

Vertical and horizontal vegetation cover synergistically shape prey behaviour

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An animal's perception of predation risk varies across a heterogeneous landscape. Animals rely on indirect cues in the environment, including availability of protective cover, openness of sightlines and distance to refuge to evaluate potential predation risk. Interactions between the indirect cues that influence an animal's perception of predation risk are poorly understood, especially for prey at risk of avian and terrestrial predation. We conducted a giving-up density (GUD) study to examine how interactions between terrestrial predator presence, ceiling (canopy) cover, wall (shrub/grass) cover and distance to nearest tree influence fox squirrel, *Sciurus niger*, risk perception. The GUD indicates an animal's perceived predation risk, such that increased GUD (decreased foraging) corresponds to greater perceived risk. We found that fox squirrels perceived cues of predation risk in response to a synergistic interaction between ceiling and wall cover. In open canopy areas, fox squirrels increased GUD where there was also increased wall cover. However, fox squirrels reduced GUD in closed canopy areas where there was also increased wall cover. We attribute the differential effects of wall cover depending on ceiling cover to the effectiveness of open sightlines in decreasing predation risk from avian or terrestrial predators. Our study shows that the effect of vegetation structure on prey risk perception and antipredator behaviour depends on the relative risk posed by avian and terrestrial predators that use different hunting strategies.

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An animal's perception of predation risk varies across heterogeneous landscapes (Brown, 1999; Laundré, Hernández, & Altendorf, 2001). When animals perceive risk they experience a fear response, which can alter behaviours (Lima & Dill, 1990) including their use of resources (Brown, Laundré, & Gurung, 1999; Laundré, Hernández, & Ripple, 2010). An animal's survival depends on adjusting its fear and behaviours to its perception of risk in the immediate vicinity (Brown & Kotler, 2004; Kotler, Brown, & Hickey, 1999). Researchers commonly quantify an animal's level of fear by measuring their antipredator behaviours (Brown, 1988, 1992; Lima & Dill, 1990). These antipredator behaviours trade off with other fitness-improving activities such as reproduction and foraging (Lima & Dill, 1990). For example, an animal that reduces foraging to engage in antipredator behaviour loses potential caloric gain, but if it fails to react to a predation threat, it may be killed (Brown, 1988). An animal must determine its level of fear to maximize foraging

potential while minimizing risk of predation (Brown et al., 1999; Charnov, 1976).

In a heterogeneous landscape, predator communities and the abundance of individual predators vary spatially, creating spatial variation in a prey animal's fear (Brown & Kotler, 2004). Most prey species are preyed upon by multiple predators (Blumstein, 2006), but not all predators impact an animal's fear in the same way (Brock, Bednekoff, Pafilis, & Foutopoulos, 2015). Predators with greater lethality generate more risk and fear (Brown, 1999), and each predator species may provoke specific antipredator behaviours based on its hunting domain (i.e. avian or terrestrial) and hunting strategy (i.e. ambush, sit-and-pursue or active; Preisser, Orrock, & Schmitz, 2012; Schmitz, 2007). Large avian predators typically hunt using a sit-and-wait or sit-and-pursue strategy (Leyhe & Ritchison, 2004), while terrestrial predators typically rely on an active hunting strategy, such as stalking or chasing their prey (Rosenzweig, 1966). Prey have imperfect knowledge about the presence and movement of predators (Brown et al., 1999) and often rely on indirect cues based on local environmental and vegetation features as surrogates for predation risk (Brown & Kotler, 2004).

Vegetation structure often provides important indirect cues of predation risk, significantly impacting an animal's antipredator

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behaviour. For example, oldfield mice, *Peromyscus polionotus*, foraged significantly more at sites with vegetation cover than at exposed sites (Orrock, Danielson, & Brinkerhoff, 2004). In addition to cues of predation risk, vegetation structure can also provide an animal with protective cover (Lima & Dill, 1990; Mysterud & Østbye, 1999), concealing the animal from predators and decreasing that animal's level of fear (Thorson, Morgan, Brown, & Norman, 1998). Vegetation cover can exist along horizontal and vertical axes, with horizontal (ceiling) cover providing concealment from avian predators, while vertical (wall) cover is important for concealment from terrestrial predators (Wywiałowski, 1987). However, cover can also increase an animal's fear by inhibiting sightlines that prey rely on to detect and respond to predators (Camp, Rachlow, Woods, Johnson, & Shipley, 2013; Embar, Kotler, & Mukherjee, 2011; Iribarren & Kotler, 2012a). The relative importance of cover versus open sightlines can be confounded by interactions with other environmental features that influence perceived predation risk, such as distance to refuge (Iribarren & Kotler, 2012a) and temporal activity patterns (Jacob & Brown, 2000). Furthermore, indirect cues of predation risk are more reliable for sit-and-pursue predators than for active predators (Preisser et al., 2012), potentially creating interactions between antipredator behaviour and vegetation structure in a multipredator environment (Jacob & Brown, 2000). In general, animals that rely on concealment to avoid being detected by predators perceive lower risk with greater levels of cover while animals that rely on early predator detection and fleeing to refuge perceive lower risk with open sightlines (Arenz & Leger, 1997; Lima & Dill, 1990).

Sightlines, protective cover and escape routes alter the effectiveness of vigilance, which is defined as the ability for a wary animal to identify and escape from a potential predator (Brown, 1999; Iribarren & Kotler, 2012a). For prey with aerial and terrestrial predators, vigilance may be effective against one type of predator but ineffective towards the other, depending on vegetation structure (Wywiałowski, 1987). Vigilance is most effective when animals have open sightlines (Embar et al., 2011; Iribarren & Kotler, 2012b), but areas with open sightlines can be risky as they generally have less protective cover (Camp, Rachlow, Woods, Johnson, & Shipley, 2012). Open sightlines are particularly important for animals that primarily use their visual sense to identify predation risk (Iribarren & Kotler, 2012b).

There have been a number of investigations of the isolated effects of multiple predators or variation in vegetation structure on the antipredator behaviour of prey species (Arenz & Leger, 1997; Brown, Kotler, Smith, & Wirtz, 1988; Esparza-Carlos, Iníguez-Dávalos, & Laundré, 2018; Jacob & Brown, 2000; Orrock et al., 2004). However, there has been little consideration of the relative strength or potential interactions between these dominant drivers of animals' fear. Our objective for this study was to investigate the interactions between terrestrial predators, avian predators and vegetation structure on perceived predation risk by the fox squirrel, *Sciurus niger*. Fox squirrels are preyed upon by both avian and terrestrial predators and are found in a variety of forest ecosystems around the eastern United States (Steele & Koprowski, 2001). We hypothesized that different predator types interact with vegetation structure on fox squirrel perceived predation risk. Specifically, we predicted that (1) in the presence of terrestrial predators, fox squirrels perceive less predation risk in areas with greater wall cover because the protective cover provides concealment from terrestrial predators, (2) in the absence of terrestrial predators, wall cover does not influence fox squirrel perception of risk, (3) fox squirrels perceive less predation risk in areas with greater ceiling cover because of concealment from avian predators, (4) fox squirrels perceive the least overall predation risk in areas where terrestrial predators are absent and ceiling cover is greatest and (5)

fox squirrels perceive greatest predation risk at greater distances to the nearest tree, which would provide spatial refuges from predators (Thorson et al., 1998).

METHODS

Study Area

We conducted this research at The Jones Center at Ichauway (Jones Center) in Newton, Georgia, U.S.A., from 25 May 2017 to 7 July 2017. The Jones Center is a privately owned research facility dominated by longleaf pine, *Pinus palustris*, canopy and by wiregrass, *Aristida stricta*, understory. Large oaks (*Quercus* sp.) occur sporadically throughout the forest and serve as important food and refuge sources for fox squirrels (Conner & Godbois, 2003). The Jones Center manages for longleaf pine using prescribed burns on a 2-year rotation to prevent hardwood encroachment on pine forests. Elevation at the Jones Center ranges from 30 m to 70 m and the topography is relatively flat. The mean summer temperature at the Jones Center is 27°C and precipitation averages 132 cm/year (Conner et al., 2016).

In 2003, the Jones Center built four 40 ha mammalian predator exclosures. We conducted our experiment in two of the exclosures. The exclosures have been actively maintained to reduce use by the terrestrial predators of fox squirrel including coyote, *Canis latrans*, bobcat, *Lynx rufus*, grey fox, *Urocyon cinereoargenteus*, and red fox, *Vulpes vulpes*. The exclosures also reduce use by raccoon, *Procyon lotor*, Virginia opossum, *Didelphis virginiana*, and striped skunk, *Mephitis mephitis*, while permitting access to white-tailed deer, *Odocoileus virginianus* (Conner et al., 2010, 2016). The exclosures do not inhibit use by aerial predators of fox squirrels, including the red-tailed hawk, *Buteo jamaicensis*. Each experimental exclosure has a 1.22 m tall woven wire fence and an electrified wire running along the top, middle and bottom of the fence (Conner et al., 2016). Small animals, including fox squirrels, are able to enter and exit the exclosures through gaps in the wire fence. Each exclosure is paired with a nearby 40 ha control site that does not alter terrestrial predator use. All exclosure and control sites experienced a prescribed fire during the first week of March 2017, prior to the start of our study.

Giving-up Densities

We measured antipredator behaviours in fox squirrels using a giving-up density (GUD) methodology (Brown, 1988). This approach uses patches with a consistent amount of food thoroughly mixed within an inedible matrix, such that, as the patch depletes, additional foraging becomes more difficult. The GUD reflects the point at which the benefit of additional foraging becomes less than a foraging animal's perceived risk (Brown, 1988; Brown & Kotler, 2004).

We selected foraging sites for our GUD experiment in two of the predator exclosures (treatment) and two control areas with ambient levels of terrestrial predators (control) in areas with longleaf pine-dominated canopy and a wiregrass-dominated or open understory (Perkins & Conner, 2004). Starting in April 2017, we prebaited areas where we found signs of recent fox squirrel activity with four to five whole pecans placed on an overturned 3.8-litre round (27.9 × 10.2 cm), rubber tray (Fortiflex Inc., Durango, Puerto Rico) approximately 1 m from the base of a tree. These trays would eventually become our GUD patches. We also mounted a remote camera (UWAY Model VH400 or Model SR1; UWAY Outdoors Canada, Lethbridge, AB, Canada; or Bushnell Trophy Cam Model 119436c; Bushnell Outdoor Products, Overland Park, KS, U.S.A.) at each tray. We visited each tray every 1–3 days to restock

bait and check cameras. Once squirrels appeared at a tray on consecutive days, we created transects by adding two more trays at an increasing distance from the base tree (Thorson et al., 1998). We created transects between two trees that were a minimum of 10 m apart, and placed tray 1 1 m from a tree, tray 2 one-fourth of the distance between the two trees, and tray 3 at the midpoint between the two trees. Tray 2 ranged from 2.5 m to 5.0 m from the tree, and tray 3 ranged from 5.0 m to 10.0 m from the tree. We only created transects in locations where no other tree occurred within a radius of the distance between the tray and the base tree.

Once we established transects, we created GUDs by mixing 5.0 g pieces of crushed pecan with 3 litres of fine sand, harvested from the local environment and sifted to remove debris. We dried the pecans at 70 °C for 24 h before weighing them for GUD deployment. We fastened six pieces of 20-gauge aluminium wire in a grid pattern across the top of each tray, which permitted squirrels access to the tray but limited their ability to dig out large amounts of sand (Shrader, Brown, Kerley, & Kotler, 2008). Between 25 May and 7 July 2017 we collected GUD data from 15 transects ($N_{\text{Treatment}} = 9$, $N_{\text{Control}} = 6$). Midway through the sampling period we moved each transect to a nearby tree, approximately 20–50 m away, to capture greater variability in vegetation structure. All transects within 100 m were defined as a transect block (Bowers, Jefferson, & Kuebler, 1993). We had nine transect blocks ($N_{\text{Treatment}} = 6$, $N_{\text{Control}} = 3$).

We visited transects every morning within 2 h after sunrise to open and provision trays and revisited them every evening within 2 h before sunset to sift out the remaining pecans. We dried the remaining pecans for 24 h at 70 °C before weighing each sample. The remaining weight was the GUD. Any patch that was not foraged by a fox squirrel was assumed to have a GUD of 5.0 g (Darracq, Conner, Brown, & McCleery, 2016). For our analysis, we only included data from GUDs where a fox squirrel was the final animal to forage at the patch (Brown, 1988). All methods were approved by the University of Florida Institutional Animal Care and Use Committee (IACUC no. 201709906).

Environmental Variables

At every patch, we measured structural variables that we believed served as ceiling cover and/or wall cover, or that affected sightlines (Embar et al., 2011; Wywiałowski, 1987). For ceiling cover, we measured overhead canopy closure (Ceiling) using a convex spherical densiometer (Little, Streich, Chamberlain, Mike Conner, & Warren, 2014). We used a Robel pole to measure visual obstruction, which we used as our explanatory variable for wall cover (Wall_Cover). We divided the Robel pole into decimetre segments, each labelled with an integer, with 1 being the lowest possible value (Robel, Briggs, Dayton, & Hulbert, 1970). We viewed the pole from 5 m away at 1 m height in all cardinal directions (Little et al., 2014; Robel et al., 1970) and recorded the lowest visible segment. We used the mean value from all four directions as our measurement of wall cover. We also recorded the distance (Dist) from the GUD patch to the tree where the transect started (Thorson et al., 1998).

Statistical Analysis

We used an information-theoretic approach to determine the effects of excluding terrestrial predators (Treatment), distance (Dist), ceiling cover (Ceiling) and wall cover (Wall_Cover), on GUD. We first tested for the effect of Dist and Treatment on GUD to determine whether there were differences in GUD based on our study design. Once we could confirm that there were no differences due to treatment or distance, we combined all of our GUD data to

identify the structural variables that were responsible for differences in GUD. Based on our hypotheses, we generated a total of 13 a priori models and used the package 'lme4' (Bates, Maechler, Bolker, & Walker, 2015) to fit linear mixed models using the fixed effects Treatment, Dist, Ceiling and Wall_Cover. Our a priori models consisted of eight additive and five interactive models using our fixed effect variables. For comparison, we also included a global model, which contained all additive and interactive terms found in our candidate models, and a null model (Burnham & Anderson, 2002). For the GUD analysis, we included results from all GUD patches in a transect where at least one patch had been visited by a fox squirrel. We mean-centred all continuous response variables to reduce multicollinearity, which is a common source of error in interactive models (Enders & Tofighi, 2007). Each model contained transect block (Transect_Block) as a random effect to account for spatial autocorrelation. We evaluated our models using Akaike's information criteria for small sample size (AIC_c) and considered all models with $\Delta AIC_c \leq 2.0$ to be a top model. We did not consider any model with an AIC_c score that was greater than the AIC_c score of the null model to compete as a top model. We identified informative model terms by calculating the 95% confidence intervals (CI) and considered a term informative if the CI did not contain 0 (Arnold, 2010). For our top models, we displayed model parameters graphically to check for model fit. We used R v.3.5.0 (R Core Team, 2018) for all statistical analyses.

RESULTS

We had 243 useable GUD samples ($N_{\text{Treatment}}=144$, $N_{\text{Control}}=99$) for our analysis. The only top model was an interactive model containing an interaction between Ceiling and Wall_Cover (Table 1). Wall_Cover was positively correlated with GUD ($\beta = 0.19$, $SE = 0.17$, $CI = -0.16, 0.52$) but was not a strong predictor of fox squirrel GUD because the 95% confidence interval included 0. Both Ceiling ($\beta = -1.38$, $SE = 0.70$, $CI = -2.73, 0.01$) and the interaction term Wall_Cover:Ceiling ($\beta = -4.48$, $SE = 2.00$, $CI = -8.56, -0.40$) were negatively correlated with fox squirrel GUD, but only the 95% confidence interval for the interaction term did not contain 0. The interaction between Ceiling and Wall_Cover indicates that, in areas with a closed canopy, GUD decreased (less perceived risk) as wall

Table 1

Number of model parameters (K), Akaike information criteria adjusted for small sample size (AIC_c), ΔAIC_c and model weights (w) for all a priori models used to examine the relationship between fox squirrel giving-up density (GUD, g) and the variables Treatment (exclosure, control), Ceiling (canopy cover, %), Wall_Cover (mean horizontal visual obstruction, dm) and Dist (distance from nearest tree, m)

Model	K	AIC_c	ΔAIC_c	w
Ceiling*Wall_Cover	6	630.22	0	0.65
Ceiling	4	633.70	3.48	0.12
Null	3	633.80	3.58	0.11
Treatment	4	635.50	5.28	0.05
Wall_Cover+Ceiling	5	635.99	5.77	0.04
Wall_Cover	4	636.70	6.48	0.03
Treatment*Wall_Cover	6	639.64	9.42	0.01
Distance+Ceiling	5	640.93	10.71	<0.01
Dist+Wall_Cover	5	643.12	12.90	<0.01
Dist+Wall_Cover+Ceiling	6	643.19	12.97	<0.01
Dist*Ceiling	6	644.15	13.94	<0.01
Treatment+Dist+Wall_Cover+Ceiling	7	644.81	14.59	<0.01
Dist*Wall_Cover	6	648.47	18.25	<0.01
Treatment*Dist	6	648.71	18.49	<0.01
Global	12	655.00	24.78	<0.01

All models included Transect_Block (transect block) as a random effect to account for spatial autocorrelation. The null model contained no fixed effects, and the global model contained all additive and interactive terms used in the candidate models.

cover increased. When there was more open ceiling cover, GUD increased (perceived greater risk) as wall cover increased (Fig. 1).

DISCUSSION

Our results suggest that fox squirrels were simultaneously sensitive to vegetation structure along horizontal (ceiling) and vertical (wall) planes when determining the level of predation risk and the optimal antipredator behaviour. Fox squirrels differentially associated the effects of wall cover with perceived predation risk depending on the amount of ceiling cover. We believe this result was driven by differences in the reliability of indirect cues of risk for avian and terrestrial predators that used different hunting strategies, combined with the influence of vegetation structure on the effectiveness of vigilance.

Red-tailed hawks primarily hunt in open canopy areas (Preston, 1990), leading to higher avian predation risk in areas with little to no ceiling cover (open canopy) compared to areas with increased ceiling cover (closed canopy). However, the red-tailed hawk's sit-and-pursue hunting strategy creates reliable indirect cues of predation risk for fox squirrels (Preisser et al., 2012). Thus, in open canopy areas, little or no wall cover promotes open sightlines, which allow fox squirrels to effectively use vigilant behaviour to reduce avian predation risk and abandon a foraging patch at a lower GUD (Fig. 2a). Fox squirrels increased their GUD (decreased foraging) in open canopy areas when there was higher or denser wall cover. In these areas, avian predation risk remained high due to the open canopy, but the increased wall cover obstructed sightlines and hindered the use of vigilance in decreasing predation risk (Fig. 2b). The synergistic effect of open canopy and obstructed sightlines reduced the perceived benefit of foraging to less than the perceived risk of predation, leading to high GUD or complete avoidance of foraging in those areas (Brown, 1988).

For fox squirrels foraging in areas with a closed canopy, the risk of avian predation decreased, increasing the relative predation risk from terrestrial predators. Indirect cues of predation risk for active hunters are less reliable than for stationary predators (Preisser et al., 2012), which decreases the effectiveness of vigilance in reducing predation risk (Brown, 1999). Without reliable cues for terrestrial

predation risk, the amount of time a fox squirrel would need to spend with its head up and searching for predators to effectively reduce predation risk comes at too high of a missed opportunity cost of additional foraging (Preisser et al., 2012). When vigilance is ineffective, open sightlines do not reduce predation risk (Brown & Kotler, 2004; Embar et al., 2011), and increased wall cover instead reduces predation risk through concealment. Thus, in a closed canopy area, wall cover had the opposite effect on risk perception than in an open canopy area. In closed canopy areas without wall cover, using vigilance was less effective than abandoning a patch at a higher GUD (Fig. 2c). Fox squirrels had the lowest GUD in closed canopy areas with increased wall cover, where concealing vegetation decreased the risk of detection by terrestrial predators, and lost sightlines had little effect on GUD because vigilance was ineffective at reducing predation risk (Fig. 2d).

Differences in GUD between open and closed canopy areas relative to the amount of wall cover suggest that fox squirrels rely on vigilance and concealment differently, depending on the primary predation threat. Our results differ from previous studies that found antipredator behaviour of rodents in response to variable ground cover was not a function of overhead cover (Arenz & Leger, 1997; Embar et al., 2011). The antipredator behaviour response to ground cover reflects an animal's primary antipredator strategy for either vigilance or concealment (Arenz & Leger, 1997; Lima & Dill, 1990). However, we have shown that prey use concealment and vigilance under different environmental conditions to minimize hunting domain-dependent or hunting strategy-dependent predation risk.

We were surprised to find that fox squirrel risk perception did not differ between exclosures and controls. We expected that, by reducing one predation risk component, the overall predation risk would decrease, causing fox squirrels to perceive less risk inside the exclosures. Instead, our results suggest that the predation risk from avian predators, which were not excluded from our treatments, perpetuated the same level of fear in fox squirrels as in areas with both avian and terrestrial predators (Blumstein, 2006). Fox squirrels show a more intense antipredator response to avian predators than to terrestrial predators (McCleery, 2009), which indicates that avian predators pose greater risk of lethality to fox squirrels (Brown, 1999). If fox squirrels are primarily determining their overall predation risk based on indirect cues of avian predation risk, then excluding terrestrial predators would be unlikely to significantly change fox squirrel risk perception. Furthermore, unreliable cues for terrestrial predation risk may make differences in risk perception between terrestrial predator exclosures and controls imperceptible.

We acknowledge three alternative reasons for why we did not observe a difference in fear levels between the exclosures and control areas. First, fox squirrels may not have perceived a difference in terrestrial predator abundance within the predator exclosures. From radiotelemetry and observation data, we know that fox squirrels use habitat inside and outside of the exclosures, and may not differentiate between the two areas. Second, the added risk from snakes, which are increased in these exclosures (L.M. Conner, personal observations), may have offset the reduction in predation risk that resulted from decreasing mammalian predators. Lastly, fox squirrels may not alter their antipredator response based on terrestrial predators as the southeastern fox squirrel's diel cycle does not significantly overlap with activity cycles of terrestrial predators at the Jones Center. Fox squirrels are diurnal and exhibit peak activity in the mid–late morning (Moore, 1957; Weigl, Steele, Sherman, & Ha, 1989), avoiding the nocturnal and crepuscular hours when coyotes, bobcats and foxes are most active (Chamberlain, Leopold, & Conner, 2003; Deuel et al., 2017; Holzman, Conroy, & Picerking, 1992).

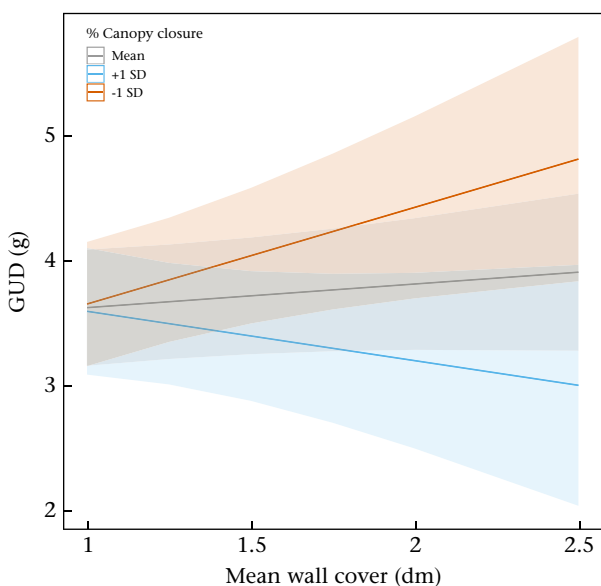


Figure 1. Predicted values with 95% confidence intervals (CIs) showing the relation between percentage of canopy cover (ceiling cover) and mean wall cover (vertical cover) on fox squirrel giving-up density (GUD). Mean canopy cover was $67.3 \pm 12.8\%$.

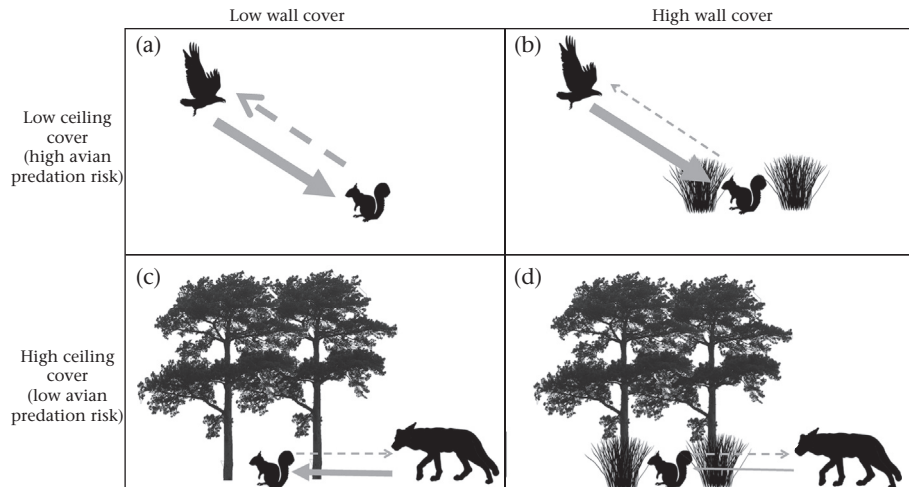


Figure 2. A conceptual diagram showing how interactions between ceiling (canopy) and wall (grass/shrub) cover influence fox squirrel antipredator behaviour. Solid lines indicate predation risk, with thicker lines representing greater risk. Dashed lines indicate sightlines, with thicker lines representing greater effectiveness of sightlines at reducing predation risk. In (a), open canopy areas with no wall cover are associated with high avian predation risk, but open sightlines allow fox squirrels to use vigilance to detect approaching avian predators. In (b), high wall cover in an area with an open canopy limits the fox squirrel's ability to detect approaching avian predators, leading to high perceived predation risk and high giving-up density (GUD). Avian predation risk is reduced in closed canopy areas, but unreliable cues for terrestrial predators make open sightlines (c) ineffective at reducing predation risk. Instead, closed canopy areas with high wall cover (d) reduce predation risk from all predators, resulting in low perceived predation risk and low GUD.

We did not find support for our prediction that greater distance to the nearest tree would increase fox squirrel risk perception. In the midwestern United States, fox squirrels increase their GUD 97% at a distance of 4–6 m from the base of a tree (Thorson et al., 1998). However, southeastern fox squirrels are larger than their midwestern counterparts (Koprowski, 1994) and may therefore perceive less predation risk farther from refuge, at least over the distances tested in the present study. Furthermore, fox squirrels may have been perceiving predation risk based on the relative amounts of ceiling and wall cover in their immediate surroundings rather than perceiving risk based on distance to refuge. This would explain why we did not observe the distance to nearest tree as having an influence on fox squirrel GUD.

We have shown that the role of vegetation structure in determining prey's perceived predation risk can change depending on the source, strength and plane of predation risk. Trade-offs between sightlines and protective cover have been studied previously (Arenz & Leger, 1997; Camp et al., 2012; Embar et al., 2011; Iribarren & Kotler, 2012a), but we believe we are the first to show that prey adjust the trade-off between protective cover and open sightlines depending on the vegetation structure along multiple spatial planes. Our results suggest that, in a heterogeneous landscape, prey can perceive different predation risks independently and optimize their foraging by using vigilance or concealment depending on environmental cues. Most prey animals must identify and respond to predation risk in a multipredator system (Preisser et al., 2012), so interactions between multiple environmental cues are likely to have synergistic effects on prey risk perception. Identifying such interactions could have implications for habitat management as well as furthering current understanding of the role of environmental cues in determining prey's antipredator behaviour, resource selection and habitat requirements.

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