HABITAT SELECTION BY MULE DEER: FORAGE BENEFITS OR RISK OF PREDATION?

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Abstract: Risk of predation may affect individuals in prey populations by limiting their use of high-quality habitat. Predation risk, however, cannot be implicated as a factor in habitat selection by prey without data comparing quality of selected and avoided habitats, along with the predation risk associated with those habitats. If forage benefits and predation risk are not positively correlated among habitat types, then predation risk may have little influence on the habitat selected by prey. We evaluated habitat selection by mountain lions (*Puma concolor*) and mule deer (*Odocoileus hemionus*) in the eastern Sierra Nevada, California, USA, from 1994 to 1997, to determine how forage benefit or risk of predation by mountain lions affects habitat selection by mule deer. Mountain lions were the primary predator of mule deer in our study area. Stands of bitterbrush (*Purshia tridentata*) in the Great Basin provided more cover for mule deer than surrounding patches of rabbitbrush (*Chrysothamnus nauseosum*) or desert peach (*Prunus andersonii*). Bitterbrush also was important forage for mule deer during winter. We hypothesized that mountain lions would be more successful at stalking and killing mule deer in habitats with more concealment cover than in habitats with less cover, and therefore mule deer would choose between foraging on bitterbush and avoiding predation by mountain lions. We collected data on habitat characteristics in 3 types of locations: random locations (n = 180), deer foraging locations (n = 179), and locations where mountain lions killed deer (n = 41). Mule deer selected habitat at greater elevations ($P < 0.001$) with more bitterbrush ($P < 0.001$) and less rabbitbrush ($P = 0.033$) when compared with random locations. Logistic regression indicated that mountain lions killed deer in relatively open areas with more desert peach ($P < 0.001$) than at locations in which deer foraged. Therefore, deer were not confronted with a trade-off when selecting habitat on winter range, and they minimized the ratio of predation risk to forage benefit by selecting habitat with more bitterbrush. Changes in diet among seasons, which occur for herds of migratory deer, lead to individuals experiencing changing predation risk to forage benefit ratios throughout the year. Hence, migratory populations of mule deer likely adopt different strategies of habitat selection among seasons.

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Selection of habitats to maximize reproductive fitness can involve a trade-off between maximizing foraging benefits while minimizing risk of predation (Festa-Bianchet 1988, Molvar and Bowyer 1994, Bleich et al. 1997, Nicholson et al. 1997). This trade-off has been proposed in an array of environments (Sih 1980, Pierce et al. 1992, Rachlow and Bowyer 1998, Barten et al. 2001), but it can occur only if foraging benefits and predation risk are positively correlated (Bowyer et al. 1998). An understanding of how forage benefit and risk of predation vary across the landscape and how those factors are interrelated is necessary for understanding habitat selection (Bleich et al. 1997, Kie 1999). Most research examining habitat selection by ungulates has focused on resource acquisition; however, some recent studies have emphasized the importance of avoiding predators while acquiring those resources (Van Ballenberghe and Ballard 1994; Sinclair and Arcese 1995; Bowyer et al. 1998). Few studies have examined the manner in which risk of predation and forage are arrayed in natural environments or have tested for effects of such landscape patterns on outcomes from encounters between large carnivores and their primary prey.

We studied habitat selection (as defined in Block and Brennan 1993) by mule deer in relation to predation by mountain lions on a winter range in the eastern Sierra Nevada, California, USA. Predators that stalk and ambush prey prefer areas with dense concealment cover for hunting (stalking cover; Schaller 1972, Russell 1978, Beier et al. 1995). Indeed, mountain lions were more successful at hunting pronghorns (*Antilocapra*

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americana) that inhabited rugged terrain with more vegetation than those that occurred in open prairie (Ockenfels 1994). The primary forage of mule deer on our study area was bitterbrush (Kucera 1997), which often occurs in homogeneous stands >2 m in height and provides substantial stalking cover. We hypothesized that stands of bitterbrush would provide ideal habitat for mountain lions engaged in hunting, and, because of the importance of bitterbrush as forage, we predicted that a positive relationship would exist between predation risk and foraging benefit to mule deer. Under such conditions, mule deer should make a trade-off (i.e., incur a cost), thereby accepting greater risk of predation to meet forage requirements.

We collected data on the locations where deer foraged and the locations where mountain lions preyed upon deer to determine which parameters were most important for habitat selection by these 2 large mammals and to determine the strategy for habitat selection by mule deer. If risk of predation by mountain lions is constant across habitats occupied by mule deer, or if mountain lions are more successful at killing deer in habitats with low foraging benefits, no trade-off exists for mule deer when selecting foraging habitat. Under such circumstances, mule deer should seek to maximize foraging benefits, thereby reducing the predation risk to forage benefit ratio (Pulliam 1989). If, however, mountain lions are more effective hunters in areas with stalking cover, habitat selection by mule deer would be more complex, and a trade-off between use of a particular habitat and predation risk might occur. We examined the role of forage availability and predation risk by mountain lions in the selection of habitat by mule deer. Because habitat selection in herbivores likely affects reproductive fitness, strategies of habitat selection can be linked to population dynamics.

STUDY AREA

We conducted our study in Round Valley (approx 130 km^2; 37°24′N, 118°34′W), which is located on the east side of the Sierra Nevada in eastern California, USA. Mount Tom (4,161 m) and Wheeler Ridge (3,640 m) form a steep boundary along the western edge of Round Valley and rocky alluvial fans extend eastward from their bases. The south end of the valley is composed of large boulders and granitic ridges that support tall bitterbrush, pinyon pines (*Pinus monophylla*), and Utah junipers (*Juniperus osteosperma*). The valley floor (1,375 m) rises northward to the top of Sherwin Grade at 2,135 m. The Tungsten Hills provide relatively dry and open habitat to the southeast. The eastern boundary of Round Valley is delineated by Highway 395, the main north–south route from Reno, Nevada, to the Los Angeles basin, California, and is coincident with a geological shift into the Volcanic Tablelands. Approximately 18.3 km^2 of open pasture occurred in the eastern portion of the valley, and 3.2 km^2 of the study area was developed as residential housing. Deer used those pastures only when heavy snows drove them to lower elevations from areas dominated by bitterbrush. Deer inhabited about 90 km^2 of Round Valley during November–April (Kucera 1988), but the area used varied with snow depth.

The vegetation association in Round Valley was characteristic of the Great Basin and typical for the sagebrush belt (Storer and Usinger 1968). Winter range was composed of bitterbrush, sagebrush (*Artemisia tridentata*), and rabbitbrush in a mosaic where patches dominated by blackbrush (*Coleogyne ramosissima*), desert peach, and Mormon tea (*Ephedra nevadensis*) were common. Riparian areas supported the growth of willow (*Salix* sp.), Rose (*Rosa* sp.), and water birch (*Betula occidentalis,* but forbs and graminoids were uncommon in Round Valley during winter.

In June 1995, a fire burned approximately 22 km^2 of winter range near the center of our study area. This fire occurred in an area dominated by bitterbrush and sagebrush and was of such intensity that no measurable regrowth of bitterbrush occurred from the charred stumps. In years following the fire, desert peach and cheat grass (*Bromus tectorum*) dominated vegetative growth and provided little concealment cover for deer or mountain lions and little forage value for deer. During the late 1980s, forage availability in Round Valley, as indexed by leader growth of bitterbrush, declined sharply in response to a prolonged drought (Kucera 1988). A decline in the migratory population of mule deer, from about 6,000 (66 deer/km^2) in 1985 to <1,000 (10 deer/km^2) in 1991, coincided with the decrease in carrying capacity of the winter range through 1988 (Kucera 1988). Our study began in November 1991, coincident with the end of that drought. Estimated numbers of deer on the winter range increased gradually from 1,344 (15 deer/km^2) in 1993 to 1,913 (21 deer/km^2) in 1997, while the density of mountain lions declined from 6.1 in winter 1992–1993 to 3.0 in 1996–1997 (Pierce et al. 2000*a*).

METHODS

Sampling Design

We captured mule deer (217 F, 93 M) in Round Valley and fitted them with radiocollars during winter or spring from 1993 to 1997. Deer were captured with Clover traps (n = 9; Clover 1956), drop nets (n = 2; Conner et al. 1987), or a net gun fired from a helicopter (n = 299; Krausman et al. 1985). We captured deer throughout their winter range, and we avoided animals in groups that already included >1 radiomarked animal. We distributed radiocollars among adult (≥1 yr old) males and females in the approximate proportion of their occurrence in the population (1:3). The majority (109/113) of young (<1 yr old) captured were fitted with brown, expandable collars close to a 1:1 sex ratio (Bleich and Pierce 1999). Differences in age and sex can play an important role in habitat selection (Bowyer 1984, Loft et al. 1987, Clutton-Brock 1991, Bleich et al. 1997). For this reason, we tested for differences in use of habitats between the sexes of mule deer before evaluating risk of predation. Adult mountain lions (12 F, 9 M) were captured and fitted with radiocollars from November 1991 to May 1995, following capture techniques described by Davis et al. (1996).

Mountain lions are important predators of mule deer in the Great Basin (Bleich and Taylor 1998), including our study area (Pierce et al. 1998, 2000*a*, 2000*b*). Nonetheless, to confirm the potential for mountain lions to pose significant risks to mule deer, and thereby to influence habitat selection by those ungulates, we compared the proportion of mortality in radiomarked mule deer caused by mountain lions with that of mortality caused by bobcats (*Lynx rufus*) and coyotes (*Canis latrans*). We located mule deer killed by mountain lions (n = 229) by back-tracking lions from daytime positions, investigating mortality signals from radiomarked deer, locating mountain lions at night via radiotelemetry, and investigating locations where numerous birds were observed scavenging. We monitored all radiomarked deer daily for mortality signals, and we determined causes of mortality by examining wounds, tracks, and feces in the vicinity of the carcass; predator identification often was confirmed with remote photography (Pierce et al. 1998). Only instances that occurred from November through April 1994–1997, within the boundaries of the study area, and for which the location where the deer was actually killed could be identified (n = 41) were used in our analyses. Each month, we randomly selected 10 radiomarked deer (deer forage locations), and we located them visually during daylight hours from November through April 1994–1997. In addition, during that same period, 10 random locations were selected each month within an area that encompassed the area deer were known to have used in previous winters (100 km^2). For random locations, we randomly selected Universal Transverse Mercator (UTM) coordinates and used a handheld Global Positioning System unit to identify the location in the field. We used those locations to sample availability of habitat for deer.

We defined habitat by the suite of characteristics we measured, which included important variables for survival and reproduction in mule deer (Leopold 1933, Hall et al. 1997). We defined habitat selection as a disproportional use of those variables (used – available) among the types of locations (Block and Brennan 1993). We used the line-intercept method (Canfield 1941) to sample cover of shrubs at all locations of deer killed by mountain lions, deer foraging locations, and random locations. We determined total distance of every browse species intersected by a 50-m tape oriented in a random direction and extending away from the location being sampled. Only bitterbrush, sagebrush, rabbitbrush, desert peach, Mormon tea, and blackbrush were included in analyses because each composed ≥5% of total vegetation measured. We performed an arcsine square-root transformation on the proportion of the 50-m measurement that each plant species comprised at each location. We viewed a 2-m tall cover pole (Bowyer et al. 1999) divided into 8 equal sections from the 4 cardinal directions at a distance of 15 m. We recorded the number of sections that were ≥50% obstructed from view from each direction as an index to stalking cover. We collected samples of bitterbrush ($\bar{x}$ = 80 g) from plants within a 50-m radius of the location being characterized. Samples taken from bitterbrush were about 10 cm in length and included more than current annual growth; those samples were typical of leaders removed by foraging deer. All samples were placed in paper bags, returned to the laboratory, and dried to a constant weight. We calculated moisture content of bitterbrush for all samples collected during 1996–1997 by subtracting weight after air drying from weight at time of collection and dividing the difference by the original weight. We determined in-vitro dry matter digestibility (IVDMD) and percent nitrogen (N) for all samples collected using standard techniques (Van Soest 1982).

Table 1. Variables used in stepwise logistic regression to model habitat selection by foraging mule deer and hunting mountain lions in Round Valley, California, USA, 1994–1997.

	Random (n = 180)		Lion kill (n = 41)		Deer location (n = 179)		
Variables	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	Description
Vegetation[a]							
Bitterbrush (m)	0.15	0.21	0.19	0.16	0.23	0.30	Proportion of a 50-m transect run in a random direction from the location being sampled that was intersected by the indicated plant species (continuous)
Sagebrush (m)	0.19	0.23	0.25	0.23	0.20	0.25	
Blackbrush (m)	0.11	0.19	0.11	0.21	0.14	0.20	
Rabbitbrush (m)	0.13	0.20	0.13	0.21	0.10	0.17	
Mormon tea (m)	0.15	0.22	0.15	0.16	0.18	0.22	
Desert peach (m)	0.07	0.17	0.21	0.32	0.08	0.18	
Snow depth (cm)	0.18	0.39	0.20	0.40	0.12	0.32	(Continuous)
Elevation (m)	1,385.21	624.64	1,377.49	559.52	1,343.63	578.47	(Continuous)
Distance to nearest water (m)	360.65	343.47	337.90	305.48	347.11	324.54	(Continuous)
Distance to nearest road (m)	1,193.82	1,379.29	1,514.47	1,382.43	1,253.05	1,169.01	(Continuous)
Cover pole index	4.57	4.31	5.88	4.87	5.64	4.85	No. 25-cm segments of a vertical 2-m pole ≥50% obstructed when viewed from 15 m from the 4 cardinal directions (discrete)
Terrain ruggedness index	29.79	38.35	19.48	20.66	26.29	60.72	Determined by multiplying the angular deviation of aspect by the SD of slope (continuous; Nicholson et al. 1997)
Visibility	210.68	100.72	241.93	82.95	203.14	102.22	No. of pixels (30-m^2 units) that could be seen by a deer with its head at a height of 1 m to a maximum of 400 m (discrete)

[a] The arcsine square-root transformation of vegetation values was used in the stepwise logistic regression.

Each month during November through April, we collected 20 fresh samples of mule deer fecal pellets from throughout our study area. We grouped 5 pellets from each sample into composite samples each month. Microhistological identification of plant fragments (Sparks and Malechek 1968) was completed for composite samples by the Composition Analysis Laboratory, Fort Collins, Colorado, USA.

We used the Geographic Information System (GIS) ARCINFO (Environmental Systems Research Institute 1998) to derive several variables including elevation, slope, distance to the nearest paved road, and distance to the nearest riparian zone. Viewshed was determined as the number of pixels (30-m^2 units) that could be seen by a deer with its head at a height of 1 m, out to a maximum distance of 400 m. We determined an index of terrain ruggedness by multiplying the angular deviation of aspect by the standard deviation of slope (Nicholson et al. 1997) for a radius of 210 m around the point being characterized.

Data Analyses

We used stepwise logistic regression (Agresti 1990; α to enter and remain = 0.15) to test for differences in habitat selection between male and female mule deer on winter range. We used the same method to determine the variables most influential in predicting the locations of deer from random locations and the locations of deer killed by mountain lions from locations of foraging deer. We controlled for multicollinearity by eliminating 1 of any pair of variables with $r^2 \geq 0.5$; as a result, 13 variables considered biologically relevant were available for inclusion in regressions (Table 1). The final model was based on the approximate chi-square distribution of the reduction in deviance achieved by adding variables (McCullagh and Nelder 1989). We used Hosmer-Lemeshow goodness-of-fit tests to assure aptness of the models. We used analysis of variance (ANOVA) to test for differences in measures of forage quality (IVDMD, N, moisture content) of bitterbrush among the 3 types of locations (i.e., random, deer, and kills made by lions) and applied post hoc tests (Tukey's HSD) as appropriate (Neter et al. 1990).

We used chi-square analysis (Zar 1984) to test for differences in the proportion of mule deer killed by mountain lions (n = 41), coyotes (n = 17), and bobcats (n = 2) between January 1993

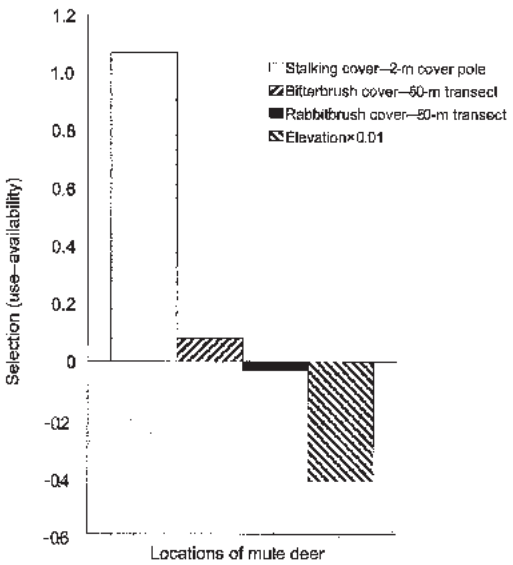

Fig. 1. Significant variables in model of habitat selection (mean of use minus mean of available) by mule deer in Round Valley, California, USA, 1994–1997. Stepwise logistic regression indicated mule deer selected habitat with more bitterbrush and greater stalking cover and that was at lower elevations, but they avoided habitat with an abundance of rabbitbrush.

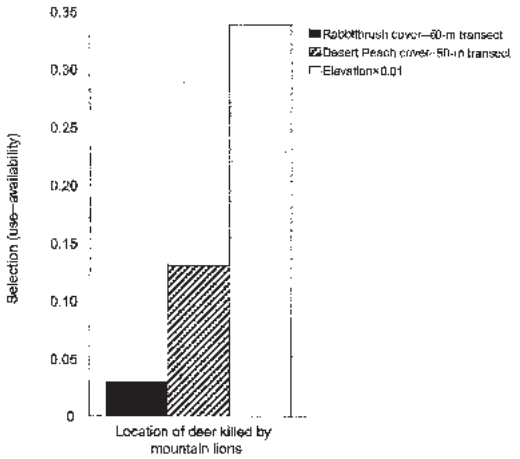

Fig. 2. Significant variables in model of habitat selection (mean of use minus mean of available) in which mountain lions killed mule deer in Round Valley, California, USA, 1994–1997. Stepwise logistic regression indicated mountain lions selected habitat with more desert peach and rabbitbrush at greater elevations to kill deer than locations where deer chose to forage.

and April 1998. We used only radiomarked mule deer for this analysis to eliminate potential biases associated with our ability to locate deer that died from different sources of predation. We used linear regression (Neter et al. 1990) to examine the relationship between the value from our cover pole and the percentage of canopy cover of bitterbrush, and we tested for a potential trade-off between predation risk and forage benefit. We used SAS (SAS Institute 1988) or SPSS (Norusis 1993) statistical packages for analyses of data and set $\alpha = 0.05$ for all tests.

RESULTS

Mountain lions (68%), coyotes (28%), and bobcats (4%) accounted for all predator-caused mortality among radiomarked mule deer ($n = 60$). Mountain lions were the primary predator of mule deer ($\chi^2_2 = 37.8$, $P < 0.001$).

Logistic regression indicated that adult male and female mule deer did not use habitat differently in Round Valley during winter ($P > 0.15$); therefore, we pooled data for males and females for subsequent analyses. Young were still traveling with their mothers and hence were included with adult females for analysis. Although linear regression of cover and bitterbrush did not produce a highly predictive model ($r^2 = 0.061$), results indicated a significant outcome ($P < 0.001$) in a positive direction. Logistic regression produced a significant model ($P < 0.001$) that distinguished locations of mule deer from random locations: {log (deer locations) = 4.0954 + 0.0450(cover) + 3.789(bitterbrush) – 2.0963(rabbitbrush) – 0.00288(elevation)}. That outcome indicated that mule deer did not occur equally across available habitats but selected areas with more bitterbrush ($P < 0.001$), less rabbitbrush ($P = 0.033$), and at lower elevations ($P < 0.001$; Fig. 1). Concordance of the final model for habitat selection by mule deer was 70%, and the goodness-of-fit test indicated that the model was apt ($\chi^2_8 = 11.72$, $P = 0.16$).

Areas where mountain lions were successful at killing mule deer differed from areas where deer foraged most frequently. The resulting model ($P = 0.0019$) for areas where mountain lions killed deer was {log (lion kills) = –4.2098 + 2.3635(rabbitbrush) + 3.1229(desert peach) + 0.00138(elevation)}. Mountain lions killed prey in areas more likely to have desert peach ($P = 0.002$) than areas where deer foraged (Fig. 2). Elevation ($P = 0.09$) and rabbitbrush ($P = 0.07$) also improved the ability of the model to distinguish locations where deer were killed by mountain lions from the locations where deer foraged. Concordance of the overall model for locations where deer were killed by mountain lions was 66%, and the

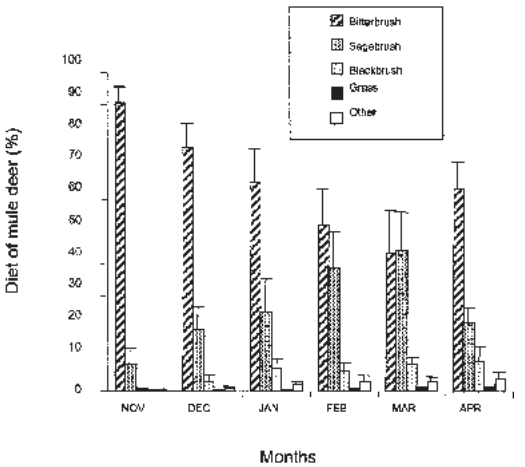

Fig. 3. Mean (± SE) diet composition of mule deer on a winter range in Round Valley, a winter range in the Great Basin of eastern California, USA, 1992–1997.

goodness-of-fit test indicated the model was apt ($\chi^2_8 = 6.405$, $P = 0.60$).

Microhistological analyses of fecal pellets collected from mule deer confirmed that bitterbrush was their primary forage on winter range (Fig. 3). Although proportion of sagebrush increased in the diet of mule deer throughout winter, bitterbrush averaged >65% of their diet during November–April. Analyses of bitterbrush indicated that percent moisture content ($F_{2,84} = 1.07$, $P = 0.347$) and percent nitrogen ($F_{2,224} = 1.97$, $P = 0.14$) did not vary among random locations (27.95 ± 2.27% [$\bar{x}$ ± SE]; 1.41 ± 0.03%), deer locations (32.46 ± 2.05%; 1.44 ± 0.03%), or locations of lion-killed deer (30.71 ± 3.05%; 1.36 ± 0.03%). We found no difference in forage digestibility between random locations (50.25 ± 0.91%) and those selected by deer (48.32 ± 0.81%; Tukey's HSD, $P > 0.05$). Mule deer, however, were killed by mountain lions in areas where the digestibility of bitterbrush was lower (42.22 ± 1.25%) than locations where deer foraged, and locations of random sites within the study area (Tukey's HSD, $P < 0.001$).

DISCUSSION

Contrary to our prediction based on the literature, cover did not enhance the likelihood of a mountain lion killing a deer in our study area. This contradiction may be a result of other studies using daytime locations that encompassed the general habitat used by mountain lions and not focusing on hunting locations or effects of the distribution of prey. Mountain lions are nocturnal and hunt and feed primarily at night (Beier et al. 1995; Pierce et al. 1998, 2000*a*). These solitary carnivores may select areas for resting during the day that are very different from the habitat where they hunt. Deer in Round Valley foraged throughout the day. A lack of distinct activity peaks is not uncommon for mule deer during short daylight periods in winter (Dusek 1975). Furthermore, individual deer in Round Valley were located repeatedly in the same areas on a daily basis. Although we were unable to document locations of randomly selected deer at night, data collected from locations of daytime foraging on winter range likely were representative of foraging locations of deer while mountain lions were hunting actively.

Mountain lions in our study area posed the most significant threat of mortality to mule deer compared with other large carnivores. If mule deer selected habitat in response to levels of predation risk, then predation by mountain lions should play an important role in habitat selection for mule deer. Further, selective pressure from mountain lions could differ for male and female mule deer; however, we observed no significant difference in habitat selection between sexes during winter. Sexual segregation at parturition is common in *Odocoileus* (McCullough et al. 1989, Bowyer 1984, Bowyer et al. 1996, Kie and Bowyer 1999), but not all populations segregate in winter (Bowyer 1984). Results from our study indicated that differences in risk of predation between sexes did not affect selection of habitat by mule deer on the winter range. The potential for a trade-off by mule deer between predation risk and forage benefit, however, existed. Such a trade-off was contingent on a situation in which predation risk was greater in habitats with more cover, and habitat composed mostly of bitterbrush provided the best forage.

Mule deer selected habitats that had a relatively high proportion of bitterbrush and low proportion of rabbitbrush. These locations tended to be at lower elevations and had more stalking cover than did random locations. If mountain lions were more successful at killing deer in areas with substantial concealment cover, our results indicate that mule deer would make a trade-off by accepting more risk for greater foraging benefits. This hypothesis, however, was rejected. Mountain lions killed more deer in habitat with desert peach and rabbitbrush, 2 low-lying shrubs associated with more open terrain than at locations where foraging deer occurred.

We postulate that for mule deer to minimize predation risk from mountain lions in the Great Basin, they should attempt to forage in areas with cover nearby, particularly stands of bitterbrush. Such a strategy does not require a trade-off if bitterbrush is the best available forage. Thus, mule deer wintering in the Great Basin or similar regions should seek to minimize their predation risk to forage ratio (Pulliam 1989) by remaining in habitat with a high proportion of bitterbrush.

Mule deer were killed by mountain lions in relatively open habitat compared with the locations where deer chose to forage. We acknowledge that we were unable to determine the locations where deer initially were pursued by mountain lions, and deer killed by mountain lions may have been foraging in habitat with substantial cover when pursuit by the mountain lion began. Our data does not allow us to determine the entire predation sequence; however, our results suggest that habitat with more stalking cover is not more risky in our study area, and prescribed burns to enhance deer habitat may increase predation risk in bitterbrush habitats.

A strategy of selecting stands of bitterbrush with substantial cover may allow mule deer to minimize risk from other predators. Stotting behavior by mule deer may be an adaptive behavior for eluding predators in habitats with numerous obstacles (Lingle 1992). Additionally, risk of predation by coyotes may be less in areas with substantial cover. Bowyer et al. (2001) reported that group size increased significantly for mule deer as they moved >30 m from concealment cover, indicating that deer sensed greater risk of predation in more open areas. Moreover, Bowyer (1987) reported that mule deer were as apt to flee from coyotes as to stand their ground, and Bleich (1999) suggested that proximity to concealment cover was an important factor in the outcome of such encounters. Studies of other canids indicate that they often pursue prey for relatively long distances (Mech 1966, Estes and Goddard 1967) in which open terrain might be an advantage to those coursing predators by allowing the more vulnerable members of a herd to be identified.

Our results were dependent on a situation in which cover was correlated with availability of high-quality food. Many populations of mule deer are migratory (Nicholson et al. 1997), including our study population (Kucera 1992, Pierce et al. 1999). Forage quality and availability change dramatically with season for deer in Round Valley (Kucera 1997). During periods when diets of mule deer were comprised predominantly of forbs and graminoids, strategies involving a trade-off between predation risk and forage benefits may prevail. Nevertheless, mule deer did not abandon areas of greatest forage value as a result of predation risk, as Wehausen (1996) reported for mountain sheep (*Ovis canadensis*) that are sympatric with deer during winter.

We found that concealment cover still may be a necessary component of the habitat where mountain lions stalked mule deer, but that mountain lions were more likely to capture and kill deer in habitat that was more open than where deer normally occurred. For that reason, mule deer in Round Valley do not have to make a trade-off between foraging benefit and predation risk when selecting habitat during winter. Mule deer can minimize their predation risk to forage benefit ratio by selecting habitat with a high proportion of bitterbrush that is away from the open terrain associated with desert peach or recent wildfires.

MANAGEMENT IMPLICATIONS

Our results were surprising in that bitterbrush habitat, which we predicted to be associated with the greatest risk of predation, appeared to be less risky than more open habitat in the surrounding area. We assumed that because mule deer selected bitterbrush habitat, they were sacrificing safety to gain greater nutrition. Indeed, mule deer in our study area appear to incur little cost from predation risk because the best place to forage also is the safest.

Assumptions about predation risk and forage benefit can be misleading and can result in poor management decisions. If forage benefit does not differ between 2 areas and individuals avoid the risky area, predation has not had a negative effect on forage acquired by those individuals. If costs to individual fitness associated with habitat selection are attributed wrongly to predation risk, then managers may focus too ardently on predator control. Often, an approach that considers factors affecting relative foraging benefits between habitats, in addition to predation risk, may be far more useful in determining costs associated with habitat selection. Certainly, a multifactorial approach to management should always be attempted in the absence of a cost–benefit evaluation that clearly defines a single factor as being solely responsible for habitat selection by prey.

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