When to Run and When to Hide: The Influence of Concealment, Visibility, and Proximity to Refugia on Perceptions of Risk

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Abstract

An animal’s ability to avoid predation likely depends on its ability to detect approaching predators, conceal itself, and seek refuge or protection from predators. Habitat, especially vegetation structure, can influence all of these factors concurrently. Binary categorical assessments of habitat as ‘open’ or ‘closed’, however, confound at least two functions of habitat structure that could influence the perceived risk of predation: concealment, which functions to hide an individual, and visibility, which enhances detection of a potential predator. Both can influence predation risk independently and simultaneously. In this study, we decoupled these functional properties of vegetation and studied the effects of concealment, visibility, and proximity to a refuge on the distance at which pygmy rabbits (Brachylagus idahoensis) fled from an approaching threat (flight initiation distance; FID). Concealment by vegetation decreased perceptions of risk; however, pygmy rabbits exhibited elevated risk at high levels of visibility, regardless of the amount of concealment. Proximity to burrow entrances also influenced perceptions of risk, such that risk was significantly lower when rabbits were on or near burrow systems. Disentangling the functional properties of habitat can provide a more comprehensive understanding of the factors that influence perceived risk and escape behaviors of prey and provide insight into how habitat structure mechanistically relates to predation risk.

Introduction

For prey species, avoiding predation is a complex process that involves interactions between habitat use and decisions about when and how to flee (Lima & Dill 1990). This process is affected by the ability of the prey to remain concealed, to detect approaching predators, and to seek refuge or protection from predators (Bonenfant & Kramer 1996; Cooper 2000; Embar et al. 2011; Javůrková et al. 2012). Habitat, especially vegetation structure, can influence all of these factors concurrently. Concealment is the functional property of the habitat that allows an animal to remain hidden from a predator, and visibility is the property that provides sightlines to allow a prey animal to visually detect oncoming predators. Although concealment is important for reducing probability of predation, visibility that facilitates early detection of predators also might influence how habitat structure relates to predation risk. For example, sightlines that allowed detection of predators increased the amount of time that gerbils (Gerbillus andersoni allenbyi) spent foraging; when animals had fewer sightlines, they perceived a food patch to be riskier, likely because vigilance was less effective for assessing risk (Embar et al. 2011). Furthermore, the ability of prey to visually detect characteristics about approaching predators, such as head and gaze orientation, speed of approach, and directness of approach, influences escape decisions (Cooper 2008; Braun et al. 2010; Cooper 2010; Bateman & Fleming 2011; Javůrková et al. 2012). As concealment increases, the ability of
prey to visually detect these cues might decrease. Thus, both visibility and concealment might simultaneously influence perceptions of risk by prey species.

Regardless of the degree to which the habitat provides concealment or obstructs vision of prey, vegetation structure, or cover, influences escape decisions and thus perceived risk across diverse taxonomic groups including mammals (Blumstein 1998; Blumstein et al. 2004; De Boer et al. 2004), lizards (Cooper & Whiting 2007; Cooper 2010), birds (Boyer et al. 2006), fish (Dill 1990), and insects (Cooper 2006). For species that escape to a refuge, perceived risk often increases with distance from refugia such as burrows, trees, or rocky terrain as reflected by an increase in flight initiation distance (FID), which is the distance at which an animal flees with the approach of a predator (Cooper 1997, 2000; Côté & Hamel 2007). For example, woodchucks (Marmota monax) demonstrated increased FID with increasing distance from their burrows (Bonenfant & Kramer 1996), and gray squirrels (Sciurus carolinensis) demonstrated increased FID with distance from trees (Dill & Houtman 1989).

One limitation to previous studies that link vegetation structure to perceived predation risk is that habitats typically have been defined as binary categories of ‘open’ or ‘closed’ cover (e.g., Lazarus & Symonds 1992; Brown et al. 1997; Whittingham et al. 2004; Beauchamp 2010; Embar et al. 2011). These designations collapse at least two functions of cover (concealment and visibility) that have been shown to influence perceptions of predation risk (Cooper et al. 2009; Embar et al. 2011). Because concealment and visibility can influence predation risk both independently and simultaneously, decoupling these functions might provide a more complete understanding of how vegetation structure shapes antipredator behavior.

Ecologists have used FID to quantify risk and identify factors that influence perceptions of risk. Ydenberg & Dill (1986) suggested that although fleeing may enable an animal to escape predation, it also incurs a fitness cost in terms of ceasing other important activities, such as feeding or finding mates. Fleeing also has a higher energetic cost than hiding, and it could draw the attention of the predator and make the prey more visible (Ydenberg & Dill 1986). Therefore, when a prey animal detects an approaching predator, it must decide when to flee, and because it should do so in a way that maximizes fitness, the optimal FID is expected to increase as risk of capture increases (Cooper & Frederick 2007, 2010). Using a behavioral measure, such as FID, for evaluating predation risk can provide more insight than investigation of mortality sites because it includes the animals’ perceptions of risk and actions that they take to avoid predation (Kotler & Blaustein 1995).

In this study, we examined the effects of cover separately and simultaneously, along with the distance to refugia, on the perceptions of risk by the pygmy rabbit (Brachylagus idahoensis), a small, cryptic lagomorph. This species digs and consistently uses extensive burrow systems with one to several entrances that are connected underground with tunnels and chambers (Green & Flinders 1980). Predation is one of the leading causes of mortality for pygmy rabbits (Sanchez 2007; Estes-Zumpf & Rachlow 2009; Crawford et al. 2010; Price et al. 2010) that rely on both shrubs and burrows for protection from predators (Green & Flinders 1980; Katzner et al. 1997; Larrucea & Brussard 2008). Consequently, pygmy rabbits behave like central-place foragers (Rosenberg & McKelvey 1999) and tend to restrict their movements to areas close to burrow systems (Heady & Laundre 2005; Sanchez & Rachlow 2008; Price 2009). This system is ideal for studying relationships between predation risk and habitat because pygmy rabbits live in a narrow range of habitat types, use burrow systems for refugia, and experience high rates of predation. Therefore, strong selective pressures have likely shaped interactions among pygmy rabbits, predation risk, and their habitat.

Although the functional properties of concealment and visibility are inversely related at our study sites, they are not perfectly correlated (Camp 2012). Consequently, we expected that both functions could influence perceptions of risk by pygmy rabbits. We predicted that perceived risk, as indexed by FID, would decrease with increasing concealment. In addition, because sightlines facilitate early detection of oncoming predators and enhance the prey’s ability to gather information about the predator, we expected that visibility would influence perceived risk such that FIDs would increase with increasing visibility. In addition, because burrows provide refuges from predators, we expected that proximity to burrow entrances also would influence perceptions of risk. We predicted that FIDs would be shorter when rabbits were in close proximity to burrow entrances because they could immediately escape to a refuge if a threat became imminent.

This study is the first that we know of to simultaneously evaluate the effects of both functional properties of cover (concealment and visibility), together with proximity to burrow entrances, on the perceived risk. Because avoiding predators is a complex process
that involves interactions between an animal and its habitat, concurrent assessment of the effects of multiple interacting components of habitat on perceptions of risk is needed to gain a better understanding of how animals strategically use habitat to reduce predation.

**Methods**

**Animals and Study Sites**

To evaluate perceptions of risk by pygmy rabbits, we collected data at two study sites in southwestern Montana and one site in east-central Idaho near the Montana border during May–Aug., 2010. All three study sites were dominated by big sagebrush (*Artemisia tridentata*) with grass and forb understories, although the subspecies of big sagebrush and the density of both shrub and understory vegetation differed across sites. All three sites supported terrestrial predators including badgers (*Taxidea taxus*), coyotes (*Canis latrans*), and weasels (*Mustela* spp.). We trapped approx. 15 adult pygmy rabbits per study site using wire box traps and fitted the captured animals with a collar-style radio-transmitter (5 g; Holohil Systems Ltd., Carp, Ontario, Canada). We radio-tracked rabbits three to four times a week from the time the animal was radio-tagged, in late May, until the beginning of August. We removed collars after completing the trials. All procedures were approved by the University of Idaho Animal Care and Use Committee (Protocol #2010–19) and are consistent with published guidelines for use of wild mammals in research (Sikes & Gannon 2011).

**Field Methods**

To conduct FID trials, we located individual animals by following the radio signal with a hand-held telemetry receiver until the rabbit was sighted. When a rabbit was visually located, a person (hereafter called the ‘flusher’) approached it at a consistent walking pace (approx 0.5 m/s). When the animal fled, the flusher placed a flag at his or her location. We considered movement of any distance by the rabbit to be ‘fleeing’. A second person, the ‘observer’, placed a flag at the location from which the rabbit fled and noted its location after fleeing and whether it went into a burrow. In conducting the FID trials, we acknowledge that rabbits might not respond to humans in the same way they would to their natural predators. However, we assumed that an approaching human represented a threat and that pygmy rabbits would display evasive behaviors that were related to their level of perceived risk (Frid & Dill 2002). We also assumed that rabbits were able to detect our presence before we started the trials and that they had adjusted their location according to their level of perceived risk. We measured FID as the distance between the location of the flusher and the rabbit when it fled, and this measure represented our index of perceived risk. We conducted FID trials at intervals of >2 d to avoid habituation of the rabbits. Our data included 49 rabbits with approx. 5 (x = 4.54, SE = 0.15) FID events per animal.

To evaluate the influence of proximity of a refuge on perceptions of risk, we measured the distance to the closest burrow entrance from the initial location of the rabbit before it flushed. We defined the rabbit location as ‘on a burrow system’ if the distance to the nearest entrance was ≤ 1 m and ‘off a burrow system’ if the distance was >1 m. After conducting a trial, we searched for the nearest burrow by walking in concentric circles starting from the location of the rabbit moving outward. Burrow systems created by pygmy rabbits typically include two to five or more entrances that span a distance of 2–4 m, and because burrow systems tend to be patchily distributed across the landscape, the area encompassed by burrow entrances belonging to a single burrow system is typically discrete, meaning the burrow systems do not overlap.

We measured concealment of the rabbit during FID trials from the direction of the flusher. Concealment was defined as the extent to which vegetation would conceal a rabbit-sized animal from potential predators using a 15 × 15-cm profile board with 25 3 × 3-cm red and white squares, which we constructed. We viewed the profile board from a horizontal distance of 4 m and a height of 1 m. 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.

We measured visibility from the point of view of the rabbit toward the flusher at the rabbit’s initial location before it fled. To measure visibility, we used a camera on a tripod at a height of 8 cm to represent the approximate eye level of a rabbit. We photographed a 1 × 1-m board placed upright on the ground at 4 m from locations used by rabbits in the direction of the flusher. 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). This count provided an index of percent visibility of terrestrial predators. The measure of visibility that
we used was a finer scale than the measure of concealment because prey might be able to monitor approaching predators through a small gap in the vegetation, even if concealment is high.

Data Analyses
To test our predictions that FID would decrease with increasing concealment or decreasing visibility and that FID would be lower for rabbits near burrow systems, we used a mixed-effects linear model (PROC MIXED; SAS Institute, Inc., Cary, NC, USA). Standard tests for normality and heteroscedasticity do not easily generalize to multilevel mixed models because of the dependencies among observations within units (here individual rabbits). Therefore, we examined several plots of level-1 residuals (responses within individual rabbits) and the empirical distribution of the estimates of the random effects to look for patterns that suggested deviations from approximate normality and homoscedasticity. We did not find any evidence of either. However, we did model FID on the (natural) log scale to better meet these assumptions. Furthermore, we used empirical ‘sandwich’ estimators for standard errors to protect against heteroscedasticity. Therefore, we are reasonably confident that the statistical assumptions for parametric analyses were adequately met.

We included the fixed effects of site, trial number, concealment, visibility, proximity to a burrow system (on or off), and the interaction between concealment and visibility, and the three-way interaction among concealment, visibility, and proximity to burrow. To illustrate the effect of the interaction between concealment and visibility on FID, we used the model to graph the estimated FID relative to concealment at four set levels of visibility (20%, 40%, 60%, and 80%) while holding the other variables constant. Upon initial exploration of the data, we did not detect a significant effect (p > 0.05) for distance to burrow as a continuous variable. However, this was in contrast to our observations of rabbits during the trials in the field; they would consistently allow us to approach them at close distances before fleeing when they were on a burrow system. Therefore, we modeled proximity to burrow as a binary variable (i.e., either on or off of a burrow system). Because each rabbit was relocated five times, we specified the individual rabbit as a random effect. We conducted a z-test to compare the proportion of times that rabbits flushed into a burrow when they were on versus off burrow systems.

Concealment and visibility were highly correlated. The correlations were −0.82, −0.77, and −0.83 at the sites BP, CG, and RVC, respectively. While the presence of collinearity might inflate standard errors, the purpose of the study was to model the relationship between FID and these variables simultaneously. Leaving one of the two variables out of the model, or using two separate models, would make this impossible. Furthermore, if only one of the two variables was included, then its apparent effect would be confounded with the other because of their correlation, which is precisely what we wanted to avoid. While the presence of the collinearity makes it more difficult to detect the effects of these variables, the standard errors and tests are adjusted appropriately by the analysis.

Results
As predicted, concealment by vegetation decreased perceptions of risk by pygmy rabbits as they were evading a potential predator. Our measure of risk, FID, decreased significantly with increasing values of concealment (F1,172 = 13.58, p < 0.001, η2 = 1.95%; overall model η2 = 47%, rabbit (within site) η2 = 33%, Fig. 1a). In contrast, visibility alone did not significantly influence perceived risk (F1,172 = 0.06, p = 0.810, η2 = 0.11%; Fig 1b); however, the interaction between concealment and visibility was significant (F1,172 = 4.11, p = 0.040, η2 = 0.93%). Risk decreased with increasing concealment; however, as visibility increased, the relationship between FID and concealment became less pronounced (Fig. 2). These data reflected elevated perceptions of risk at high levels of visibility, regardless of the amount of concealment provided by vegetation. Nevertheless, concealment seemed to be the more important functional property influencing perceptions of predation risk by pygmy rabbits because the estimated FID was lowest at the point of maximum concealment and minimum visibility.

Proximity of burrows also influenced behavior of rabbits (Fig. 3). During our trials, pygmy rabbits were always located relatively close to burrow systems; the average distance from a burrow ranged from 9 to 67 m (n = 227, SD = 10.10). Rabbits <1 m from burrow systems flushed into burrow entrances during 70% of the trials, whereas those that were off burrow systems flushed into burrows during only 11% of the trials. Flight initiation distances were significantly shorter when rabbits were on burrow systems than when they were off systems (F1,172 = 5.87, p = 0.020, η2 = 1.6%), presumably because they could quickly
escape into a burrow entrance. Indeed, rabbits were significantly more likely to flush into a burrow entrance when they were on burrow systems than when they were away from burrow systems ($z$-test: $z = 9.52$, $p < 0.001$). The three-way interaction between concealment, visibility, and proximity to burrow was not significant ($F_{1,172} = 3.96$, $p = 0.05$, $\eta^2 = 0.50\%$), however, suggesting that the functional properties of concealment and visibility did not alter animal behavior relative to the immediate proximity of a refuge.

The effect of study site was not significant ($F_{1,172} = 0.830$, $p = 0.35$, $\eta^2 = 0.30\%$), but the effect of trial number was significant ($F_{1,17} = 1.72$, $p = 0.020$, $\eta^2 = 2.08\%$), indicating that 2 d might not have been an adequate amount of time to avoid habituation. However, when we accounted for habituation by including trial number in the model, there were still significant relationships between FID and concealment, visibility, and distance to burrow.

Discussion

Our study demonstrated that the different functions provided by habitat structure can influence perceptions of risk in opposing and interacting ways. Habitat
structure markedly influenced perceptions of risk by pygmy rabbits when they were evading a simulated potential predator. The FID decreased when animals were increasingly concealed by vegetation. However, perceived risk also was influenced by the interaction between the functional properties of concealment and visibility, indicating that both factors affected how rabbits might interact with their environment to manage risk. In addition, perceived risk was lower when animals were near the refuge of a burrow. These results suggest that disentangling the different functional relationships between habitat structure and predation risk might enhance understanding of habitat selection and antipredator behavior.

In our study, rabbits that were well concealed by sagebrush vegetation exhibited shorter FIDs and seemed to use a strategy of remaining still and relying on crypsis to escape detection. A well-camouflaged individual that flees from a predator might actually increase probability of capture by attracting the attention of the predator (Ydenberg & Dill 1986). Indeed, a strategy of using protective cover in conjunction with crypsis is well documented across taxa (e.g., frogs, Cooper et al. 2008; lizards, Martín et al. 2009; mice, Vignieri et al. 2010). For example, round-tailed horned lizards (Phrynosoma modestum), which have coloring that resembles small stones, exhibited shorter FIDs on rocky substrates compared with sandy ones, presumably in response to the effectiveness of their crypsis (Cooper & Sherbrooke 2010). The gray-brown pelage of pygmy rabbits closely matches the color of the woody bases of sagebrush (Stoner et al. 2003), and selecting habitat that provides high concealment with cryptic coloration might be a strategy for avoiding detection by predators. Shorter FIDs likely represented decreased perceptions of risk for well-concealed individuals.

Although obstruction of visibility alone did not significantly influence perceived risk, rabbits in our study had longer FIDs at high levels of visibility, regardless of the amount of concealment provided by vegetation. Higher levels of visibility might have allowed rabbits to detect our direct approach early and flee sooner than when they had high levels of concealment and low levels of visibility. For some species, predation risk, indexed by foraging behavior, is lower in open habitats, which provide visibility of oncoming predators and allow for escape by fleeing rather than hiding (Lima & Dill 1990; Lazarus & Symonds 1992; Embar et al. 2011). Visibility can reduce perceptions of risk by predation for foraging animals (Brown et al. 1997; Altendorf et al. 2001; Whittingham & Evans 2004; Embar et al. 2011), presumably because sightlines increase the effectiveness of vigilance and consequently, the efficiency of foraging. We examined response behaviors in the presence of an immediate threat (i.e., a simulated predator), which could explain why increased visibility alone did not influence perceived risk in our study. In contrast to our results, Woods (2012) documented that foraging pygmy rabbits perceived lower risk of predation under cover that provided sightlines in comparison with cover under which sightlines were occluded. Therefore, the influence of visibility on risk might depend on the activities of the prey animal and the type of threat. Visibility might be more important to animals that are moving through the landscape or foraging than to animals that are faced with an immediate threat.

Proximity to the refuge of burrow systems reduced perceptions of risk. Pygmy rabbits spend much of their time near burrows (Heady & Laudré 2005; Sanchez & Rachlow 2008), presumably in response to predation risk. Similarly, European rabbits spent less time foraging at increasing distances from their burrows (Bakker et al. 2005). In our study, rabbits flushed into burrows more often when they were near a burrow entrance, but did so only when the threat was very close (i.e., FIDs were shortest). Pygmy rabbits often have less shrub cover close to burrow systems (Price 2009). However, perceptions of risk were, nonetheless, lowest when animals were close to their burrow entrances, suggesting that concealment might be less important for rabbits closer to a refuge.

There were some methodological challenges associated with this work, specifically the collinearity between concealment and visibility and the relatively low effect sizes. The low effect sizes are likely a result of the complexity of this type of field work and possibly measurement error associated with concealment and visibility. We attempted to deal with these potential problems by adjusting our analysis appropriately. Nevertheless, we acknowledge that future studies collecting this type of data should seek to reduce these potential challenges.

Because patterns of habitat use by prey are shaped by decisions to avoid predation and improve fitness, an understanding of the mechanisms that influence those decisions can help quantify how habitat components influence individual fitness and population persistence. For example, pygmy rabbits in Utah avoided areas that had undergone sagebrush removal through mechanical thinning (Pierce et al. 2011; Wilson et al. 2011), and our work provides insight into one mechanism that might influence their preference for areas of untreated sagebrush.
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Literature Cited


Beauchamp, G. 2010: Relationship between distance to cover, vigilance and group size in staging flocks of semipalmated sandpipers. Ethology 116, 645—652.


Cooper, W. E. 2000: Effect of temperature on escape behaviour by an ectothermic vertebrate, the keeled earless lizard (Holbrookia propinqua). Behaviour 137, 1299—1315.


Kotler, B. & Blaustein, L. 1995: Titrating food and safety in a heterogeneous environment: when are the risky and safe patches of equal value? Oikos 74, 251—258.


