peut augmenter les risques de prédation chez les rongeurs diurnes du désert et que les différents aspects des risques reliés à l'habitat peuvent varier dans le temps.
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Introduction

Predation risk can influence many features of an animal's ecology (Lima and Dill 1990), such as habitat selection, activity, diet, reproduction, social behavior, and inter-specific interactions (e.g., Sih 1982; Lima et al. 1985; Holbrook and Schmitt 1988; Taylor 1988; Holmes 1991; Hedrick and Dill 1993; Suhonen et al. 1994; Norrdahl and Korpimäki 1995). One needs to consider habitat-specific predation risk for a species to understand patterns of habitat selection, behavior, and survival within particular habitats.

For terrestrial vertebrates, the relationship of vegetative cover to predation risk has been a common focus of investigations (Anderson 1986; Wywiałowski 1987; Lima 1990; Cassini 1991; Dickman 1992). In particular, extensive research on desert rodents indicates that shrub microhabitat may be safer than open microhabitat for these small mammals because vegetative cover can provide shelter from predators (e.g., Rosenzweig 1973; Thompson 1982; Kotler 1984; Bowers 1988; Kotler and Brown 1988; Longland and Price 1991).

Habitat-specific risk may influence activity times, foraging behavior, space partitioning, and species coexistence of desert rodents (Price and Brown 1983; Kotler and Brown 1988; but see Brown 1989). Previous research, however, has focused on small nocturnal rodents (mainly heteromyids and *Peromyscus* spp.), which can use shrubs as protective cover from predation by owls (but see Kotler et al. 1992; Pierce et al. 1992; Bouskila 1995). Vegetative cover can also obstruct an animal's vision (Metcalf 1984; Carey 1985; Lima et al. 1987; Lazarus and Symonds 1992) and perhaps its locomotion. This obstructive property of cover may be especially relevant to the likelihood of escape for prey that detect predators visually and then retreat to a refuge such as a burrow. Studies of predation risk often focus on habitat-specific attack rates and predator abundances, whereas escape probabilities are ignored or assumed to be constant among habitats (Lima and Dill 1990; Lima 1992).

We compared several components of predation risk for Townsend's ground squirrels (*Spermophilus townsendii*) between shrub and open habitats in a shrub-steppe ecosystem. Our emphasis was on the ways in which vegetative cover could influence the chance of escape (Lima 1992) for a diurnal desert rodent that visually scans for predators and typically runs to a burrow for shelter. Shrub habitats were dominated by winterfat (*Ceratoides lanata*), whereas open

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habitats were burned areas with virtually no shrubs. Winterfat shrubs did not appear to provide protective cover for Townsend's ground squirrels because of their small size and structure. We hypothesized that shrubs might actually increase risk for squirrels by increasing their escape time to a refuge and reducing the distance from which they could detect predators. We used experimental running trials to test running speeds of squirrels in winterfat and open areas, and we compared predator-detection distances between these two habitats. Escape time also depends on the distance of the squirrel from a refuge, so we compared densities of burrow entrances (refuges) between habitats.

Study site and predator – prey system

The Snake River Birds of Prey National Conservation Area in southwestern Idaho, U.S.A. (43°20'N, 116°22'W), includes approximately 195 325 ha of shrub–steppe habitat. We conducted our study on the benchlands of this area, where the topography was generally flat (900–950 m elevation). The area contains the Snake River Canyon, however, which includes basalt cliffs that are ≤ 125 m high. The primary natural vegetation in the area included shrub associations of big sagebrush (*Artemisia tridentata*), winterfat, and shadscale (*Atriplex confertifolia*). About 50% of the area had burned since 1980 (Kochert and Pellant 1986), resulting in open habitat dominated by a native bunchgrass (*Poa secunda*) and many exotic grasses and forbs (e.g., *Bromus tectorum*, *Salsola iberica*, *Descurainia* spp., and *Lepidium perfoliatum*; Yensen et al. 1992). Annual precipitation in the area averages 20 cm, but years with ≤ 12 cm are not rare (United States Department of the Interior 1979).

Townsend's ground squirrels occurred in both shrub and open habitats. Adult squirrels mated soon after they emerged from hibernation in late January or February. Juvenile squirrels were first active above ground between late March and late April, and most individuals entered estivation by late June. The Snake River Birds of Prey National Conservation Area contains one of the highest densities of breeding raptors in the world (Marti et al. 1993). The primary raptor species that prey on ground squirrels are the prairie falcon (*Falco mexicanus*), northern harrier (*Circus cyaneus*), red-tailed hawk (*Buteo jamaicensis*), and ferruginous hawk (*B. regalis*). Mammalian predators include coyotes (*Canis latrans*) and badgers (*Taxidea taxus*; Messick and Hornocker 1981). Several snakes (western rattlesnakes, *Crotalus viridis*; gopher snakes, *Pituophis melanoleucus*) also prey on juvenile squirrels (Diller and Johnson 1988).

Methods

Running speeds

We conducted a field experiment from 18 May to 5 June 1994 to compare the running speeds of juvenile squirrels between winterfat and open habitats. We captured squirrels in wire cage traps (Model 201, Tomahawk Live Trap Co., Tomahawk, Wis.) from an area that included open habitat and patches of winterfat. Animals were therefore captured in a habitat that was intermediate in vegetation structure to the two habitats in our experiment. We recorded the sex and body mass of captured squirrels and marked them with black hair dye (Lady Clairrol, Nice'n Easy, No. 124) so that each

individual was used in only one time trial. We kept the squirrels in covered cages in the shade prior to trials. The juveniles were of the age (ca. 60–70 days) and body mass (95–232 g) of potential dispersers from natal areas, so our experiment simulated a situation in which a dispersing juvenile might encounter a predator while exploring novel habitat.

We constructed two running tracks (1 × 10 m) with particle board walls (0.4 m high) in the field. We marked start (0 m) and finish (10 m) lines on each track. Incline can influence running speeds of sciurids (Blumstein 1992), so our tracks were level and we ran all individuals in the same direction (back towards the area where they had been trapped). Track 1 was in a patch of winterfat. We removed all other vegetation (grasses and forbs) on the track because rapid growth of these plants during the study period could have confounded our results. The height of winterfat shrubs on our track ($\bar{x} = 14.8$ cm, SD = 5.1 cm; $n = 69$) was similar to that of typical winterfat habitat, whereas the density of shrubs on the track (6.9/m²) was slightly greater than typical winterfat areas (5.4/m²; Van Horne et al. 1992). Track 2 was in an open area with no shrubs. Again, we removed all other vegetation from the track, so that the only difference between the two tracks was the presence of winterfat shrubs on track 1.

We used a between-subjects design to test for habitat effects on running speed. Individuals were randomly assigned to either the winterfat or the open track. When possible, we paired captured squirrels by body mass and sex and then randomly assigned the members of the pair to treatments. We alternated trials between the two tracks within a day. The median time of day for trials was 12:13 MST (range 08:36–19:50; $n = 32$).

For each trial, we briefly familiarized an individual with the track by placing it for ca. 1 min at both the finish line and the halfway point (5 m). We then released it from its trap 1.5 m before the start line and one person chased it down the track, yelling loudly and beating the ground with a small (ca. 1 m long) broom. We released the squirrels before the start line to avoid timing them before they had responded to the chaser. Other researchers (Trombulak 1989; Blumstein 1992; Smith 1995) have used similar methods to encourage sciurids to run at maximum speed. We also used a domesticated dog (a 38-kg male) to stimulate the squirrels. The dog was staked near the start line, so that the "predator" and "prey" could see each other, but no physical contact was allowed. The ends of the tracks were not blocked, so the squirrels continued to run past the finish line.

One person recorded the times (s/10 m) for all trials with a hand-held stopwatch while seated in a stand 3 m above the ground. If a squirrel hesitated during a trial, we excluded its time from our analysis. We used an analysis of covariance to test for the effects of habitat (winterfat or open), sex, habitat × sex, body mass, and time of day on running speed (m/s).

Density of refuges

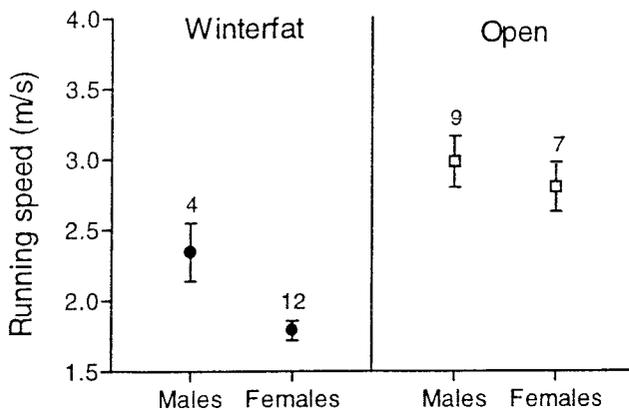
Burrows are the primary refuge from predators for Townsend's ground squirrels in winterfat and open habitats. From 1 to 13 June in 1992 and 1993, we walked adjacent transects and counted all entrances to squirrel burrows on 2 winterfat sites and 8 open sites. The area of each study site was 2.25, 4.5, or 9.0 ha in 1992 and all sites were 4.5 ha in 1993. The unequal sampling of habitats and areas was due to design considerations of a concurrent demographic study. We compared the density (number per hectare) of burrow entrances between habitats and years with a repeated-measures analysis of variance (ANOVA). Habitat was a between-subjects effect and year was a within-subject effect. We used a multivariate approach to test for the within-subject effect and for an interaction of the between-subjects and within-subject effects (SAS Institute Inc. 1989).

Table 1. Results of separate ANOVA models from investigations of three aspects of predation risk for Townsend's ground squirrels.

Response variable	Source of variation	df	MS	Wilks' λ	F	P
Running speed	Habitat	1	969.44		29.98	0.0001
	Sex	1	200.86		6.21	0.0189
	Habitat \times sex	1	47.93		1.48	0.2336
	Error	28	32.34			
Refuge density	Habitat	1	211.25		9.15	0.0164
	Error	8	23.09			
	Year	1,8		0.238	25.60	0.0010
	Habitat \times year	1,8		0.101	71.11	0.0001
Detection distance	Habitat	4,22		0.471	6.18	0.0017
	Year	4,22		0.954	0.26	0.8985
	Habitat \times year	4,22		0.517	5.14	0.0044

Note: The ANOVA of running speeds (m/s) is for juvenile squirrels timed in experimental trials. Refuge densities (burrow entrances per hectare) were analyzed with a repeated-measures ANOVA that included habitat as a between-subjects effect and year as a within-subject effect. Predator-detection distances were analyzed with a multivariate ANOVA.

Fig. 1. Running speeds ($\bar{x} \pm 1$ SE) of juvenile Townsend's ground squirrels, based on experimental trials. The numbers above the bars indicate the number of individuals timed in each group. Running speeds were greater in open habitat than in winterfat habitat and males ran faster than females (Table 1).



Predator-detection distances

Because it would be difficult to quantify the distance at which a squirrel could see an approaching predator, we used an index to estimate the maximum predator-detection distances for squirrels in winterfat and open habitat instead. We calculated this index in May 1993 and in late March – early April 1994. Within the two habitats, we selected random points (5 in 1993 and 10 in 1994) and extended a 200-m tape along a random bearing from each point. One person moved slowly along the transect, away from the initial random point, carrying a pole with attached wooden forms representative of potential predators of squirrels. We depicted a mammalian predator (coyote or badger) by a 30 \times 30 cm square attached to the pole 20 cm above ground level and a northern harrier by a 1 \times 0.1 m rectangle attached 4 m above ground level. Both forms were painted red. One of us (P.B.S.) viewed the predator forms from the initial random point through a small cylindrical opening (ca. 6 mm in diameter, 13 mm deep) drilled through a wooden board. He viewed the forms at two heights above the ground that were typical of the eye level of a ground squirrel in a quadrupedal (5 cm) and a bipedal (18 cm) vigilance posture. We then recorded the maximum distance (≤ 200 m) at which each predator form could

be seen from the two viewing heights. Therefore, we estimated maximum detection distances for four combinations of squirrel posture and predator type (quadrupedal-coyote, bipedal-coyote, quadrupedal-harrier, bipedal-harrier) at each random point. We used these four distances as response variables in a multivariate ANOVA that included habitat, year, and habitat \times year as effects.

We performed all analyses on rank-transformed data (Conover and Iman 1981). Rank transformation may be inappropriate for some ANOVA models that include interactions, but it was suitable for our experimental design, which included two main effects that had only two levels each (Thompson 1991; Seaman et al. 1994). We present untransformed data in our figures.

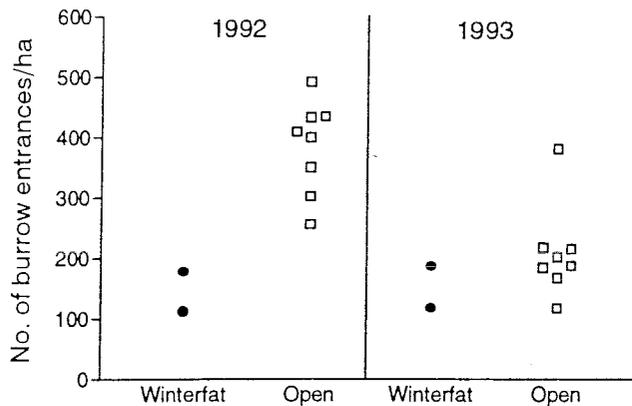
Results

We conducted running trials for 32 individual squirrels (16 in each habitat). Our random-assignment procedure resulted in similar distributions of body mass for individuals tested in winterfat habitat ($\bar{x} = 158.1$ g, SD = 31.20 g) and in open habitat ($\bar{x} = 160.2$ g, SD = 35.19 g). Our initial analysis of covariance indicated that neither body mass ($P = 0.5583$) nor time of day ($P = 0.5418$) was a significant covariate, so we removed them from our ANOVA model. Based on the reduced model, habitat and sex both influenced running speed and there was no interaction between these effects (Table 1). Running speeds were greater in the open habitat than in the winterfat habitat, and males ran faster than females (Fig. 1). The greatest difference in means between two groups was > 1 m/s (males-open vs. females-winterfat; Fig. 1).

There was a habitat \times year interaction in our model of refuge density (Table 1), therefore we compared refuge densities between habitats separately for the 2 years with Holm's sequential Bonferroni t tests (Rice 1989; Wright 1992) on rank-transformed data. We controlled the experimentwise error rate at 0.05. In 1992, the density of refuges was greater in open habitats than in winterfat areas ($P \leq 0.05$; Fig. 2). In contrast, refuge densities did not differ between habitats in 1993 ($P > 0.05$; Fig. 2).

There was also a habitat \times year interaction in our multivariate model of predator-detection distances (Table 1, Fig. 3). We explored the basis for this interaction by comparing

Fig. 2. Density of refuges (burrow entrances) of Townsend's ground squirrels for 1992–1993 in two habitats in a shrub–steppe ecosystem. Points were total counts from separate study sites. The density of refuges was greater in open habitats than in winterfat habitats in 1992 ($P \leq 0.05$), but there was no difference between habitats in 1993 ($P > 0.05$).



detection distances between habitats within years for individual prey posture – predator type combinations. We used sequential Bonferroni t tests but employed an experiment-wise error rate of 0.10 to maintain reasonable power for the 8 tests. In 1993, predator-detection distances were greater in open habitat than in winterfat habitat for all prey–predator combinations ($P \leq 0.10$; Fig. 3). In contrast, the only habitat difference in 1994 was for the bipedal-coyote combination ($P \leq 0.10$; Fig. 3); detection distances did not differ between habitats for the other three combinations ($P > 0.10$). These annual differences resulted from a general decrease in detection distances in open habitat from 1993 to 1994 (Fig. 3).

Discussion

Our comparisons of running speeds, refuge densities, and predator-detection distances all suggest that winterfat shrub habitat could be riskier than open habitat for Townsend's ground squirrels in some years. Compared with open areas, squirrels in winterfat habitat may have a reduced ability to detect predators and lower escape speeds to refuges that are less abundant. These results contrast with the prevailing view of predation risk for many desert rodents (see the Introduction), which can use shrubs for refuge and may rely less on detecting predators visually than do Townsend's ground squirrels. Our results are more consistent with those for yellow-bellied marmots (*Marmota flaviventris*), which are montane diurnal sciurids with antipredator tactics similar to those of Townsend's ground squirrels. Patch use by these marmots is negatively associated with high, dense vegetation that can obstruct their view of predators (Carey 1985). Likewise, Armitage (1982) described a few instances of coyotes using tall vegetation for concealment while preying on yellow-bellied marmots.

There are several caveats related to our approach and inferences. Our investigation was restricted to winterfat shrub habitat and we recognize that risk to squirrels might differ in other shrub communities, such as big sagebrush, where the size and structure of shrubs might allow squirrels to use them for refuge. However, we predict that running

speeds of squirrels and predator-detection distances will typically be reduced in most shrub communities relative to more open areas. We also emphasize that our comparisons were between two macrohabitats and that we did not investigate risk for squirrels near shrubs versus open spaces within winterfat habitat. Also, although open habitat typically contains less vegetation structure than does shrub habitat, growth of annual plants during years with unusually high precipitation can reduce the structural differences between these two habitats. Lastly, unlike running speeds and predator-detection distances, refuge densities were not necessarily directly related to shrub cover. Instead, low densities of burrow entrances were simply associated with lower squirrel densities on shrub sites than in open areas in some years (Van Horne et al. 1992).

We highlighted components of risk that mainly influence the probability of escape for squirrels in different habitats. Some features of predator–prey interactions could ameliorate such effects, including habitat-dependent attack rates, predator attack speeds, prey detectability, and prey movements. A greater probability of attack in open than in winterfat habitat could offset habitat-specific escape probabilities. This difference in attack rates needs to be large, however, if there are substantial differences in escape probabilities (Lima 1992), as suggested by our study. Our data related to attack rates are limited and pertain only to avian predators. Nevertheless, the number of raptors observed on our sites during behavioral observations of squirrels did not differ between winterfat and open areas in 1992 or 1993 (Sharpe and Van Horne 1993), although there were species differences (i.e., northern harriers were most common on winterfat areas and prairie falcons were most common on open areas). Shrubs could reduce the attack speed of terrestrial predators as well as prey. Because winterfat shrubs are short (ca. 15 cm), however, we expect that they would have a negligible effect on the running speed of a mammalian predator such as a coyote. The potential effect of shrub cover on the attack speed of raptors is less clear and likely depends on the hunting behavior of particular species. We suggest that the hunting style of northern harriers is well adapted to vegetation structure similar to that of winterfat habitat. Northern harriers generally hunt <3 m above vegetation with a search–pause–pounce technique (Palmer 1988). Prey may also be more difficult for predators to detect in habitats with high structural complexity (Armitage 1982), but we contend that the visual obstruction of winterfat shrubs is probably a net disadvantage to prey such as Townsend's ground squirrels, whose predator-avoidance strategy involves detection of a predator prior to an attack.

Animals that are familiar with the location of refuges within their home ranges (Clarke et al. 1993) could adjust their movements in response to perceived risk (e.g., Anderson 1986). For instance, consider a simple scenario in which a juvenile squirrel settles in either winterfat or open habitat and then typically restricts its movements relative to a refuge so as to allow adequate time for retreat from a predator. If we assume that this minimum escape time is ca. 3.4 s (chosen only to illustrate a point and not empirically derived), then a male in open habitat could travel 10 m from a refuge, whereas a female in shrub habitat could range only 6 m from a refuge (Fig. 4). If a squirrel had a circular home range centered on a single burrow entrance, then a male in an open area

Fig. 3. Predator-detection distances ($\bar{x} \pm 1$ SE) for Townsend's ground squirrels for 1993–1994 in two habitats. The distances were based on an index that included four combinations of squirrel vigilance posture and predator type. Distances were truncated at 200 m. Each mean was estimated from 5 random points in 1993 and 10 random points in 1994. Detection distances were greater in open habitat than in winterfat habitat for all combinations in 1993 ($P \leq 0.10$), whereas the only difference between habitats in 1994 was for the bipedal-coyote combination ($P \leq 0.10$).

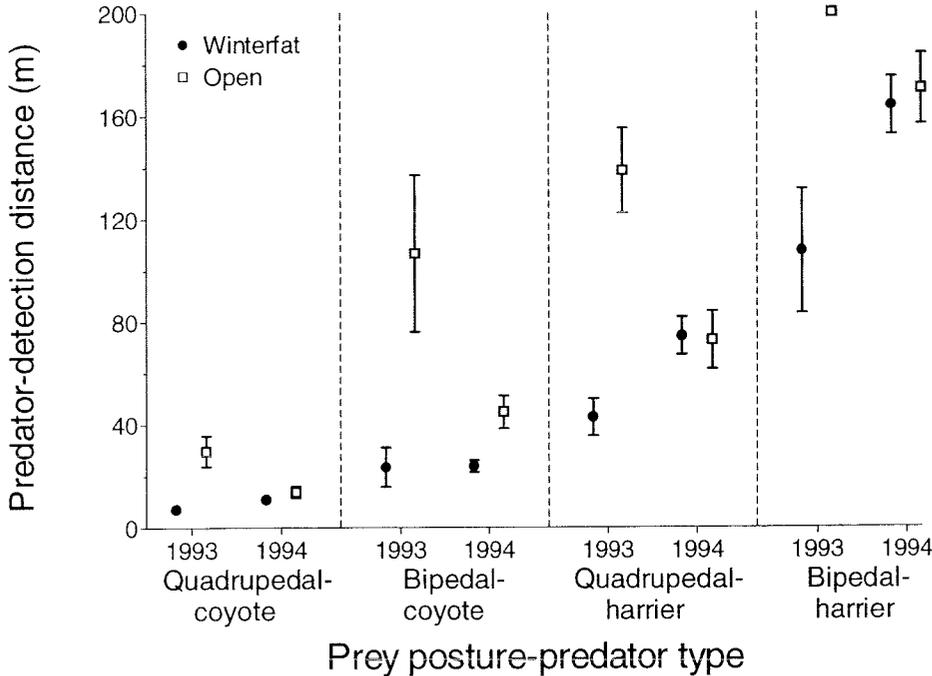
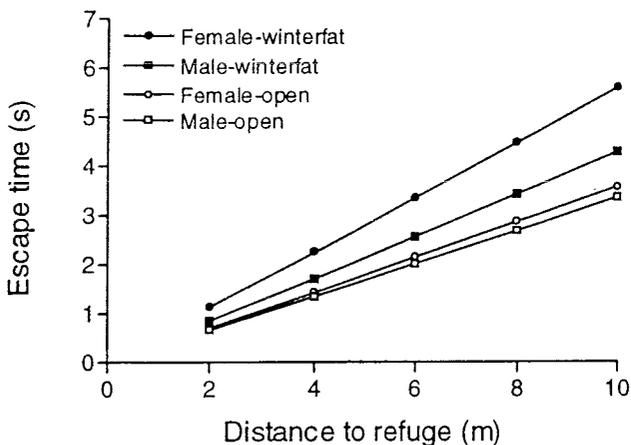


Fig. 4. Relationship between distance to a refuge and escape time from a predator for juvenile Townsend's ground squirrels. The relationship is based on average sex- and habitat-specific running speeds (m/s) obtained during a field experiment (see Fig. 1).



would have a “safe” range of 314 m² compared with only 113 m² for a female in winterfat habitat. Such predation-sensitive movement by a central-place forager like a ground squirrel could potentially affect the spatial distribution of animals among habitats. For animals exploring novel habitat, such as a juvenile dispersing from its natal area or an adult that might increase its movements during the mating period,

the general abundance of refuges (Fig. 2) is probably most relevant to predation risk. Unfamiliarity with refuge locations could be one cost of dispersal and reproduction.

If Townsend's ground squirrels perceive winterfat habitat to be riskier than open areas, one would expect squirrels in winterfat habitat to allocate more time to vigilant postures that allow them to scan for predators. This prediction is supported by the activity budgets of squirrels derived from behavioral observations of focal animals (Sharpe and Van Horne 1993). In 1992, squirrels in winterfat habitat allocated 58% of their activity budget to vigilance compared with $\leq 8\%$ for squirrels in open habitat. This habitat-specific pattern of vigilance was repeated in 1993 (73% for winterfat, $\leq 28\%$ for open). Increased vigilance has been associated with environments with reduced visibility for several species of birds (Metcalf 1984; Lazarus and Symonds 1992; Martella et al. 1995) and large mammals (Underwood 1982; Lagory 1986).

Besides environmental variables, other factors could influence running speeds and predation risk of sciurids, such as age, body mass, and sex. We must limit inferences from our experiment to juvenile squirrels, but we predict that a similar habitat effect would be obtained for adults. Body mass was not a significant covariate in our experiment, and also did not influence the maximum running speed of adult golden marmots (*Marmota caudata*; Blumstein 1992). In contrast, Trombulak (1989) reported that the running speed of Belding's ground squirrels (*Spermophilus beldingi*) was negatively correlated with body mass. The significant effect of sex on running speed in our study (males were faster than females)

was unexpected and difficult to explain. We suggest that larger sample sizes are needed for a conclusive test of sexual differences in running speed.

Temporal variation in environmental conditions can affect the relative risk that prey experience in different habitats. In our arid shrub-steppe system, annual variation in precipitation translated into habitat \times year interactions for both refuge availability and predator-detection distances. The decrease in densities of burrow entrances on open areas from 1992 to 1993 was related to a substantial population decline of squirrels after a severe drought in the summer of 1992. Although squirrel densities also declined on winterfat sites, burrow entrances persist longer on winterfat than on open habitat (Van Horne et al. 1993a). Our index indicated a consistent decrease in predator-detection distances in the open from 1993 to 1994. This decrease was related to unusually high precipitation in 1993 that was associated with a growth flush of forbs (especially *Salsola iberica* and *Descurainia* spp.) late in the active season of the squirrels, especially on open areas (Van Horne et al. 1993b). Substantial dead biomass of these forbs was present on open areas during 1994, and this cover reduced detection distances. Other ecosystems may exhibit similar temporal dynamics that influence predator-prey interactions.

In conclusion, our study indicated that shrub cover can increase some aspects of predation risk for a desert rodent, especially components related to the likelihood of escape (Lima 1992). The activity budgets of the ground squirrels are consistent with this perceived habitat-specific risk; squirrels are more vigilant in winterfat shrub habitat than in open habitat. These results emphasize the need to consider the details of habitat-predator-prey systems instead of assuming that cover is necessarily beneficial to prey. Finally, our results illustrate that factors influencing predation risk can vary greatly in time as well as in space. These temporal effects may be underappreciated in studies of habitat-specific predation risk.

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