

# INFLUENCE OF HABITAT ON BEHAVIOR OF TOWNSEND'S GROUND SQUIRRELS (*SPERMOPHILUS TOWNSENDII*)

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Trade-offs between foraging and predator avoidance may affect an animal's survival and reproduction. These trade-offs may be influenced by differences in vegetative cover, especially if foraging profitability and predation risk differ among habitats. We examined above-ground activity of Townsend's ground squirrels (*Spermophilus townsendii*) in four habitats in the Snake River Birds of Prey National Conservation Area in southwestern Idaho to determine if behavior of ground squirrels varied among habitats, and we assessed factors that might affect perceived predation risk (i.e. predator detectability, predation pressure, population density). The proportion of time spent in vigilance by ground squirrels in winterfat (*Krascheninnikovia lanata*) and mosaic habitats of winterfat-sagebrush (*Artemisia tridentata*) was more than twice that of ground squirrels in burned and unburned sagebrush habitats. We found no evidence for the "many-eyes" hypothesis as an explanation for differences in vigilance among habitats. Instead, environmental heterogeneity, especially vegetation structure, likely influenced activity budgets of ground squirrels. Differences in vigilance may have been caused by differences in predator detectability and refuge availability, because ground squirrels in the winterfat and mosaic habitats also spent more time in upright vigilant postures than ground squirrels in burned-sagebrush or sagebrush habitats. Such postures may enhance predator detection in low-growing winterfat.

Key words: *Spermophilus townsendii*, Townsend's ground squirrel, activity budgets, foraging, predator detection, predation risk, vigilance

For many animals, reproductive success and survivorship may be linked to a trade-off between conflicting demands of foraging efficiency and predator avoidance (MacWhirter, 1991). If foraging profitability and predation risk vary with habitat or patch type (Lima and Dill, 1990), one might expect animals in heterogeneous environments to vary time allocated to various activities in a manner reflecting the risk trade-off of foraging-predation (Leger et al., 1983).

Predation risk may be influenced strongly by vegetative cover (Cassini and Galante, 1992; Lima, 1990; Martín and López, 1995; Sparrowe, 1972). Cover can provide concealment from predators and obstacles to pursuing predators (Wywiałowski, 1987). Conversely, cover can obstruct an animal's view of its surroundings, shortening the dis-

tance at which prey can detect predators visually (Carey and Moore, 1986; Martella et al., 1995; Metcalfe, 1984). There may be some trade-off between concealment of prey and predator so that predictions of patterns of prey activity may vary depending if vegetation acts in an obstructive or protective manner (Lazarus and Symonds, 1992; Schooley et al., 1996).

One of the most conspicuous components of an animal's activity budget is the amount of time devoted to antipredator behavior (Loughry, 1993). Several antipredator defenses are common: increased individual vigilance, increased group vigilance (the "many eyes" hypothesis—Pulliam, 1973), remaining close to refuges, and avoidance of detection by hiding or crypsis (Hoogland, 1981). Although many studies have examined the relationship between

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predation risk and activity of prey species (Elgar, 1989; Lima and Dill, 1990), precise benefits of trade-offs between foraging and vigilance are not clear. For instance, low rates of scanning allow more time for foraging but increase risk of failing to detect predators (Elgar et al., 1986; Lima, 1994). Because predation risk is an important aspect of animal decision-making, it is important to understand how an animal perceives predation risk (Lima and Dill, 1990). Allocation of time to vigilance compared with foraging often has been used as an indicator of the perception of risk by prey (Cassini, 1991; Watts, 1990). Because characteristics of prey movement can contribute to a predator's success or selection of prey (Lima and Dill, 1990; Sarno and Gubanich, 1995; Sparrowe, 1972), perceived predation risk also may be estimated by the amount and timing of prey movements.

The trade-off between simultaneous demands of foraging and predator avoidance (Sih, 1980) is likely important to Townsend's ground squirrels (*Spermophilus townsendii*). These ground squirrels are active only 4–4.5 months of the year (Alcorn, 1940), requiring them to store enough fat during the active season to survive an extended period of hibernation. Townsend's ground squirrels also are an important prey species for many predators. They are included in the diets of red-tailed hawks (*Buteo jamaicensis*), golden eagles (*Aquila chrysaetos*), and prairie falcons (*Falco mexicanus*—Ogden and Hornocker, 1977; Steenhof and Kochert, 1988). They are also preyed upon by badgers (*Taxidea taxus*—Messick and Hornocker, 1981), coyotes (*Canis latrans*—Smith and Johnson, 1985), western rattlesnakes (*Crotalus viridis*), and gopher snakes (*Pituophis melanoleucus*—Diller and Johnson, 1988). Therefore, risk of predation likely influences strongly decision-making processes of this ground squirrel, as has been shown with other species of ground-dwelling squirrels (Armitage, 1982; Carey and Moore, 1986; Holmes, 1984).

We examined behavior of Townsend's ground squirrels in a heterogeneous shrub-steppe environment to determine if ground squirrels differed in the percentage of above-ground activity spent in vigilance, foraging, and locomotion in a way that could be attributed to differences in habitat and perceived predation risk. We also assessed effects of other factors that might affect perception of risk, such as predator detectability, predation pressure, and density of ground squirrels.

### MATERIALS AND METHODS

*Study area.*—The Snake River Birds of Prey National Conservation Area in southwestern Idaho (43°20'N, 116°22'W) encompasses 244,000 ha of shrub-steppe habitat along 130 km of the Snake River. Annual precipitation averages ca. 20 cm, mostly as rain or snow from November to April. Summers are dry, with a mean daily temperature of ca. 24°C in July; winters are generally mild with a daily mean temperature of ca. -1.0°C in January (United States Department of Interior, 1979).

The primary natural vegetation in the area included shrub associations of big sagebrush (*Artemisia tridentata*), winterfat (*Krascheninnikovia lanata*), and shadscale (*Atriplex confertifolia*). However, since 1980, wildfires have burned ca. 50% of the shrub habitats (Kochert and Pellant, 1986), converting them to open habitats dominated by native bunchgrasses (Sandberg's bluegrass, *Poa secunda*) and exotic annuals, especially cheat grass (*Bromus tectorum*), tumble mustard (*Sisymbrium altissimum*), tansy mustards (*Descurainia*), and peppergrass (*Lepidium perfoliatum*). Densities of ground squirrels apparently are correlated negatively with exotic annuals and are more stable in shrub-dominated communities (Yensen et al., 1992). Native species, especially Sandberg's bluegrass, winterfat, and big sagebrush, made up a majority of the diet of ground squirrels (Yensen and Quinney, 1992).

We established six 9-ha observational sites in four habitat types. Two sagebrush sites were dominated by big sagebrush, with mean heights and densities of ca. 40 cm and 1.6 shrubs/m<sup>2</sup>, respectively. Sagebrush accounted for ca. 50% of the vegetative cover on the sites, with moss and native bunchgrasses comprising the majority

of remaining vegetation. Sagebrush could obstruct both a ground squirrels' vision and pursuing mammalian predators, while providing a refuge from avian predators. The winterfat site had ca. 60% winterfat shrub cover with mean heights of 16.8 cm and mean densities of 5.6 shrubs/m<sup>2</sup>. Moss and native bunchgrasses comprised the majority of the remaining vegetation on this site. Winterfat would likely obstruct a ground squirrel's vision but provide little refuge from mammalian or avian predators because of the shrubs' short stature and growth form. Although winterfat can affect greatly a ground squirrel's ability to reach a refuge quickly, it is unlikely that those shrubs would impede movements of most predators (Schooley et al., 1996). One site was a mosaic of big sagebrush and winterfat, with ca. 40% sagebrush and 20% winterfat cover. The obstructive-protective properties of the vegetation would depend on if a ground squirrel was in a patch of winterfat or sagebrush. Sandberg's bluegrass accounted for the majority of the remaining vegetation. Two burned-sagebrush sites (burned in 1981) were dominated by Sandberg's bluegrass (ca. 5–10 cm tall), which accounted for ca. 60% of the vegetative cover. Cheatgrass and exotic annuals comprised most of the remaining vegetation. Therefore, there were few, if any, refuges available aboveground for ground squirrels on the burned-sagebrush sites. Topography of all sites was flat to rolling, with elevations ranging from 900 to 950 m (Yensen et al., 1992).

As a result of higher than normal early spring precipitation, there was increased vegetative cover (less bare ground) on all sites in 1993, primarily as a result of increased growth of exotic annuals and new growth on shrubs. The mean proportion of each site with vegetative cover increased from 64% in 1992 to 73% in 1993. Vegetative cover was even higher in 1994 (83%), especially in burned-sagebrush habitats where dead plant material remained from the 1993 growing season (86% cover in 1994 compared with 66% and 57% in 1993 and 1992, respectively).

**Predator detection.**—We were interested in quantifying the obstructive properties of different habitats and determining how this affected a ground squirrel's ability to detect predators. Because it was difficult to quantify how far a ground squirrel could see an approaching predator, we developed an index to estimate maxi-

imum distances at which ground squirrels could detect predators. On each site, we selected random points (5 in 1993, 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 point of origin, carrying a pole with attached wooden forms (painted red) that represented potential predators of ground squirrels. We depicted a mammalian predator (badger or coyote) with a 30- by 30-cm square attached to the pole at 20 cm above the ground, and an avian predator (e.g., northern harrier, *Circus cyaneus*) with a 1- by 0.1-m rectangle attached at 4.0 m above the ground. One of us (P. B. Sharpe) viewed the predator forms from the point of origin through small cylindrical openings (ca. 6 mm diameter, 13 mm deep) drilled through a wooden board at two heights above the ground that were typical of the eye level of a ground squirrel in a quadrupedal (5 cm) and a sitting (13 cm; posterior in contact with the substrate, forelegs raised off substrate) vigilant posture, the two most common postures. We recorded the distance ( $\leq 200$  m) that each predator form could be seen from each of the two viewing heights. We thus estimated maximum detection distances for four combinations of ground squirrel postures and predator types (quadrupedal-mammalian, sitting-mammalian, quadrupedal-avian, sitting-avian) at each random point. This index was measured in May 1993 and late March through early April 1994 on each of the six sites used for behavioral observations.

**Behavioral observations.**—We recorded behavior of Townsend's ground squirrels from January through June, 1992–1994. Most observations were made on ground squirrels that were marked uniquely with hair dye (Clairol Nice 'n Easy® blue-black—Schooley et al., 1993), although we observed unmarked ground squirrels when we could not locate marked individuals. We observed ground squirrels from a portable 3-m hunter's stand (Hunter's Equipment, Inc., San Angelo, TX) using a 15–60 zoom spotting scope mounted on the stand's railing. We attempted to observe focal animals (Altmann, 1974) for 30 min/day. At 20-s intervals, we recorded the focal animal's behavior on a Poly-corder electronic notebook (Omnidata International, Inc., Logan, UT). We discontinued focal observations if the individual disappeared into a burrow for  $>5$  min or was out of sight for  $>3$  min. If 30 min of observations were not col-

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lected for a focal animal, we attempted to relo-  
cate the individual during the day for further ob-  
servations. If  $\geq 10$  min of observations were not  
collected on a specific animal within a day, we  
dropped the data from analyses. As a result of  
our technique, behavioral observations primarily  
represent above-ground activity and the relative,  
not absolute, amount of time spent in different  
activities.

Because it was difficult and time consuming  
to locate randomly selected individuals, we set  
the hunter's stand in areas likely to allow detec-  
tion of animals and recorded observations on  
any individuals that were detected. If there was  
an opportunity, we recorded data for individuals  
that had not been observed previously. After an  
individual was chosen, we waited 2–3 min be-  
fore recording observations to reduce any bias  
toward conspicuous behavior (Wiens et al.,  
1987). Attempts were made to sample age and  
sex classes equally throughout the active season  
and individuals throughout the daylight. We col-  
lected behavioral observations on 167, 127, and  
95 individuals in 1992, 1993, and 1994, respec-  
tively. Each animal was observed for mean  
times of 25.7, 40.4, and 31.6 min (1–6 different  
days) in 1992, 1993, and 1994, respectively.

Behavior was classified as: 1) below ground,  
2) foraging (head down and ingesting forage,  
chewing between bites with head up for <3 s,  
or chewing while sitting on haunches), 3) vigi-  
lant (quadrupedal with head above horizontal  
plane for  $\geq 3$  s, sitting on haunches while not  
chewing, bipedal posture, or sitting in a shrub  
and not foraging), 4) locomotion (walking or  
running), and 5) other (e.g., grooming, excavat-  
ing). We noted foraging on specific plant-species  
or food items whenever possible, and we re-  
corded specific vigilant postures used by ground  
squirrels.

One person (P. B. Sharpe) collected all behav-  
ioral observations in 1992 and 1993. In 1994, a  
technician assisted with behavioral observations.  
During calibration periods in late February to  
early March and late May, we tested for observ-  
er agreement by simultaneously recording behav-  
ior of focal animals, using the observation  
techniques described above, and compared ob-  
servations between the two observers. We si-  
multaneously observed 14 individuals (seven  
during each calibration period) and recorded the  
same category of behavior (e.g., foraging, vigi-  
lance) for 92.8% of 402 observations.

*Predation pressure.*—We recorded number  
and species of raptors observed hunting over  
each site during 15-min periods throughout the  
daylight to measure relative predation pressure  
by raptors. Observations of mammalian predat-  
ors on sites also were noted.

*Density of ground squirrels.*—Population  
densities of adult Townsend's ground squirrels  
were calculated using the no-recruitment special  
case of the Jolly-Seber model for open popula-  
tions (Pollock et al., 1990; Seber, 1982). That  
model assumed that there was no recruitment  
(through birth or immigration) into the popula-  
tion, which was a reasonable assumption for  
adult Townsend's ground squirrels in most years  
because of the relatively low levels of immigra-  
tion (Smith and Johnson, 1985). However, adults  
apparently dispersed during the latter part of the  
active season in May 1992 as a result of a  
drought. Therefore, in 1992, data were truncated  
at the date of juvenile emergence (late March–  
early April). Data for estimates of density were  
collected by mark-recapture of known individ-  
uals that had been injected with passive-inte-  
grated-transponder (PIT) tags (Schooley et al.,  
1993). Only adult densities were used, because  
observations of Townsend's ground squirrels in-  
dicated that adult vigilance was more important  
in relation to the "many-eyes" hypothesis (Pul-  
liam, 1973). Adults generally did not respond to  
juvenile alarm calls, but most animals became  
vigilant upon hearing an adult's call (P. B. Sharpe,  
in litt.). We also found no significant differences  
between vigilance levels of adults within any  
habitat type when we compared periods before  
and after juvenile emergence ( $P > 0.23$ ). Lough-  
ry (1993) also reported that number of adults  
present was more influential than number of  
young in determining individual vigilance levels  
in black-tailed prairie dogs (*Cynomys ludovici-*  
*anus*).

*Statistical analyses.*—For the predator-dete-  
ction study, we performed analyses on rank-trans-  
formed data (Conover and Iman, 1981) when  
comparing habitat types but present non-trans-  
formed data for estimated detection distances in  
our figures. We used the maximum detection  
distances from the four combinations of ground-  
squirrel postures and predator types as response  
variables in a multivariate analysis of variance  
(MANOVA) that included habitat, year, and  
habitat by year as independent variables. Within  
each habitat type, we also tested for the effect

of posture on non-transformed detection distances for each predator type using *t*-tests.

For the behavioral part of our study, all observations for a specific individual within a year were combined to calculate the percentage of time spent in various activities. We compared three general categories of behavior among ground squirrels: percentage of time spent vigilant, foraging, and in locomotion. Those behaviors constituted a large part of observed daily behavior, and we believe that they were most influenced by predation risk. Use of a subset of all behaviors also reduced problems associated with analyses of proportions that sum to 1.0 (i.e., unit-sum constraint—Aebischer et al., 1993). Statistical analyses were conducted on arcsine-transformed data using the SAS statistical package (SAS Institute, Inc., 1989). MANOVA models were run under the GLM procedure with locomotion, foraging, and vigilance as dependent variables to test for differences in overall behavioral patterns using Wilks' lambda ( $\Lambda$ ). Significant differences were investigated using ANOVA models with the experiment-wise error rate controlled with Holm's sequential Bonferroni *t*-tests (Rice, 1989; Wright, 1992). We primarily were interested in behavioral differences among habitats, but prior to combining data from individuals within a habitat type, we determined if behavior differed by age, sex, and time period (pre- and post-juvenile emergence), or between paired sites within a habitat. We compared animals of known age and sex for the period in which both juveniles and adults were active (April–May). We then compared male behavior with that of females prior to juvenile emergence and adult behavior prior to juvenile emergence with that following juvenile emergence. Next, we ran a model that included only sagebrush and burned-sagebrush habitats to determine if there were differences when sites were nested within habitat type. In 1994, there were too few ground squirrels present on the winterfat and mosaic sites to justify collecting behavioral data. Therefore, we tested for behavioral differences among habitats with two separate models, using habitat and year as effects. The first model included data from 1992 to 1993, the period in which we had data from all habitats. The second model included data for sagebrush and burned-sagebrush sites from 1992 to 1994. This allowed us to test for differences between those habitats among years and within years.

We compared avian predation pressure among behavioral sites using ANOVA models with year and habitat as effects. As with the behavioral data, we used two models: one model included the 1992 to 1993 data for all sites and one model included data for sagebrush and burned-sagebrush sites from 1992 to 1994.

## RESULTS

*Predator detection.*—We compared estimated detection distances (as determined by our predator-detection index) for a model mammalian and a model avian predator from ground squirrels in quadrupedal and sitting postures to quantify obstructive properties of each habitat. There were no statistically significant year by habitat ( $F = 0.62$ ,  $\Lambda = 0.91$ ,  $d.f. = 12$ , 206,  $P = 0.83$ ) or year ( $F = 2.16$ ,  $\Lambda = 0.90$ ,  $d.f. = 4$ , 78,  $P = 0.08$ ) effects, but there was a significant habitat ( $F = 9.02$ ,  $\Lambda = 0.33$ ,  $d.f. = 12$ , 206,  $P = 0.0001$ ) effect on maximum detection distances. Therefore, we combined all data within a habitat type and examined each combination of prey posture-predator height separately, controlling the experiment-wise error rate at 0.1 for the 24 tests to increase power. For all combinations of prey posture and predator type, detection distances were significantly farther in burned sagebrush than in any other habitat ( $P < 0.1$ ; Fig. 1). The mosaic habitat had significantly shorter detection distances than other habitats for all comparisons ( $P < 0.1$ ). Intermediate detection distances were found in the winterfat and sagebrush habitats (Fig. 1), and they differed from each other only in detection distances from a sitting vigilant posture ( $P < 0.1$ ). Although detection distances were always farther from a sitting posture than a standing posture within each habitat type and predator type combination, distances differed significantly only in burned-sagebrush and winterfat habitats ( $P < 0.05$ ; Fig. 1).

*Behavioral observations.*—There were no sex effects on behavior either prior to ( $F = 0.51$ ,  $\Lambda = 0.99$ ,  $d.f. = 3$ , 125,  $P = 0.68$ ) or following ( $F = 0.42$ ,  $\Lambda = 1.0$ ,  $d.f. = 3$ ,

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167,  $P = 0.74$ ) juvenile emergence. There were no significant differences when adult behavior prior to juvenile emergence was compared with that recorded after juvenile emergence ( $F = 2.16, \Lambda = 0.98, d.f. = 3, 280, P = 0.09$ ). There also were no differences between juvenile and adult behavior ( $F = 1.62, \Lambda = 0.97, d.f. = 3, 167, P = 0.19$ ), so we combined age and sex classes within each site in each year. The comparison of sagebrush and burned-sagebrush habitats indicated no significant site-nested-within-habitat effect ( $F = 0.77, \Lambda = 0.99, d.f. = 6, 650, P = 0.59$ ), but a significant year by habitat interaction ( $F = 4.96, \Lambda = 0.91, d.f. = 6, 652, P = 0.0001$ ). We therefore combined paired sites within each habitat for subsequent analyses.

Data from 1992 and 1993 showed significant year ( $F = 5.84, \Lambda = 0.94, d.f. = 3,$

262,  $P = 0.0007$ ), habitat ( $F = 18.98, \Lambda = 0.56, d.f. = 9, 638, P = 0.0001$ ), and year by habitat ( $F = 2.51, \Lambda = 0.92, d.f. = 9, 638, P = 0.0078$ ) effects. The effect of year resulted primarily from an increase in vigilance ( $P = 0.0006$ ) on all but the sagebrush sites from 1992 to 1993. The model including only burned-sagebrush and sagebrush sites also detected a significant year effect ( $F = 4.50, \Lambda = 0.92, d.f. = 6, 604, P = 0.0002$ ), that also resulted from differences in vigilance in 1992 compared with 1993, habitat ( $F = 7.22, \Lambda = 0.93, d.f. = 3, 302, P = 0.0001$ ), and year by habitat ( $F = 5.88, \Lambda = 0.89, d.f. = 6, 604, P = 0.0001$ ). Because of significant interaction effects in both models, we chose to examine habitat differences in behavior of ground squirrels for each year separately.

Ground squirrel behavior differed signif-

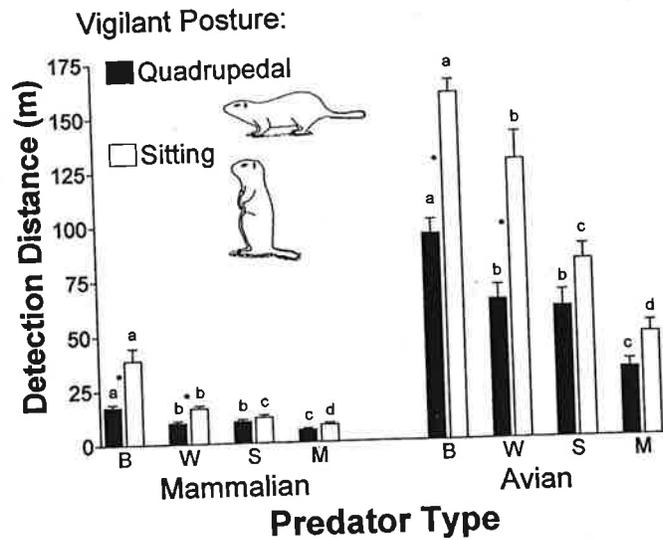


FIG. 1.—Estimated maximum predator-detection distances ( $\bar{X} \pm 1 SE, n = 15$  random points on each of six sites) for Townsend's ground squirrels in the Snake River Birds of Prey National Conservation Area, Idaho, 1993–1994. Maximum detection distances were estimated for two classes of predator (mammalian and avian) and for two vigilant postures (quadrupedal and sitting) of ground squirrels in four habitat types (B = burned sagebrush, W = winterfat, S = sagebrush, M = mosaic) using an index that measured maximum distance that a human could see forms representative of ground squirrel predators from two viewing heights representative of the eye level of ground squirrels in the two most common vigilant postures. Bars within each vigilant posture-predator type combination (e.g., sitting posture, mammalian predator) with the same letter do not differ significantly at  $P = 0.1$ ; an asterisk between two bars indicates that detection distances from standing and sitting postures within a habitat type differ significantly at  $P = 0.05$ .

TABLE 1.—Time (%) spent in three major activities by Townsend's ground squirrels in the Snake River Birds of Prey National Conservation Area, Idaho, 1992–1994.

Year	Habitat	n <sup>a</sup>	Activity					
			Locomotion		Foraging		Vigilant	
			$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
1992								
	Burned sagebrush	68	13.6A <sup>b</sup>	1.2	57.0A	2.6	7.7A	0.8
	Sagebrush	58	8.9B	1.1	55.2A	3.9	26.5B	4.1
	Winterfat	23	8.2B	1.6	23.4B	4.8	58.2C	6.9
	Mosaic	18	5.3B	1.4	23.0B	6.6	58.1C	7.7
1993								
	Burned sagebrush	68	9.7A	0.7	52.2A	2.5	23.5A	2.2
	Sagebrush	46	11.2AB	1.1	51.2A	3.6	28.0A	3.3
	Winterfat	7	6.2BC	2.4	17.4B	6.2	73.1B	8.7
	Mosaic	6	1.1C	0.6	9.2B	3.9	87.2B	3.7
1994								
	Burned sagebrush	57	9.4A	0.9	52.9A	3.3	23.2A	2.9
	Sagebrush	38	8.5A	0.8	55.5A	4.1	19.3A	3.4

<sup>a</sup> Number of individuals observed.

<sup>b</sup> Column values within a year that have the same letter do not differ significantly at  $P = 0.05$  (Holm's sequential Bonferroni  $t$ -tests—Rice, 1989; Wright, 1992).

icantly among habitats in 1992 ( $F = 11.39$ ,  $\Lambda = 0.57$ ,  $d.f. = 9$ , 391,  $P = 0.0001$ ) and 1993 ( $F = 9.35$ ,  $\Lambda = 0.54$ ,  $d.f. = 2$ , 295,  $P = 0.0001$ ), but not in 1994 when only two habitats were included ( $F = 0.76$ ,  $\Lambda = 0.98$ ,  $d.f. = 3$ , 91,  $P = 0.52$ ). Behavioral differences were investigated by comparing separately each behavior among habitats within years. In all years, ground squirrels in burned-sagebrush and sagebrush habitats spent similar amounts of time foraging, but ground squirrels spent less time vigilant and more time in locomotion in burned sagebrush in 1992 (Table 1). Ground squirrels in winterfat and mosaic habitats had similar activity budgets; they spent a significantly greater proportion of their time vigilant and less time foraging than did ground squirrels in sagebrush or burned-sagebrush habitats (Table 1). Ground squirrels in mosaic and winterfat habitats also spent less time in locomotion than did those in sagebrush and burned sagebrush, although differences were not always significant (Table 1).

Locomotion, foraging, and vigilance comprised 78–97% of observed diurnal ac-

tivity, with foraging and vigilance comprising 65–96% of daily activity in all habitats (Table 1). There was a strong negative correlation between foraging and vigilance ( $r_s = -0.76$ ,  $P = 0.0001$ ,  $n = 389$ ).

We examined relative use of three types of vigilant postures (quadrupedal, sitting, bipedal) to determine if ground squirrels differed in the proportion of overall vigilance spent in different postures in different habitats. In 1992 and 1993, as with behavior in general, there were significant effects of habitat ( $F = 9.10$ ,  $\Lambda = 0.75$ ,  $d.f. = 9$ , 638,  $P = 0.0001$ ), year ( $F = 2.78$ ,  $\Lambda = 0.97$ ,  $d.f. = 3$ , 262,  $P = 0.04$ ), and year by habitat ( $F = 3.35$ ,  $\Lambda = 0.89$ ,  $d.f. = 9$ , 638,  $P = 0.0005$ ) on the proportion of vigilance spent in different postures. The model using only sagebrush and burned-sagebrush sites also had significant effects of year ( $F = 6.95$ ,  $\Lambda = 0.88$ ,  $d.f. = 6$ , 604,  $P = 0.0001$ ), habitat ( $F = 9.04$ ,  $\Lambda = 0.92$ ,  $d.f. = 3$ , 302,  $P = 0.0001$ ), and year by habitat ( $F = 5.00$ ,  $\Lambda = 0.91$ ,  $d.f. = 6$ , 604,  $P = 0.0001$ ). In both models, effect of year was primarily a result of a decrease in the use of quadru-

## Squirrels in the Snake

Vigilant	
$\bar{X}$	SE
7.7A	0.8
26.5B	4.1
58.2C	6.9
58.1C	7.7
23.5A	2.2
28.0A	3.3
73.1B	8.7
87.2B	3.7
23.2A	2.9
19.3A	3.4

TABLE 2.—Percent vigilance spent in three major postures by Townsend's ground squirrels in the Snake River Birds of Prey National Conservation Area, Idaho, 1992–1994.

Year	Habitat	$n^a$	Vigilant posture					
			Quadrupedal		Sitting		Bipedal	
			$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
1992								
	Burned sagebrush	60	77.4A <sup>b</sup>	3.6	14.8A	2.9	7.8A	2.6
	Sagebrush	49	67.4A	4.9	28.1AB	4.9	4.6A	1.5
	Winterfat	32	30.5B	6.8	40.7BC	6.0	28.7B	5.5
	Mosaic	17	31.2B	7.9	51.0C	8.4	17.8AB	6.1
1993								
	Burned sagebrush	68	64.7A	3.0	27.6A	2.7	7.0A	1.5
	Sagebrush	43	47.4B	4.7	30.6AB	3.9	8.4A	2.0
	Winterfat	7	23.8B	8.7	59.5BC	12.2	16.3A	5.0
	Mosaic	6	23.3B	7.3	66.7C	12.0	9.9A	6.1
1994								
	Burned sagebrush	56	44.2A	4.4	34.4A	3.6	21.2A	4.4
	Sagebrush	34	50.5A	6.2	25.5A	3.9	12.5A	3.9

<sup>a</sup> Number of individuals observed.

<sup>b</sup> Column values within a year that have the same letter do not differ significantly at  $P = 0.05$  (Holm's sequential Bonferroni  $t$ -tests—Rice, 1989; Wright, 1992).

vigilance comprising in all habitats among negative correlation and vigilance ( $n = 389$ ).

Use of three types of quadrupedal, sitting, and bipedal ground squirrels in different postures in different years, as with behavior, significant effects ( $F = 0.75$ ,  $d.f. = 9$ ,  $P = 0.04$ ), and year by habitat ( $F = 2.78$ ,  $d.f. = 9$ ,  $P = 0.04$ ), and year by habitat ( $F = 2.78$ ,  $d.f. = 9$ ,  $P = 0.04$ ), and year by habitat ( $F = 2.78$ ,  $d.f. = 9$ ,  $P = 0.04$ ).

The model using burned-sagebrush sites of year ( $F = 7.26$ ,  $d.f. = 3$ ,  $P = 0.0001$ ), sagebrush habitat ( $F = 5.00$ ,  $d.f. = 3$ ,  $P = 0.0001$ ). In winterfat habitat did not differ significantly

pedal vigilance ( $P < 0.02$ ) and an increased use of the sitting posture ( $P < 0.005$ ) from 1992 to 1993. Use of bipedal vigilance increased on the sagebrush and burned-sagebrush sites from 1993 to 1994 ( $P < 0.05$ ).

We examined each year separately because of the significant year by habitat interactions, with significant effects of habitat on the proportion of vigilance spent in different postures in 1992 ( $F = 7.26$ ,  $\Lambda = 0.66$ ,  $d.f. = 9$ ,  $P = 0.0001$ ), 1993 ( $F = 5.19$ ,  $\Lambda = 0.69$ ,  $d.f. = 9$ ,  $P = 0.0001$ ), and 1994 ( $F = 6.38$ ,  $\Lambda = 0.82$ ,  $d.f. = 3$ ,  $P = 0.0006$ ). Ground squirrels in burned-sagebrush and sagebrush sites differed significantly in the proportion of vigilance spent in a quadrupedal posture in 1993 only (Table 2). Although the overall model indicated significant differences in the use of difference vigilant postures between ground squirrels in different habitats in 1994, there were no significant differences when each vigilant posture was examined separately. Ground squirrels in winterfat habitat did not differ significantly

from those in mosaic sites in the use of vigilant postures.

There was a trend toward less quadrupedal and more bipedal and sitting vigilance by ground squirrels in winterfat and mosaic habitats, where low-stature cover predominated compared with ground squirrels in burned-sagebrush and sagebrush habitats. Ground squirrels in burned-sagebrush used quadrupedal vigilance more and sitting-vigilant postures less than those in winterfat or mosaic sites in both 1992 and 1993 (Table 2). The proportion of vigilance spent in different vigilant postures in sagebrush was generally intermediate between that found in burned-sagebrush, winterfat, or mosaic sites (Table 2).

**Predation pressure.**—During 1992–1993, frequency at which raptors were observed over study sites—our index of avian predation pressure—varied significantly by year and habitat (ANOVA,  $F = 5.40$ ,  $d.f. = 7$ ,  $P = 0.0001$ ; year effect,  $P = 0.004$ ; habitat effect,  $P = 0.03$ ; year-by-habitat interaction,  $P = 0.33$ ). Although

TABLE 3.—Number and frequency (number per 15 min) of raptors observed over behavioral sites in four habitat types within the Snake River Birds of Prey National Conservation Area, Idaho, 1992–1994. Raptors are grouped by taxa.

Habitat <sup>a</sup> Year	Periods <sup>b</sup>	Number of raptors				Frequency	
		Buteo	Falcon	Harrier	Other <sup>c</sup>	$\bar{X}$	SE
Burned sagebrush							
1992	97				9	0.09	0.04
1993	208	5	17	10	5	0.18	0.03
1994	280	3	6	3	1	0.05	0.01
Sagebrush							
1992	280				35	0.13	0.02
1993	295	2	9	69	12	0.31	0.04
1994	256	1	2	9	2	0.06	0.02
Mosaic							
1992	66				9	0.14	0.05
1993	58	3	4	12	0	0.33	0.08
Winterfat							
1992	105				8	0.08	0.03
1993	22	0	0	2	0	0.09	0.06

<sup>a</sup> Observations were made on two sites in both burned sagebrush and sagebrush habitats in 1992–1994; observations were made on one site in mosaic and winterfat habitats and only in 1992 and 1993.

<sup>b</sup> Number of 15-min observation periods during which we searched for raptors.

<sup>c</sup> Unidentified or rare occurrences; raptors were not identified by type in 1992.

overall predation pressure increased from 1992 to 1993, there were no significant differences among habitats when the comparison-wise error rate was controlled ( $P > 0.05$ ). An examination of only burned-sagebrush and sagebrush sites across all years also showed significant year and habitat effects (ANOVA,  $F = 41.52$ ,  $d.f. = 5, 1410$ ,  $P = 0.0001$ ; year effect,  $P = 0.0001$ ; habitat effect,  $P = 0.02$ ; year-by-habitat interaction,  $P = 0.06$ ). More raptors were observed in sagebrush than burned sagebrush, and more raptors were observed over all sites in 1993 compared with other years (Table 3).

Although frequency of raptors generally did not differ among sites, types of raptors present differed ( $\chi^2 = 43.25$ ,  $d.f. = 6$ ,  $P < 0.001$ ). At burned sagebrush sites, both buteos and falcons (primarily prairie falcons) were observed more frequently than other raptors, but in shrub-dominated habitats, northern harriers were observed more often than other species (Table 3).

*Density of ground squirrels.*—During the

3 years of this study, densities of ground squirrels on winterfat and mosaic sites were low, but there was a wide range of densities within sagebrush and burned-sagebrush habitats. In years when densities were low in sagebrush and burned-sagebrush habitats, ground squirrels did not increase their vigilance to levels observed in winterfat or mosaic habitats (Fig. 2); rather, vigilance decreased slightly with decreasing densities of ground squirrels in sagebrush.

#### DISCUSSION

As reported for other species of ground squirrels (Betts, 1976; Leger et al., 1983), Townsend's ground squirrels spent the majority of their above-ground activity in foraging, vigilance, and locomotion. Our results suggest that perceived predation risk varied with habitat. Our estimated predator-detection distances were farthest in burned-sagebrush habitats and shortest in mosaics of sagebrush and winterfat. The proportion of activity spent in vigilance was lowest, and time spent foraging and in locomotion

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ation Area, Idaho, 1992–

Frequency	
$\bar{X}$	SE
0.09	0.04
0.18	0.03
0.05	0.01
0.13	0.02
0.31	0.04
0.06	0.02
0.14	0.05
0.33	0.08
0.08	0.03
0.09	0.06

1994; observations were made

densities of ground  
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wide range of densities  
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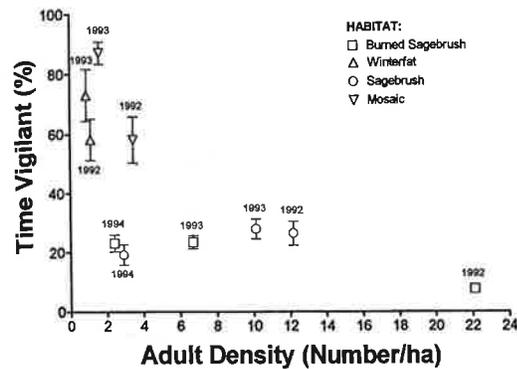


FIG. 2.—Relationship between density of adult Townsend's ground squirrels and proportion (%) of above-ground activity ( $\bar{X} \pm 1 SE$ ) devoted to vigilance in four different habitats in the Snake River Birds of Prey National Conservation Area, Idaho, 1992–1994. No density estimates were available for winterfat or mosaic habitats in 1994.

was highest by ground squirrels in burned sagebrush, but the reverse was true in mosaic habitats. Ground squirrels in burned sagebrush used quadrupedal vigilance more often than other postures, but ground squirrels in winterfat and mosaic habitats used sitting postures more often than other postures. Because there was a strong negative correlation between levels of foraging and vigilance, there appears to be a trade-off between these two activities; the balance, of which, differs with habitat. Differences in ground-squirrel behavior among habitats could be influenced by three factors.

**Vegetative structure.**—Differences in vegetative structure of habitats that we studied could have caused differences in observed activity, although this was likely a complex relationship partly tied to differences in obstructive and protective properties of vegetative cover. Although winterfat and sagebrush shrubs reduced detection distances to similar levels, levels of vigilance were lower in sagebrush. Differences in vigilance may occur because sagebrush provides escape cover for ground squirrels or barriers to pursuing predators, unlike winterfat shrubs. Therefore, levels of vigilance

in sagebrush may be affected by the non-standard environment (Lima, 1992) provided by sagebrush. Sagebrush simultaneously can act as protection from predators (especially avian predators) and as an obstruction to detection of predators. Winterfat shrubs, on the other hand, obstruct a ground squirrel's vision and provide little protection from predators. In response, ground squirrels used more upright vigilance postures and spent more time in vigilance.

Our results suggest that the combination of predator detectability and refuge availability may determine a ground squirrel's perceived predation risk. For instance, ground squirrels in burned-sagebrush and sagebrush habitats differed in their ability to detect predators because of differences in vegetative structure (Fig. 1), but levels of vigilance generally did not differ between habitats. Burned-sagebrush sites generally had little vegetative cover and few above-ground refuges. The lower number of above-ground refuges may have been compensated partially for by presence of more below-ground refuges (burrow entrances) than were found on shrub-dominated sites in some years (Schooley et al., 1996). Estimated predator-detection distances also were significantly farther in burned sagebrush compared with sagebrush (Fig. 1), which could have further compensated for a difference in refuge densities by providing more time to reach a refuge.

Ground squirrels on winterfat and mosaic sites did not differ in the proportion of time spent vigilant, despite mosaic habitats having large patches of sagebrush that could have provided protective cover. Decreased predator-detection distances may have offset benefits of increased cover, further supporting the hypothesis that an interaction between detectability of predators and refuge density influences perceived risk.

Variability in use of upright versus quadrupedal vigilant postures among habitats also suggests that both detectability of predators and refuge density influence perceived risk. Ground squirrels in burned sagebrush

(high visibility, intermediate refuge density) and sagebrush (intermediate visibility, high refuge density) used quadrupedal vigilant postures more often than upright postures. In contrast, ground squirrels in winterfat (intermediate visibility, low refuge density) and mosaic (low visibility, intermediate refuge density) habitats used upright vigilant postures (sitting and bipedal) more often than quadrupedal postures. Loughry (1993) noted a similar increase in use of bipedal postures among black-tailed prairie dogs when they were in vegetation that would be higher than the top of their heads if they remained in quadrupedal postures. Upright postures would allow ground squirrels to detect predators at a farther distance and possibly increase time available for escape after a predator was detected, which should be more important in habitats with few refuges and short detection distances.

The possible relationship between predator detectability and perceived risk is further supported by changes in vigilance within habitats across years. Time spent in vigilance and use of more upright vigilant postures increased from 1992 to 1993 in conjunction with the increase in vegetative cover of exotic annuals and more new growth on shrubs (decreased detection distances) on all sites.

*Predation pressure.*—Predation pressure could have influenced behavioral differences observed among habitats. We have no evidence, however, that predation pressure, at least by raptors, differed significantly among habitat types in a manner that can explain observed differences in vigilance rates among ground squirrels in different habitats. Because northern harriers were the most common species over sagebrush, winterfat, and mosaic habitats, it also is unlikely that differences in types of raptors hunting in different habitats were responsible for observed behavioral differences among ground squirrels. It is possible that mammalian predators use habitats differentially, but we cannot determine if differences exist

because few mammalian predators were observed.

*Density of ground squirrels.*—Animals in larger groups may decrease time devoted to vigilance because more eyes are present to detect predators at any one time (Pulliam, 1973). Alternatively, increased group size may increase competition for limited food resources. If so, decreases in vigilance may be a result of increased competition instead of many eyes (Elgar, 1989; Hoogland, 1979; Lima and Dill, 1990). Previous studies have found a decrease in vigilance with an increase in group size (Burger and Gochfeld, 1992; Hoogland, 1979; Kildaw, 1995; Lima, 1987; Martella et al., 1995), but it is not clear if this was the case in our study. Although the two sites that generally had the lowest densities (winterfat and mosaic) had the highest vigilance rates, it did not appear that those differences resulted from a simple relationship with population density. When densities of ground squirrels in sagebrush and burned sagebrush decreased to similar levels as those that were previously observed in winterfat and mosaic sites, ground squirrels still exhibited significantly lower levels of vigilance on sagebrush and burned-sagebrush sites (Fig. 2).

Although not feasible in this study, examining absolute time spent in different activities throughout the day may have given additional insight into differences in behavioral patterns. Nonetheless, our study indicates that Townsend's ground squirrels exhibited significant differences in behavior among habitats, which appear to be a result of differences in perceived predation risk in those habitats. Ground squirrels in winterfat and mosaic habitats spent more than twice as much of their above-ground activity in vigilance behavior compared with ground squirrels in sagebrush and burned-sagebrush habitats. Furthermore, it appears that relationships between habitat type and activity remain relatively constant across time and population densities. It does not appear, however, that predation pressure differs among habitats, although predation risk af-

an predators were observed. In this study, expenditure in different activity categories may have given different differences in behavior. However, our study indicates that ground squirrels experience differences in behavior that appear to be a result of perceived predation risk in winterfat sites more than twice as much as ground activity in burned-sagebrush sites. It does not appear that predation risk af-

fects on predators were observed. Previous studies (Burger and Gochfeld 1979; Kildaw, 1995; Stapp et al., 1995), but it is the case in our study. Sites that generally had higher winterfat and mosaic cover, it did not result from differences in population density of ground squirrels in sagebrush sites (Fig. 2).

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**EDITOR'S ADDENDUM**—The population of ground squirrels examined in this paper is currently recognized as *Spermophilus mollis*. Rationale for use of *S. townsendii* is presented in Van Horne et al. (*Journal of Mammalogy*, 79:522, 1998).

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