Examining functional components of cover: the relationship between concealment and visibility in shrub-steppe habitat

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Abstract. The term “cover” has been used broadly in ecology, with a wide range of meanings, from thermal cover to security cover, to escape cover. Some habitat features could provide both thermal and security cover, or both concealment and escape cover; but in other cases, habitat features such as vegetation could impose a tradeoff between opposing functions of cover. Cover that conceals an animal from a predator also could reduce the animal’s visibility and thus, its ability to detect a predator early enough to escape capture. We quantified the opposing functional properties of cover (concealment and visibility) and evaluated the relationship between these properties using continuous measures in sagebrush-steppe and grassland habitats. We hypothesized that concealment and visibility would be inversely related and that the slope of this relationship would differ among sites with varying density and patchiness of shrub vegetation, imposing differing tradeoff scenarios. Concealment and visibility were inversely, but not perfectly related, implying that animals must make tradeoffs between the properties of cover, but they could achieve higher levels of one property while giving up relatively less of the other. In addition, we examined potential tradeoffs by pygmy rabbits (Brachylagus idahoensis) by comparing concealment and visibility at locations used by rabbits with measurements collected at random locations. At a small scale, pygmy rabbits traded off visibility for concealment in dense and sparse vegetation, but not in patchy vegetation. Although cover is an intuitively simple concept, it is functionally more complex, and this study provides insight into the opposing mechanisms of cover that might influence habitat use. Our work provides an initial step towards more fully understanding how cover functionally relates to predation risk.

Key words: Brachylagus idahoensis; predation risk; pygmy rabbit; tradeoffs.

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INTRODUCTION

The term “cover” has been used widely in ecology, its meaning varying from the proportion of vegetation or vegetation community within an area (Bonham 1989), to habitat features used by animals to reduce heat exchange with the environment (thermal cover, Cook et al. 1998), or the risk of stressors such as predators (security cover, Peek and Scott 1985). Furthermore, security cover might include habitat features that make an animal harder to detect (concealment cover, Robinson and Bolen 1984), features that physically separate an animal from the threat (e.g., tree cavity, cliff), or features that allow an individual to detect its predator and/or flee from...
it, such as a perch or trail (escape cover, Giles 1978). Some habitat features could provide both thermal and security cover, or both concealment and escape cover; but in other cases, habitat features such as vegetation could impose a tradeoff between various functions. For example, vegetation that conceals an animal from a predator also could reduce the animal’s visibility and thus, its ability to detect a predator early enough to escape capture.

Concealment is the property of cover that hides a prey animal from a predator, and visibility is the property that provides sightlines, which allow an individual to visually detect predators. Both of these properties can influence the perceived and realized risk of predation for a variety of prey species (e.g., Longland and Price 1991, Tabor and Wutsbaugh 1991, Bowyer et al. 1999, Budnik et al. 2002, Ripple and Beschta 2004, Pietrek et al. 2009, Embar et al. 2011). Prey species might alter habitat use to increase visibility or concealment as their perception of safety changes (Whittingham and Evans 2004), which could depend on the characteristics of the animal and its potential predators, the habitat, and environmental factors, such as weather and moonlight (Stankowich and Blumstein 2005, Kotler et al. 2010). Because concealment and visibility are opposing properties of cover that likely influence how an animal interacts with the environment to increase fitness, individuals might tradeoff one property to increase the other.

Although tradeoffs between foraging and predation risk are well documented (e.g., Sih 1980, Lima 1985, Houston et al. 1993, Rachlow and Bowyer 1998, Grand 2002), tradeoffs between the functional properties of cover in relation to predation risk are not well understood. A first step to understanding if and how animals make tradeoffs between concealment and visibility is to quantify the relationship between these properties across habitats and scales of measurement. One previous impediment to evaluating the functional relationships between cover and predation risk was the binary categorization of cover as “open” or “closed” (e.g., Lima 1985, Brown 1988, Götmark et al. 1995, Candolin and Salesto 2005, Lee et al. 2005, Carrascal and Alonso 2006, Druce et al. 2006, Druce et al. 2009). However, cover is not simply present or absent in, but occurs at a range of values in the landscape. Likewise, visibility, commonly termed “sightlines”, often has been characterized as “open” or “obscured” (Whittingham et al. 2004, Hannon et al. 2006, Jones et al. 2006, Embar et al. 2011). In many cases, concealment has been measured (and called “cover”), and visibility was assumed to be the lack of cover. Tradeoffs between concealment and visibility likely influence habitat selection by prey, and both functions have been shown to influence predation risk (e.g., Longland and Price 1991, Embar et al. 2011); however, to our knowledge, the relationship between concealment and visibility in cover provided by the habitat has not been quantified.

Our objective was to quantify the functional properties of cover in a continuous manner as they pertain to a small prey species in sagebrush-steppe and grassland habitats. We quantified concealment and visibility independently for both aerial and terrestrial predators and then quantified the relationship between the two properties. Additionally, we examined how these properties and their relationship were manifested in habitat selection by pygmy rabbits (Brachylagus idahoensis), a sagebrush-dependent species that occupies areas in the Great Basin and the surrounding intermountain region of the western USA (Dobler and Dixon 1990). Because predation by both aerial and terrestrial predators is an important source of mortality for pygmy rabbits (Green and Flinders 1980, Estes-Zumptf and Rachlow 2009, Crawford et al. 2010, Price et al. 2010), and they rely, in part, on visual cues to detect predators, both concealment and visibility likely are important for this species. In this study, we isolated the predation response of pygmy rabbits from other behaviors such as foraging and resting by measuring habitat selection in the presence of disturbance.

We quantified concealment and visibility horizontally to represent the relationship between terrestrial predators and prey, and also vertically to represent the relationship between a ground dwelling prey species and aerial predators. We investigated whether concealment and visibility and their relationship differed among three study sites with varying density and patchiness of shrub vegetation and across three scales of measurement for terrestrial cover. Because the relationship between concealment and visibility...
likely varies with both of these factors, we predicted that: (1) horizontal concealment and visibility would differ across distances for terrestrial predators such that concealment increased and visibility decreased with distance between the prey and predator; (2) concealment and visibility would differ among our study sites because of differences in vegetation structure among sites; and (3) concealment and visibility would be inversely related, but that the slope of the relationship also would differ among sites. In addition, we examined how the relationship between concealment and visibility influenced habitat selection in the presence of a potential threat. We predicted that pygmy rabbits would select locations with higher concealment and lower visibility than available in the habitat, indicating that individuals were trading off visibility for enhanced concealment.

**Methods**

**Study sites**

We examined values of concealment and visibility at two study areas in southwestern Montana and one area in east central Idaho near the Montana border during May–August 2010. All three study sites supported shrub-steppe vegetation dominated by big sagebrush (*Artemisia tridentata*) with forb and grass understories, although the subspecies of big sagebrush and the density of both shrub and understory vegetation differed across sites. The Montana areas, Reservoir Creek and Badger Pass, were both characterized by mountain big sagebrush (*Artemisia vaseyana*). The Idaho site, Cedar Gulch, was predominantly Wyoming big sagebrush (*A. t. wyomingensis*) with a sparse grass and forb understory. Cedar Gulch was characterized by mima mounds, areas of mounded microtopography, which supported relatively taller, dense patches of sagebrush shrubs. We also collected concealment and visibility data in a grassland habitat without a shrub overstory at a site adjacent to the Reservoir Creek site. Elevations at the 3 study areas ranged from 1500–2400 m and each site was approximately 100 ha.

The study sites supported a compliment of native vertebrates including other lagomorphs (blacktailed jackrabbits, *Lepus californicus*; mountain cottontail rabbits, *Sylvilagus nuttallii*), mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), and a diversity of predators known to prey on pygmy rabbits. These included both aerial predators such as the great horned owl (*Bubo virginianus*) and northern harrier (*Circus cyaneus*), and terrestrial predators such as the long-tailed weasel (*Mustela frenata*), badger (*Taxidea taxus*), and coyote (*Canis lantrans*).

**Study animals**

To compare concealment and visibility at locations selected by pygmy rabbits with random locations, we trapped 15 pygmy rabbits at Reservoir Creek, 18 at Cedar Gulch and 16 at Badger Pass using wire box traps during May–July 2010. We fitted the captured animals with a collar style radio transmitter (5 g; Holohil Systems Ltd.) and located the rabbits by following the radio signal with a handheld antenna until the rabbit was sighted. We recorded the location of the rabbit when we first saw it, before it fled, and collected habitat measurements at that location. We assumed that the rabbits were aware of our presence as we moved through the shrubs radio tracking them and that they likely adjusted their position in response to our presence, which would represent a potential threat in their vicinity. Therefore, habitat selection at the locations where we observed the rabbits likely reflected a response to elevated risk, and our assumption was that the rabbits responded to our presence in a manner similar to that of a predator. We relocated each individual rabbit 5 times at intervals >2–3 days. We removed collars after completing the trials. All procedures were approved the University of Idaho ACUC (Protocol #201019), and follow guidelines published by the American Society of Mammalogists for research on wild mammals (Sikes and Gannon 2011).

**Concealment and visibility**

We measured concealment and visibility at locations selected by pygmy rabbits, and at 2 randomly located points that were paired with the used location. We selected random points by using the rabbit locations as starting points and choosing a random direction and distance within 10 m. Because rabbits were not located in the grassland vegetation, we randomly located 60 points in the grassland habitat adjacent to the
Reservoir Creek site at which we also collected visibility and concealment to provide a contrast with those measures in the shrub-steppe vegetation.

At each site, we measured concealment as the extent to which vegetation would hide a rabbit-sized animal from potential predators using a 15 × 15 cm profile board with 25 3 × 3 cm red and white squares. For terrestrial predators, we viewed the profile board from three distances (4, 8 and 12 m) from a height of 1 m. Similarly, to measure concealment from aerial predators, we placed the profile board flat on the ground and took a perpendicular photograph from a height of 1.5 m. From both terrestrial and aerial perspectives, we recorded the number of 3 × 3 cm squares that were ≥50% visible, and converted the counts to the percent of squares that were ≥50% concealed by vegetation.

To measure visibility of potential predators from the perspective of a prey animal, we used a camera on a tripod at a height of 8 cm to represent the approximate eye level of a rabbit. We took a photograph of a 1 × 1 m board placed upright on the ground at distances of 4, 8 and 12 m from locations used by rabbits and from the randomly selected points. We estimated the percent of the 1 × 1 m board that was visible to the rabbit by placing a digital grid with 100-point intersections over the digital photograph on a computer and recording the number of intersections at which the board was visible (i.e., not obscured by vegetation or topography). This count provided an index of visibility of terrestrial predators. To assess visibility of aerial predators, we took a photograph directly upward from each of the used and random points and recorded the number of grid intersections in which the sky was visible in the photograph.

We measured shrub cover at the 3 sagebrush sites using the line-intercept method (Canfield 1941). At each site, we randomly selected 10 locations, a random direction, and conducted the line-intercept measurement for 30 m. Shrub cover was not present in the grassland area adjacent to Reservoir Creek study site.

**Statistical analyses**

First, to determine if horizontal concealment and visibility differed among the 4 study sites and among the 3 distances (4, 8, and 12 m), we used multivariate analysis of variance (MANOVA) with concealment and visibility as the dependent variables and site, distance, and the interaction between site and distance as the independent variables (PROC GLM, SAS Institute 2008). We followed significant MANOVA results with analysis of variance (ANOVA) and Tukey’s pairwise comparisons to determine which sites and distances differed significantly. We also used MANOVA and Tukey’s pairwise comparisons to determine if aerial concealment or visibility upward differed among sites.

We used a mixed-effects linear model to characterize the relationship between terrestrial visibility and concealment at the 4 study sites (3 shrub sites plus the grassland site) and across the 3 distances, and to evaluate the relationship between aerial concealment and visibility upward at the 4 sites (PROC GLIMMIX, SAS Institute 2008). We included the fixed effects of site and distance (for terrestrial measurements) as well as 2-way and 3-way interactions between concealment, site and distance. Each location used by an individual rabbit had 2 random points associated with it, and each rabbit was relocated 5 times. The individual rabbit and the event nested within rabbit were modeled as random effects (“event” is used here to represent a cluster of 3 observations—1 used location and 2 randomly selected locations). Because we did not locate rabbits in the grassland, we assigned identification and an event number to each location in the grassland to make 60 unique combinations that identified 60 random locations. We used Wald tests to compare the slopes to determine whether these relationships differed among the 4 sites and 3 distances. Because the relationship between aerial concealment and visibility was not linear, we used Spearman’s rank correlation to test those relationships.

Finally, to determine if there was a difference between the concealment and visibility at locations selected by pygmy rabbits and random points, we used a mixed-effects linear model. To account for possible habituation by the rabbits, the individual rabbit and the event nested within rabbit were modeled as random effects. We also included the fixed effects of site and distance (for terrestrial measurements) and all 2-way and 3-way interactions.
RESULTS

Functional relationships of vegetation cover

Both concealment and visibility differed across scale (i.e., the distance from which we took the measurements) of measurement with respect to cover from terrestrial predators. Together, terrestrial concealment and visibility differed significantly across distances (Wilks’ lambda = 0.86, P < 0.0001). The interaction between site and distance also was significant (Wilks’ lambda = 0.98, P = 0.0097); however, this interaction was ordinal, and therefore, we interpreted and tested the main effects. As expected, distance was positively related to concealment and negatively related to visibility (Fig. 1). Univariate tests revealed that both functional components contributed to the overall differences (concealment: \( F_{11,1527} = 113.31, P < 0.0001 \); and visibility: \( F_{11,1527} = 101.18, P < 0.0001 \)).

Sagebrush cover varied qualitatively among our study sites. The Reservoir Creek and Cedar Gulch sites both had relatively open shrub canopies (Reservoir Creek cover = 21.3%, SE = 2.7%; Cedar Gulch cover = 21.0%, SE = 2%), but the distribution of shrub cover differed. Reservoir Creek had a moderately patchy sagebrush distribution throughout the study site, while vegetation at Cedar Gulch was highly patchy, being characterized by sparse sagebrush cover with areas of dense cover associated with mima mounds. The cover on the mima mounds measured using the line intercept method ranged between 31.0% and 38.0% (Price 2009). In contrast, the sagebrush canopy at the Badger Pass site was relatively dense and continuous (cover = 34.8% ± 5.9%).

There were differences in both terrestrial and aerial measures of concealment and visibility across study sites. Together, terrestrial concealment and visibility differed among sites (Wilks’ lambda = 0.88, P < 0.0001), and univariate tests revealed that both measures contributed to the observed differences in across sites (concealment: \( F_{11,1527} = 25.73, P < 0.0001 \); visibility: \( F_{11,1527} = 44.80, P < 0.0001 \)). Pairwise multiple comparisons revealed differences among all sites for terrestrial concealment (P < 0.05), except between Badger Pass and Cedar Gulch (Fig. 2a). Concealment was highest at both the Badger Pass and Cedar Gulch sites, while visibility was lowest at these sites. Tukey’s pairwise comparisons revealed significant differences among all sites for concealment (P < 0.05), and univariate tests revealed that both measures contributed to the observed differences in across sites (concealment: \( F_{11,1527} = 25.73, P < 0.0001 \); visibility: \( F_{11,1527} = 44.80, P < 0.0001 \)).
Fig. 2. Terrestrial (a) and aerial (b) concealment and visibility (mean ± SE) provided by vegetation structure measured at 4 sites in shrub-steppe and grassland habitats. Sites are ordered from left to right from highest to lowest shrub cover. Terrestrial concealment was greatest and visibility was lowest at the sites characterized by dense shrub cover. The Cedar Gulch site had a patchy shrub distribution, but within the patches the shrub cover was >25%. Different capital letters denote significant differences among sites in concealment, and different lower case letters denote significant differences in visibility (P < 0.05).

(\(\bar{x} = 81.6\%, \text{SE} = 1.33\%\)) and Cedar Gulch (\(\bar{x} = 82.3\%, \text{SE} = 1.44\%\)) sites, which differed significantly (P < 0.05) from both the Reservoir Creek (\(\bar{x} = 72.3\%, \text{SE} = 1.65\%\)) and the grassland site (\(\bar{x} = 63.9\%, \text{SE} = 2.07\%;\) Fig. 2a). Terrestrial visibility also differed among sites (P < 0.05), except between the Reservoir Creek (\(\bar{x} = 26.4\% \text{ SE} = 1.37\%\)) and the grassland site (\(\bar{x} = 28\% \text{ SE} = 1.78\%;\) Fig. 2a), both of which had higher mean values than either Badger Pass (\(\bar{x} = 20\% \text{ SE} = 1.19\%\)) or Cedar Gulch (\(\bar{x} = 10.7\% \text{ SE} = 0.87\%\)). Cedar Gulch had the lowest mean value for
visibility ($\bar{X} = 10.7\% \ SE = 1.44\%$). Although the shrub cover across the site was relatively sparse, the cover within mima mounds was relatively high, and this likely reduced visibility and increased concealment from within the dense patches.

Concealment and visibility with respect to avian predators also differed among sites. Together, both aerial concealment and visibility differed among our study sites (Wilks’ lambda = 0.94, $P < 0.0001$), and univariate tests revealed that both measures contributed to the observed differences (concealment: $F_{3,506} = 4.45$, $P = 0.0042$; and visibility: $F_{3,506} = 4.34$, $P = 0.0050$; Fig. 2b). In general, aerial concealment was low at all sites ($\bar{X} < 20.0\%$) whereas aerial visibility was high ($\bar{X} > 80.0\%$). Not surprisingly, aerial concealment was the lowest at the site that contained only grass. Pairwise comparisons revealed significant differences ($P < 0.05$) in aerial concealment between the grassland site and both Badger Pass (dense shrub cover) and Cedar Gulch (sparse, but patchy cover associated with mima mounds). Aerial visibility differed significantly only between Cedar Gulch and Reservoir Creek (Fig. 2b).

**Relationships between concealment and visibility**

As expected, terrestrial concealment and visibility were inversely related. The interaction between concealment, site, and distance was significant ($F_{12,1118} = 178.01$, $P < 0.0001$); therefore, we examined the relationships separately across sites and distances. For all sites and distances of the terrestrial measures, the slopes between visibility and concealment were negative and significant, ranging from 0.787 to 0.349 ($P < 0.05$; Fig. 3). As with absolute values of terrestrial visibility and concealment, the relationship between the two functions differed across scales of measurement. There was a general decline in the steepness of the regression lines with increasing scale at all sites, but the differences in the slopes were significant only at the Reservoir Creek and Cedar Gulch sites (Fig. 3). Slopes of the regression lines between terrestrial visibility and concealment measured at 4 m differed significantly among all study sites ($P < 0.05$) except between Badger Pass and Reservoir Creek (Fig. 3). As expected, the site that had the most dense shrub vegetation (Badger Pass) had a steeper slope when measured from 4 m ($b = 0.63$) than the other two shrub sites (Cedar Gulch: $b = 0.53$; Reservoir Creek: $b = 0.61$), however, the grassland site had the steepest slope ($b = 0.79$). The relationships between terrestrial visibility and concealment also differed among all sites when measured at 8 m and 12 m ($P < 0.05$; Fig. 3). At all scales, the slopes were consistently shallower at the Cedar Gulch site, which was characterized by a highly patchy distribution of shrub cover (Fig. 3).

Aerial measures of visibility and concealment also were negatively related. The Spearman’s rank correlation coefficient for aerial concealment and visibility upward ranged from 0.72 to 0.37 across sites ($P < 0.05$ for all sites), indicating that the two variables were significantly and negatively correlated. We used the mixed-effects linear model to visually examine the slopes of the relationships in a qualitative evaluation and the slopes appeared to be steeper at the grass site and Cedar Gulch than at Badger Pass and Reservoir Creek.

**Selection of concealment and visibility by pygmy rabbits**

Pygmy rabbits selected locations with higher concealment relative to their surroundings when disturbed by a human on foot. Our data included 49 rabbits with 3–5 relocations (events) per individual. We collected 680 measurements of concealment and visibility at our 3 shrub study sites (227 used locations and 454 paired random points). Overall, terrestrial measurements of concealment differed significantly between used locations and random points ($F_{1,1798} = 7.22$, $P = 0.0073$). The effect of the 3-way interaction between distance, site and location also was significant ($F_{4,1798} = 2.75$, $P = 0.027$); therefore, we examined the influence of location (used or random) for each distance and site individually. Locations used by rabbits differed from random points when measured at 4 m for concealment at Badger Pass ($t_{1798} = 1.98$, $P = 0.048$) and Reservoir Creek ($t_{1798} = 4.59$, $P < 0.0001$), but not at Cedar Gulch and not any site at 8 and 12 m away (Fig. 4). Likewise, terrestrial measurements of visibility were significantly different between used and random locations ($F_{1,1798} = 5.80$, $P = 0.016$). The 3-way interaction also was significant ($F_{4,1798} = 4.45$).
2.50, \( P = 0.040 \)); visibility differed significantly between random and used sites only at 4 m at Reservoir Creek (\( t_{1798} = 5.38, P < 0.0001 \); Fig. 4). Overall, the differences reflect selection by rabbits for higher levels of terrestrial concealment and lower levels of terrestrial visibility than available in the surrounding areas, except at the Cedar Gulch site where the relationship between the two functional properties was less pronounced.

Rabbits also selected for higher aerial concealment and lower aerial visibility. Aerial measure-
ments differed between used and random points (concealment: $F_{1, 447} = 10.35, P = 0.0014$; visibility: $F_{1, 446} = 11.30, P = 0.0008$); however, the interaction between site and location also was significant for both aerial measures (concealment: $F_{2, 447} = 7.72, P = 0.0005$; visibility: $F_{2, 446} = 5.77, P = 0.0034$). Rabbits used significantly greater concealment than at random locations at Reservoir Creek ($t_{447} = 4.32, P = 0.0001$) and Badger Pass ($t_{447} = 2.40, P = 0.017$), but as with terrestrial measures, did not exhibit significant selection at Cedar Gulch (Fig. 5). Similarly, there were significant differences between used and random locations for visibility upward at both Reservoir Creek ($t_{446} = 3.88, P < 0.0001$) and Badger Pass ($t_{446} = 2.67, P = 0.0077$), but not at the Cedar Gulch site (Fig. 5). In contrast to the other 2 sites, pygmy rabbits at Cedar Gulch tended to use aerial concealment and visibility in proportion to availability.
We documented that two functional properties of cover, concealment and visibility, were inversely related, which means that animals cannot maximize both properties and must make trade-offs between them. The slopes of the relationships between concealment and visibility, however, were not 1, indicating that the two properties were not perfectly correlated; animals could achieve higher levels of one property while giving up relatively less of the other. Our results suggested that the structure of sagebrush vegetation allowed a small animal to position itself so that its body would be largely hidden from a potential predator, but it could put an eye to an opening between branches and retain a view of the surroundings.

Levels of both concealment and visibility varied across our study sites and among scales.

Fig. 5. Aerial concealment and visibility (mean ± SE) at 3 study sites in shrub-steppe habitat for locations used by pygmy rabbits and paired random points. Asterisks denote significant differences between use and availability ($P < 0.05$).
of measurement. At all sites, as scale increased, concealment of the prey animal increased and visibility of potential terrestrial predators from the perspective of the prey animal decreased. Among our study sites, concealment tended to be higher and visibility lower at the sites with relatively dense sagebrush cover (Badger Pass with dense and continuous cover and Cedar Gulch with dense patches of cover associated with mima mounds). Visibility was relatively higher at the sparse sagebrush site and the grassland site.

The relationship between concealment and visibility also differed across scales of measurement and sites, which might create differing tradeoff scenarios for prey species. Although terrestrial concealment increased and visibility decreased with scale at all sites, presumably because of the influence of intervening vegetation, the slopes of the relationship between the two became less pronounced (i.e., shallower) as the scale increased. This trend was most notable at the patchy and the sparse shrub sites, indicating that the tradeoffs animals are forced to make at those two sites might decrease with distance from a predator. The slope of the relationship between visibility and concealment was shallowest at the site characterized by overall sparse, but highly patchy cover associated with mima mounds and steepest at the site with the dense, continuous shrub cover. The steeper slopes associated with dense and continuous vegetation would require greater tradeoffs between the two functional properties; for every unit of concealment gained the dense site, a greater amount of visibility is given up relative to the other shrub sites.

In contrast to the shrub vegetation, the slope of the relationship between visibility and concealment at the grassland study site was the steepest of our 4 study sites, which suggested that in a landscape with only grass and no shrub structure, the tradeoff between visibility and concealment approaches a 1 to 1 tradeoff. Pygmy rabbits are tightly associated with shrub vegetation throughout their range (Green and Flinders 1980, Heady and Laundré 2005, Larrucea and Brussard 2008), and indeed, in our study, we never located radio-collared rabbits in areas with only grass.

Pygmy rabbits in our study tended to trade off visibility for concealment in the presence of a potential threat (i.e., a human on foot). However, selection of concealment and visibility by rabbits differed among sites and across scale of measurement. Our results suggested that pygmy rabbits traded off visibility for concealment at 4 m when they were approached by a potential predator, but with increasing distances, values converged so that we did not detect significant differences in visibility and concealment between random and used locations. Rabbits at the sparse and moderately patchy sagebrush site and the dense, continuous site selected for higher concealment and lower visibility, but rabbits at the site with highly patchy vegetation associated with mima mounds did not exhibit marked selection for either property. That site also had the shallowest slope for the relationship between concealment and visibility of the 3 sagebrush sites, so perhaps individuals did not exhibit selection at that site because they were not forced to trade off one component for the other to the same magnitude. Consequently, they simply used habitat as it was available with respect to the functional properties of cover that we measured. The highly patchy distribution of sagebrush likely allowed animals to be well concealed within the dense shrub structure associated with mima mounds, but the lack of shrub cover in the matrix between mounds might have afforded a more open view of the surroundings.

Aerial concealment and visibility followed similar patterns to terrestrial measures in our study. These functional properties were inversely related, and their relationships differed across study sites. The steepest slopes occurred at the grassland area suggesting that, in contrast to woody vegetation, grass did not provide both aerial concealment and visibility simultaneously. In this study, pygmy rabbits selected higher aerial concealment relative to their surroundings at 2 sites, but they did not exhibit selection for aerial visibility at any site. However, because our presence on foot likely simulated a terrestrial predator, our ability to evaluate selection of aerial concealment or visibility is limited. Variation in hunting modes among predators presents different types of threats to prey species and can select for different antipredator responses (Arnez and Leger 1997, Embar et al. 2011).
selection that we documented was likely more representative of a response to a terrestrial threat (Camp et al. 2012).

The tradeoff that animals must make between concealment and visibility has been hinted at in previous studies. For example, Götmark et al. (1995) suggested that nest concealment was a common tactic used for predator avoidance for song thrushes (Turdus philomelos), but that individuals also might benefit from retaining visibility from the nest that allowed detection of predators, food and conspecifics. They documented that song thrushes selected nest locations with intermediate levels of concealment from the range of values available and suggested that the thrushes were trading off concealment for visibility; however, they only measured concealment of the nest. Likewise, great bustard (Otis tarda) females also selected nest sites that had relatively open horizontal visibility, and Magaña et al. (2010) suggested that such selection represented a tradeoff between concealment and visibility, although only concealment was quantified. To our knowledge, our study is the first to quantify both concealment and visibility as continuous variables to demonstrate that an animal, indeed, must make tradeoffs between these properties.

There were some methodological challenges associated with this work. First, the fine scale at which we conducted our analyses of habitat selection relative to heterogeneity of the habitat might have influenced our results. We selected random locations within 10 m of the rabbit positions, and in many instances, the random locations were ≤5 m away. Our results would likely have differed if we had sampled at a coarser scale; for example, if we had chosen random points across the study sites. This procedural change might not have affected our results at the grassland site or the dense shrub site because those sites were more homogenous, but we expect that it would have done so at the moderately and highly patchy sites. If we had sampled over a broader scale rather than a microsite scale, the differences between the shrub patches and the matrix between patches would have resulted in more pronounced differences between used and random locations. Second, we used different methods to measure visibility (i.e., digital grid) and concealment (i.e., profile board), which also could have influenced our results because the resolution of these 2 measures differed. Profile boards are a common way to measure concealment of an animal in vegetation, but to measure visibility from an animal’s point of view and emulate an eye looking through a hole in the vegetation required a different method. Therefore, we took a photograph from within the shrub looking outward; however, this methodology resulted in a difference in precision between these two measurements. Although unlikely to introduce a directional bias, this difference might influence our ability to detect significant trends. Future research that examines the functional relationships between concealment and visibility across different scales of habitat selection using consistent precision of measurement would help to refine understanding of these concepts in relation to predation risk.

Cover, which is a critical requirement for all animals, is an intuitively simple concept, but a functionally complex reality. As we have shown, the properties of cover can vary across habitats and scale, which can influence the relationship between them, and these differences likely have consequences for prey species. Many studies have demonstrated that cover can influence vulnerability to predation (e.g., Longland and Price 1991, Eccard et al. 2008, Colombelli-Négrel and Kleindorfer 2009); however, the relationship between the opposing functional components of security cover, concealment and visibility, has remained largely unexplored until now. To understand habitat selection relative to predation risk, we must understand the properties of security cover and how they vary across habitats and scales. This study provides insight into the mechanisms of cover that might influence predation risk and habitat selection. Improving a functional understanding of cover will increase our ability to assess habitat quality by linking habitat characteristics to components of fitness (Van Horne 1983), which is needed to evaluate the effects of habitat change and to guide habitat management and restoration efforts.

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