

ASSESSING EFFECTS OF PREDATION RISK ON FORAGING BEHAVIOR OF MULE DEER

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We applied optimal foraging theory to test effects of habitat and predation risk on foraging behavior of mule deer (*Odocoileus hemionus*) subject to predation by mountain lions (*Puma concolor*). We predicted that deer would spend less time foraging, have higher giving-up densities of food (GUDs), and have higher vigilance behavior when occupying patch edges than when in open and forest interiors. We also measured GUDs in 3 microhabitats within 3 forest types. We used pellet-group surveys to estimate habitat and microhabitat use, and we assessed vigilance behavior with automatic camera systems. The GUDs (perceived predation risk) were greater in forests of Douglas fir (*Pseudotsuga menziesii*) than mountain mahogany (*Cercocarpus ledifolius*). In forests of Douglas fir, GUDs were greatest in the forest interior, declined at the forest edge, and were lowest in the open microhabitat. Microhabitat features did not influence GUDs in the mountain mahogany forest. Pellet-group data indicated more activity in the open than in the edge or forest. Based on photographs, deer were more vigilant at forest edges than in open and forest areas. We concluded that deer are responding to predation risk by biasing their feeding efforts at the scale of habitats and microhabitats and altering their habitat-specific patterns of vigilance behavior.

Key words: GUDs, Idaho, mule deer, *Odocoileus hemionus*, optimal foraging, predation risk

Predators have long been viewed solely as agents of mortality that influence abundance and population dynamics of their prey (Rosenzweig and MacArthur 1963; Taylor 1984). However, predators also have nonlethal effects on their prey because prey reduce activity times, alter habitat use, increase group size, or change vigilance levels in response to predators. These nonlethal effects cause prey to trade food for safety as they shift activity toward safer but less rewarding food patches or to heighten vigilance at the expense of feeding efficiency (Brown 1999; Lima and Dill 1990; Sih 1980). On a population level, nonlethal effects of predators scaring their prey actually

may be more important than lethal effects (Brown 1999; Brown et al. 1992; Kotler and Holt 1989).

Optimal foraging theory (MacArthur and Pianka 1966) provides a framework for considering nonlethal effects of predation risk on food and safety trade-offs. When foraging under predation risk, an animal should leave a depletable resource patch when benefits of harvesting resources no longer outweigh the metabolic, predation, and missed-opportunity costs of foraging (Brown 1988; Brown et al. 1992). Two predictions follow: Given 2 habitats with similar resource levels or productivity, animals should spend more time foraging in the safer habitat, and when offered depletable food

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patches with equal opportunity, animals should leave riskier areas at a higher giving-up density (GUD—Brown 1988; Kotler 1992; Kotler et al. 1993). Titration experiments of food and safety have provided support for these 2 predictions (Kotler 1997). Foragers bias feeding activity toward safe habitats and have higher GUDs in risky habitats; animals that are in a higher energy state perceive a higher cost of predation and avoid risks more than animals in a low energy state (Brown et al. 1992; Clark 1994; Lima 1988). Other behavioral responses to predators include adjusting vigilance levels and group sizes in response to predation risk (McNamara and Houston 1992). Vigilance levels should be higher in the risky habitat when either encounter rates with predators or the lethality of the predators increases. Predation risk and vigilance levels generally decline with group size as a consequence of the many-eyes and dilution effects (Cresswell 1994).

Large mammalian herbivores, such as ungulates, and predators that feed on them can play important roles in ecosystem dynamics (Sinclair and Arcese 1995b). If predation risk alters foraging strategies of these species, it potentially can have a major influence on dynamics of such systems (Sinclair and Arcese 1995a). Predation risk has been shown to influence habitat selection and diet (Edwards 1983), herd sizes (FitzGibbon and Lazarus 1995), vigilance (Illius and FitzGibbon 1994; Molvar and Bowyer 1994), and GUDs (Kotler et al. 1994) of several ungulate species. Kotler et al. (1994) quantified habitat-specific predation risk by using GUDs in controlled food patches to titrate for the level of fear in animals. Here, we expand on that approach by examining mule deer (*Odocoileus hemionus*) subject to predation by mountain lions (*Puma concolor*). Our goal was to simultaneously measure several indicators of predation risk to test the specific predictions that GUDs are greater in high-risk areas than in low-risk areas, number of fecal pellet groups per area and number of

photographs taken at feed boxes (measures of habitat use) are lower in high-risk areas, proportion of photographs of vigilant deer at feeding boxes are higher than expected in high-risk areas, and group sizes of deer are larger and lengths of continuous feeding bouts shorter at feed boxes in high-risk areas.

MATERIALS AND METHODS

Study area.—Our study was located in Cassia (south-central Idaho) and Box Elder counties (northwestern Utah). The site spanned about 2,500 km² and contained 5 small, isolated mountain ranges with elevations of 1,830–3,151 m. Mountain ranges were highly fragmented into open and forested habitat patches that varied in size, complexity, and isolation from nearby patches. Climate was characterized by hot, dry summers (0–35°C) and cold, windy winters (–25–4°C). Humidity rarely exceeded 40%, and precipitation was sporadic with an annual mean of 30 cm.

Forested patches were divided into 4 major types: Douglas fir (*Pseudotsuga menziesii*), quaking aspen (*Populus tremuloides*), juniper (*Juniperus osteosperma* and *J. scopulorum*), and curl-leaf mountain mahogany (*Cercocarpus ledifolius*). Dominant shrubs in open areas included big sagebrush (*Artemisia tridentata*), gray rabbitbrush (*Chrysothamnus nauseosus*), bitterbrush (*Purshia tridentata*), and buffaloberry (*Shepherdia rotundifolia*).

In our study area, mountain lions and mule deer approximate a 1 predator–1 prey system. Mountain lions occasionally preyed on porcupines (*Erethizon dorsatum*) and a variety of small mammals, including black-tailed jack rabbits (*Lepus californicus*). Other ungulates in the study area included a few pronghorn antelope (*Antilocapra americana*) and elk (*Cervus elaphus*). The other potential predators of mule deer in this system were coyotes (*Canis latrans*) and bobcat (*Lynx rufus*).

In testing our predictions, we considered 2 spatial scales over which predation risk may vary. At a large scale, we considered 4 forest types: juniper, Douglas fir, mountain mahogany, and aspen. Within a forest type, we considered 3 microhabitats regarding the risk of predation to mule deer by mountain lions (J. W. Laundré, in litt.; López González 1994): the interior of the

forest patches, open sagebrush patches (≥ 50 m from forest patches), and open-forest interfaces (edges of about ± 20 m along the forest border). Of 58 mule deer killed by mountain lions, 72% occurred in the edge microhabitat, and 14% each occurred in forest and open areas (J. W. Laundré, in litt.; López González 1994). Assuming frequency of kills represented a relative measure of risk, we predicted open and forest microhabitats should be the safest, whereas edges were the riskiest. Additionally, 63% of the kill sites were in juniper, 30% in Douglas fir, and 5% each in mountain mahogany and aspen (J. W. Laundré, in litt.). Thus, juniper and Douglas fir habitats were considered the riskiest, and the greatest differences in use of edge and open-forest interior should have been seen in those habitats.

Prediction 1: measuring GUDs.—To test our prediction of higher GUDs in high-risk areas, we used wooden trays covered with wire-mesh fencing (10 by 7 cm—Kotler et al. 1994) filled with premeasured amounts of compressed alfalfa hay pellets (6-mm diameter), corn kernels, and a plastic, nonedible substrate (#6 plastic test tube caps, 13 mm in length). That substrate provided a depletable food patch with diminishing returns; foraging effort per unit harvest increased with time spent foraging at the tray (Kotler et al. 1994). Nine trays were placed in each of 3 different forest habitats (juniper, Douglas fir, and mountain mahogany). Within each of those forest habitats, 3 feeding trays were placed in each of the 3 microhabitats (open, edge, and forest interior), about 50–100 m from one another (Fig. 1). Covered feeding trays were placed in the habitat patches about 3–5 days before each feeding trial began to habituate deer to feeding trays. During feeding trials, trays were emptied of remaining food and then refilled daily around 1200 h. Collected food was weighed to obtain estimates of GUDs.

Feeding trials were conducted from November 1995 through February 1996, January through March 1997, and December 1997 through February 1998. During the first 2 field seasons, feeding trays were filled with a mixture of 1,000 g each of alfalfa and corn and 500 g of substrate. In the 3rd season, food quantity was reduced to 500 g each and then to 250 g each of alfalfa and corn kernels. Concomitantly, substrate quantity was increased to 1,000 g and then to 1,500 g. Those reductions in food and increases in substrate ensured that patterns of GUDs

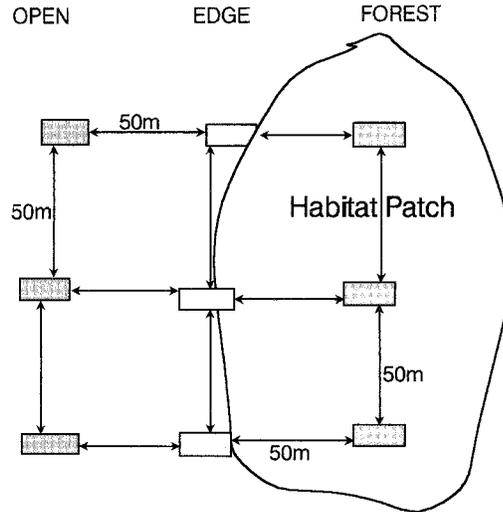


FIG. 1.—Example of feeding tray arrangement within a habitat patch; 3 trays each were set in parallel lines in the 3 microhabitats.

were the result of perceived predation risk and not simply the consequence of forager satiation.

For our prediction that GUDs would be greatest along the edge and lowest in the open microhabitats, we used a blocked 2-way analysis of variance (ANOVA—Sokal and Rohlf 1981) to test for the effect of microhabitat (open, edge, interior) on GUDs. Day–food amount was used as the blocking variable. Because that design was analogous to the paired-*t* design, blocking by day removed variability due to daily differences, including different food substrate levels, and tested for the main effect, differences among microhabitats. The GUDs were logarithmically transformed to normalize data (Brown 1988). Each habitat was tested separately. A Tukey range test was used to identify differences among treatments (Sokal and Rohlf 1981). All data were analyzed using Sigmasat statistical software (Quinton et al. 1995). All statistical testing was performed with a significance level of ≤ 0.05 , following methods outlined in Zar (1984).

Prediction 2: measuring use levels.—We tested the general prediction that deer would spend more time in low-risk versus high-risk areas with 2 methods: deer pellet-group surveys (Galina et al. 1991) and automated camera traps (Carthew and Slater 1991). Deer pellet-group surveys were conducted in 15 patches (4 each in juniper, Douglas fir, and mountain mahogany

and 3 in aspen). Each survey consisted of 3 parallel, 400-m transects, 1 along the forest edge, 1 about 50 m into open shrubland, and 1 about 50 m into the forest interior. Pellet groups were counted and removed from circular plots (20-m intervals, 20 plots/transect). Each transect was resampled for 2 consecutive seasons.

Our prediction was that open areas should have the highest density of pellet groups (adjusted for forb and grass biomass, if necessary) and that the edge should have the lowest. To test that prediction, we analyzed mean number of pellet groups with a 3-way ANOVA to test for effects of microhabitat, forest type, and year. If the null hypothesis was rejected, a pairwise Tukey test was performed (Zar 1984).

To measure levels of use with automated cameras, we used the TrailTimer TT-2000 camera system with the TT-1000 TrailTimer "Plus" Infrared Multiple Event Game Monitor (TrailTimer Company, St. Paul, Minnesota). Camera systems were positioned about 2 m in front of feeding trays in each of the habitat patches in the predation risk areas previously described. As an animal approached a tray to forage, its picture was taken, along with a record of the time and date. The latency period between consecutive shots was set at 2 min. Data from camera systems were collected from November 1995 through February 1996 and January through March 1997.

With the photographic data, we tested that fewer photos (indication of use levels) would be taken along edges compared with open and forest habitats. We used a chi-square goodness-of-fit test (Zar 1984) to determine if the number of photographs differed among the 3 risk areas. A 1:1 ratio was used to calculate expected values.

Prediction 3: measuring vigilance levels.—We used photographic data to test if deer were more vigilant along edges. Deer in each photo were categorized as either vigilant (head up) or foraging (head down). If no difference in risk was perceived by deer, we expected no differences in relative number of vigilant to feeding photos among areas. A *G*-test of independence (Neu et al. 1974; Sokal and Rohlf 1981) was used to test if the relative number of photographs showing vigilance or foraging differed among risk areas. Expected values for that analysis were calculated based on the distribution of observed photographs in each category (Sokal and Rohlf 1981).

Prediction 4: measuring group size and feed-

ing bouts.—We tested if foraging group size and mean length of foraging bouts differed among risk areas with photographic data. For group size, we recorded number of deer in each photograph containing ≥ 2 animals. For length of foraging bouts, we calculated the difference between starting and ending times of multiple photographs of the same individual deer at a food box. We tested the prediction that group size should be larger in the edge (safety in numbers) and that individual deer should spend less time feeding at the edge boxes with a 1-way ANOVA. If data violated the assumption of normality, we used a Kruskal-Wallis 1-way ANOVA on ranks.

Aboveground biomass and habitat characteristics.—To determine if pellet-group data needed to be adjusted, we measured aboveground vegetative biomass (Brower et al. 1990) along the 400-m transects in different risk areas. At 80-m intervals, visible forb and grass species were clipped at ground level and removed from randomly selected 1-m² areas, 5 m from the center of plots. Forbs and grasses were collected separately, air dried to a constant weight, and weighed.

To determine structural differences among risk areas, characteristics of trees and shrubs were measured using the point-quarter method (Brower et al. 1990). Pellet-group transects in each habitat patch and risk area were used. Selection of shrubs measured was limited to those 50 cm or higher. Shrubs <50 cm were presumed to contribute little cover for an approaching lion. For mean aboveground biomass (forbs and grasses) and 4 of the habitat variables measured (shrub density and height, slope, and aspect), a 2-way ANOVA was used to test for effects of microhabitat and forest type. If the null hypothesis was rejected in an ANOVA, a pairwise Tukey test was performed (Zar 1984). We used a paired *t*-test to determine if tree density and diameter at breast height differed between the edge and forest-interior microhabitats because the open microhabitat lacked trees.

RESULTS

Prediction 1: GUDs.—For the first 2 years (winters of 1996 and 1997), mule deer in juniper and Douglas fir habitat fed sporadically. For those 2 winters, no difference in GUDs was found among the 3 mi-

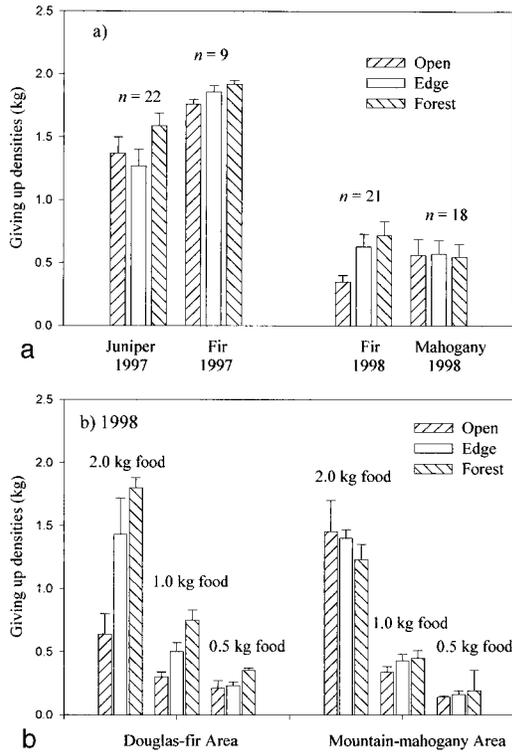


FIG. 2.—Mean giving-up densities (GUDs) \pm SE for 3 predation risk areas in the 3 habitat types, including a) the data from the different food quantities combined and b) separate GUDs for the different quantities of food used in the trays.

crohabitats (Fig. 2a). During the winter of 1998, deer fed consistently in the Douglas fir and mountain mahogany habitats but did not feed consistently enough in the juniper forest for analysis. In 1998, there were no differences in GUDs among microhabitats in the mountain mahogany habitat (Fig. 2a). There were differences among microhabitats for the Douglas fir habitat; GUDs were least in the open and greatest in the forest interior (Fig. 2a). Those differences persisted over the 3 food levels (Fig. 2b). Daily total GUDs were lower ($t = 2.401$, $P = 0.028$) in mountain mahogany habitat ($\bar{X} = 560 \text{ g} \pm 110 \text{ SE}$) than Douglas fir habitat ($660 \pm 90 \text{ g}$).

Prediction 2: use levels.—Relative to the pellet-group survey, results of a 3-way AN-

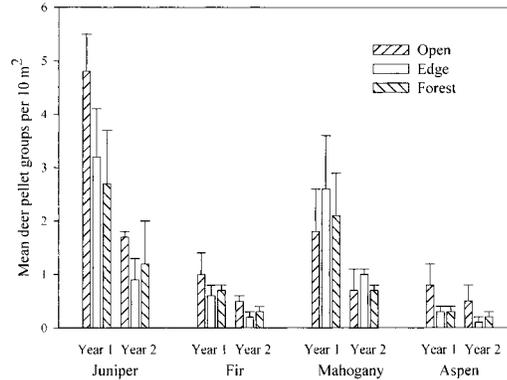


FIG. 3.—Mean density of mule deer pellet groups \pm SE in 4 habitats sampled; mean densities varied by year ($F = 80.9$, $d.f. = 1, 17$, $P < 0.001$), habitat type ($F = 27.8$, $d.f. = 3, 17$, $P < 0.001$), and microhabitat ($F = 7.26$, $d.f. = 2, 17$, $P = 0.004$).

OVA indicated significant effects of sample year, forest type, and microhabitat (Fig. 3). Tukey's test indicated that pellet-group density in the open ($1.5 \pm 0.34/10 \text{ m}^2$) was higher than for the edge ($1.1 \pm 0.26/10 \text{ m}^2$) or forest ($1.0 \pm 0.24/10 \text{ m}^2$) microhabitats. Density of pellet groups within the habitat types was higher in the open and forest than the edge for all habitats except the mountain mahogany (Fig. 3).

Eight hundred photographs were taken of mule deer in the juniper and Douglas fir sample (52% of deer foraging, 37% of deer surveying, and 11% of other activities). Only those photographs that showed foraging or surveying (700 photos) were used in the analyses (88% from the juniper area, 12% from the Douglas fir). Based on a 1:1:1 expected ratio, more photographs were taken in the edge than in the open or juniper forest ($\chi^2 = 166.1$, $d.f. = 2$; Table 1). In the Douglas fir habitat, more photographs were taken in the open than the edge or forest ($\chi^2 = 33.9$, $d.f. = 2$; Table 1).

Prediction 3: vigilance levels.—In the juniper area, more photographs were of deer foraging than surveying ($\chi^2 = 37.8$, $d.f. = 1$; Table 1). For the Douglas fir area, more total photographs showed surveying than feeding ($\chi^2 = 20.5$, $d.f. = 1$; Table 1). In

TABLE 1.—Comparison (chi-square goodness-of-fit) of observed and expected numbers of total photographs taken in the 3 risk areas for the juniper pine and Douglas fir habitats and proportion of photographs (*G*-test of independence) showing foraging and surveying activities of mule deer among the predation risk areas within these habitat types. Expected frequency of photographs per category (in parentheses) were either based on a 1:1:1 ratio (chi-square goodness-of-fit) or calculated based on ratios of observed values (*G*-test of independence). Results of comparisons between observed and expected values are given with the significant values ($P \leq 0.05$) indicated with an asterisk; individual cells where observed values were greater (+) or less (–) than expected ($P \leq 0.05$) are indicated.

Habitat and activity type	Open	Edge	Forest	<i>G</i> -test
Juniper area				
Foraging	134 (139.1)	195 (204.5)	57+ (42.4)	5.17
Surveying	89 (83.9)	133+ (123.5)	11– (25.6)	11.6*
<i>G</i> -test	0.48	1.17	15.1*	16.8*
Douglas fir area				
Foraging	10 (12.2)	9+ (4.1)	0 (2.7)	10.0*
Surveying	40 (37.8)	8 (12.8)	11 (8.3)	3.0
<i>G</i> -test	0.53	6.37*	6.1*	13.0*

the juniper habitat, a higher number of photographs than expected in the edge area were of surveying, and, conversely, in the forest, a higher number than expected of the photographs were of foraging (Table 1). For the Douglas fir habitat, only the number of photographs showing foraging in the edge was higher than expected (Table 1).

Prediction 4: group size and feeding bouts.—Two hundred twenty photographs showed groups of 2–5 deer (Table 2). Photographs with >1 individual occurred more often in the forest-interior microhabitat and significantly less frequently in the edge microhabitat (Table 2). A difference in group size among microhabitats was found with the largest groups in the forest interior and smallest groups in the edge microhabitat (Dunn’s test; Table 2).

Fifty-two sets of photographs were taken of individual mule deer foraging continuously for 3–39 min (Table 2). The number of photographs of continuous feeding among the 3 microhabitats did not differ from expected (Table 2). Likewise, no difference in the mean length of foraging bouts was found among microhabitats.

Productivity and habitat characteristics.—Mean aboveground biomass of forbs differed ($F = 2.53$, *d.f.* = 2, 11, $P = 0.031$) among the 12 sample sites (Table 3). Forb

TABLE 2.—Number of photographs of foraging groups and mean group size and number of sets of photographs of continuous feeding and mean feeding bout time for the 3 predation risk areas. Proportions of photographs taken in each risk area were compared with expected (in parentheses) with a chi-square goodness-of-fit test. Mean group sizes and mean length of foraging bouts were compared among the 3 risk areas with a 1-way analysis of variance or its nonparametric equivalent.

	Open	Edge	Forest	Statistics
Number of photographs of foraging groups (≥ 2 mule deer)				
Number of photographs	85 (84.7)	76 (109.2)	59 (26.4)	$\chi^2 = 40.4$, $P < 0.001$
Mean group size $\pm SE$	2.3 ± 0.09	2.2 ± 0.05	2.5 ± 0.09	$H = 7.503$, $P = 0.023$
Number of photographs showing continuous foraging bouts				
Number of sets of photographs	16 (20)	28 (26)	8 (6)	
Mean length (min) of foraging bout $\pm SE$	10.8 ± 1.8	8.8 ± 1.1	10.8 ± 2.6	

TABLE 3.—Characteristics of 3 different risk level areas (open, edge, and forest). Sample sizes are indicated in parentheses; differences among risk level areas for a given characteristic are marked with asterisks and similar areas, as indicated by multiple range testing, are marked with the same letter.

Characteristic	Risk level area			<i>P</i>
	Open	Edge	Forest	
Forb biomass (g/m ²)	9.9 ± 3.3 (12)	7.4 ± 2.0 (12)	5.5 ± 2.1 (12)	0.33
Grass biomass (g/m ²)	12.9 ± 1.9A (12)	12.8 ± 2.2A (12)	5.2 ± 1.4 (12)	0.001*
Tree density (no./100 m ²)		3.5 ± 0.91 (14)	10.0 ± 2.8 (14)	0.04*
Tree diameter breast height (cm)		10.9 ± 1.0 (14)	15.9 ± 2.1 (14)	0.023*
Shrub density (no./100 m ²)	22.9 ± 8.1 (14)	14.3 ± 3.8 (14)	11.8 ± 4.0 (14)	0.179
Shrub height (cm)	60.1 ± 4.3 (14)	73.3 ± 1.9A (14)	78.9 ± 3.6A (14)	<0.001*
Slope (degrees)	19.8 ± 1.8 (14)	19.4 ± 1.4 (14)	20.9 ± 1.4 (14)	0.49
Aspect (degrees)	165.7 ± 22.4 (14)	166.3 ± 25.2 (14)	146.9 ± 22.4 (14)	0.55

production was lowest in juniper forest (1.04 ± 0.44 g/m²) and highest in mountain mahogany forest (10.5 ± 3.5 g/m²). There was no difference in the mean forb biomass among the microhabitats (Table 3). Mean aboveground grass biomass differed among the 12 sample sites, ranging from 5.1 ± 1.5 g/m² for the aspen area to 14.2 ± 1.7 g/m² for mountain mahogany forest. Among the 3 risk areas, only mean grass biomass differed (Table 3), being lowest in the forest areas. Because grasses only comprised <10% of mule deer diets (Constan 1972; Deschamp et al. 1979), resource availability was considered equal among the 3 microhabitats.

Shrub density ($F = 3.64$, $d.f. = 2, 13$, $P = 0.002$), shrub height ($F = 2.15$, $d.f. = 2, 13$, $P = 0.047$), and slope ($F = 7.38$, $d.f. = 2, 13$, $P < 0.001$) differed among the 14 sample sites. With regard to microhabitat, shrubs were shorter in the open (Table 3), whereas tree density and diameter breast height were less in the edge than forest-interior microhabitats (Table 3). Slope and aspect did not differ among microhabitats. Because mountain lions stalk their prey (Hornocker 1970; Wilson 1984) and require some degree of cover, the difference in tree density and shrub height were assumed to result in microhabitat-specific differences in predation risk.

DISCUSSION

In general, we found support for the predictions of deer perceiving a higher predation risk with regard to open versus edge areas, but our results were equivocal. For example, GUDs and number of photographs taken for the juniper habitat in 1996 and 1997 did not support the predictions. However, because deer did not feed consistently during these years, those data could be considered poor tests of the predictions. In 1998, deer seemed habituated to trays, and these data should have provided a more realistic estimate of GUDs. For this year, greater GUDs in the edge versus open areas in the Douglas fir habitat persisted over 3 decreasing levels of food resources and 3 increasing levels of substrate (Fig. 2). Additionally, numbers of pellet groups found in edge areas were lower than the open (Fig. 3) in Douglas fir and juniper habitats. Lastly, there also was a higher-than-expected level of vigilance in the edge areas of the juniper habitat. Taking these factors into account, results from the Douglas fir and juniper habitats support the prediction that deer are perceiving and responding to a higher predation risk in the edge than in the open.

With regard to the forest interior areas of the Douglas fir and juniper habitats, overall numbers of pellet groups were higher than

in edge areas, supporting our prediction. However, GUDs for the forest interior in the Douglas fir habitat were consistently greater than the edge in 1998, refuting our prediction. When we reviewed the GUD data set, we noted that the greater GUDs for the forest interior were more a result of a higher proportion of the food trays that were not used in this area. This result seems to support the observations that mule deer do not forage extensively in forests. Others (Collins 1983; Collins and Urness 1981) found that deer spend more of their time in forested areas, although most of this time was spent resting. Because this structural type seems to be used for resting more often than for foraging by mule deer, testing predation risk in forested areas with GUDs and pellet-group counts may not be appropriate. Perhaps levels of vigilance, which photographic data indicated were low and thus supported our prediction, might be a more appropriate indicator that deer perceived a lower risk in this structural type.

The mountain mahogany habitat did not support our predictions for GUDs or pellet-group numbers. Based on pellet-group surveys, mountain mahogany is a well-used habitat type (Fig. 3), especially in the winter, when most of the kills were found (J. W. Laundré, in litt.). However, based on distribution of kills relative to habitat, we found only 5% in the mountain mahogany habitat (J. W. Laundré, in litt.). Additionally, overall GUDs for mountain mahogany were less than in Douglas fir habitats (Fig. 2). These data suggest the mountain mahogany habitat, in general, may be a low-risk area. It would be predicted, then, that little or no difference should exist in the pellet-group and GUD data among open, edge, and forest areas for this habitat type. Because there were no differences in the physical characteristics measured in mountain mahogany habitat compared with the other 3 habitat types (Altendorf 1997), the cause of this lowered risk level is unknown.

Our results support predictions that deer spend less time foraging, have greater

GUDs, and are more vigilant in risky areas. These results correspond to those of a number of studies ranging from aquatic species (Fraser and Cerri 1982; Sih 1980; Werner et al. 1983) to small mammals (Brown 1988; Brown et al. 1992). Regarding ungulates, Kotler et al. (1994) also reported finding greater GUDs in riskier habitats for Nubian ibex (*Capra ibex*). Others have found evidence of predation risk restricting habitat use by individuals (Berger 1991; Edwards 1983; Festa-Bianchet 1988). Results on vigilance behavior in several other ungulate species (Hunter and Skinner 1998; Molvar and Bowyer 1994) support our findings of higher vigilance in riskier habitats. These studies and ours, where we combined all 3 measures of risk, support the hypothesis that ungulates take predation risk into consideration in their foraging strategies. Our results also support the concept that fear of predation is a predominant factor in the feeding ecology of prey species (Brown et al. 1999) and that the level of predation risk, as determined by a prey's predator (or predators) and characteristics of the habitat, is a driving force in habitat use by prey (Bleich 1999; Edwards 1983). A physical landscape that varies in risk level results. The rising and falling of risk levels as an individual moves through this landscape produce the topography of a second landscape, the landscape of fear (J. W. Laundré and L. Hernández, in litt.). It is within this landscape that an individual has to make foraging decisions. Determining this landscape of fear and its consequences on the survival of individuals and, thus, populations, as well as secondary impacts on habitat, are important aspects that need to be examined further to assess the extent of nonlethal impacts of predators on their prey.

ACKNOWLEDGMENTS

We thank Earthwatch, Inc., ALSAM Foundation, and the United States Bureau of Land Management for funding this project. Logistical support was provided by the Northern Rockies

Conservation Cooperative, Idaho Department of Fish and Game, and Utah Division of Wildlife Resources. D. Streubel, K. Allred, and K. Jafek provided invaluable advice and support with the research. We also thank A. Singleton, J. MacDonald, N. Dawson, M. Gurung, B. Holmes, B. Kempf, J. Loxterman, G. Pratt, and volunteers from Earthwatch, Inc. (1995–1998) for their assistance in fieldwork and data collection.

LITERATURE CITED

- ALTENDORF, K. B. 1997. Assessing the impact of predation risk by mountain lions (*Puma concolor*) on the foraging behavior of mule deer (*Odocoileus hemionus*). M.S. thesis, Idaho State University, Pocatello.
- BERGER, J. 1991. Group size, foraging, and antipredator plays: an analysis of bighorn sheep decisions. *Behavioral Ecology and Sociobiology* 4:91–99.
- BLEICH, V. C. 1999. Mountain sheep and coyotes: patterns of predator evasion in a mountain ungulate. *Journal of Mammalogy* 80:283–289.
- BROWER, J. E., J. H. ZAR, AND C. M. VAN ENDE. 1990. Field and laboratory methods for general ecology. 3rd ed. William C. Brown Company, Dubuque, Iowa.
- BROWN, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology* 22:37–47.
- BROWN, J. S. 1999. Vigilance, patch use, and habitat selection: foraging under predation risk. *Evolutionary Ecology Research* 1:49–71.
- BROWN, J. S., J. W. LAUNDRÉ, AND M. GURUNG. 1999. The ecology of fear: optimal foraging, game theory and trophic interactions. *Journal of Mammalogy* 80:385–399.
- BROWN, J. S., R. A. MORGAN, AND B. D. DOW. 1992. Patch use under predation risk: II. A test with fox squirrels, *Sciurus niger*. *Annales Zoologici Fennici* 29:311–318.
- CARTEW, S. M., AND E. SLATER. 1991. Monitoring animal activity with automated photography. *The Journal of Wildlife Management* 55:689–692.
- CLARK, C. W. 1994. Antipredator behavior and the asset-protection principle. *Behavioral Ecology* 5:159–170.
- COLLINS, W. B. 1983. Feeding behavior and habitat selection of mule deer and elk on northern Utah summer range. *The Journal of Wildlife Management* 47:646–663.
- COLLINS, W. B., AND P. J. URNESS. 1981. Habitat preferences of mule deer as rated by pellet-group distributions. *The Journal of Wildlife Management* 45:969–972.
- CONSTAN, K. J. 1972. Winter foods and range use of three species of ungulates. *The Journal of Wildlife Management* 36:1068–1076.
- CRESSWELL, W. 1994. Flocking is an effective antipredator strategy in redshanks, *Tringa totanus*. *Animal Behavior* 47:433–442.
- DESCHAMP, J. A., P. J. URNESS, AND D. D. AUSTIN. 1979. Summer diets of mule deer from lodgepole pine habitats. *The Journal of Wildlife Management* 43:154–161.
- EDWARDS, J. 1983. Diet shifts in moose due to predator avoidance. *Oecologia* 60:185–189.
- FESTA-BIANCHET, M. 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. *Oecologia* (Berlin) 75:580–586.
- FITZGIBBON, C. D., AND J. LAZARUS. 1995. Anti-predator behavior of Serengeti ungulates: individual differences and population consequences. Pp. 274–296 in *Serengeti II: dynamics, management, and conservation of an ecosystem* (A. R. E. Sinclair and P. Arcese, eds.). The University of Chicago Press, Chicago, Illinois.
- FRASER, D. F., AND R. D. CERRI. 1982. Experimental evaluation of predator-prey relationships in a patchy environment: consequences for habitat use patterns in minnows. *Ecology* 63:307–313.
- GALLINA, S., P. GALLINA-TESSARO, AND S. ALVAREZ-CÁRDENAS. 1991. Mule deer density and pattern distribution in the pine-oak forest at the Sierra de La Laguna in Baja California Sur, México. *Ethology, Ecology, and Evolution* 3:27–33.
- HORNOCKER, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. *Wildlife Monographs* 21:1–39.
- HUNTER, L. T. B., AND J. D. SKINNER. 1998. Vigilance behaviour in African ungulates: the role of predation pressure. *Behaviour* 135:195–211.
- ILLIUS, A. W., AND C. FITZGIBBON. 1994. Costs of vigilance in foraging ungulates. *Animal Behaviour* 47:481–484.
- KOTLER, B. P. 1992. Behavioral resource depression and decaying risk of predation in two species of co-existing gerbils. *Behavioral Ecology and Sociobiology* 30:239–244.
- KOTLER, B. P. 1997. Patch use by gerbils in a risky environment: manipulating food and safety to test four models. *Oikos* 78:274–282.
- KOTLER, B. P., J. S. BROWN, R. H. SLOTOW, W. L. GOODFRIEND, AND M. STRAUSS. 1993. The influence of snakes on the foraging behavior of gerbils. *Oikos* 67:309–316.
- KOTLER, B. P., J. E. GROSS, AND W. A. MITCHELL. 1994. Applying patch use to assess aspects of foraging behavior in Nubian ibex. *The Journal of Wildlife Management* 58:299–307.
- KOTLER, B. P., AND R. D. HOLT. 1989. Predation and competition: the interaction of two types of species interaction. *Oikos* 54:256–260.
- LIMA, S. L. 1988. Initiation and termination of daily feeding in dark-eyed juncos: influences of predation risk and energy reserves. *Oikos* 53:12–26.
- LIMA, S. L., AND L. M. DILL. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- LÓPEZ GONZÁLEZ, C. A. 1994. Ecología compartimiento del puma (*Puma concolor*) en un habitat fragmentado. M.S. thesis, Universidad Nacional Autónoma de México, México City, México.
- MACARTHUR, R. H., AND E. R. PIANKA. 1966. On optimal use of a patchy environment. *The American Naturalist* 100:603–609.

- MCNAMARA, J. M., AND A. I. HOUSTON. 1992. Evolutionary stable levels of vigilance as a function of group size. *Animal Behaviour* 43:641–658.
- MOLVAR, E. M., AND R. T. BOWYER. 1994. Costs and benefits of group living in a recently social ungulate: the Alaskan moose. *Journal of Mammalogy* 75:21–630.
- NEU, C., C. R. BYERS, AND J. M. PEEK. 1974. A technique for analysis of utilization-availability data. *The Journal of Wildlife Management* 38:541–545.
- QUINTON, A., G. LEBEDEV, P. YOUTZ, T. TUERKE, R. SINKLER, AND J. KUO. 1995. *Sigmastat for Windows 95: statistical software. Version 2.0.* San Rafael, California.
- ROSENZWEIG, M. L., AND R. H. MACARTHUR. 1963. Graphical representation and stability of predator-prey interaction. *The American Naturalist* 97:209–223.
- SIH, A. 1980. Optimal behavior: can foragers balance two conflicting demands? *Science* 210:1041–1042.
- SINCLAIR, A. R. E., AND P. ARCESE. 1995a. Population consequences of predation-sensitive foraging: the Serengeti wildebeest. *Ecology* 76:882–891.
- SINCLAIR, A. R. E., AND P. ARCESE (EDS.). 1995b. *Serengeti II: dynamics, management, and conservation of an ecosystem.* The University of Chicago Press, Chicago, Illinois.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry: the principles and practice of statistics in biological research.* W. H. Freeman and Company, New York.
- TAYLOR, R. J. 1984. *Predation.* Chapman and Hall, New York.
- WERNER, E. E., J. F. GILLIAM, D. J. HALL, AND G. B. MITTELBACH. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64:1540–1548.
- WILSON, P. 1984. Puma predation on guanacos in Torres del Paine National Park, Chile. *Mammalia* 48: 515–522.
- ZAR, J. H. 1984. *Biostatistical analysis.* 2nd ed. Prentice Hall, Englewood Cliffs, New Jersey.

Submitted 7 September 1999. Accepted 12 June 2000.

Associate Editor was John A. Litvaitis.