



Effect of Downed Woody Debris on Small Mammal Anti-Predator Behavior

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Received: June 22, 2011

Initial acceptance: September 15, 2011

Final acceptance: September 24, 2011

(S. Foster)

doi: 10.1111/j.1439-0310.2011.01978.x

Abstract

Anti-predator behavior can affect prey growth, reproduction, survival, and generate emergent effects in food webs. Small mammals often lower the cost of predation by altering their behavior in response to shrubs, but the importance of other microhabitat features, such as downed woody debris, for anti-predator behavior is unknown. We used giving-up densities to quantify the degree to which downed woody debris alters perceived predation risk by small mammals in southeastern pine forests. We placed 14 foraging trays next to large downed woody debris, shrubs, and in open areas for 12 consecutive nights. Moon illumination, a common indicator of predation risk, led to a similar reduction in small mammal foraging in all three microhabitats (open, downed woody debris, and shrub). Small mammals perceived open microhabitats as riskier than shrub microhabitats, with downed woody debris habitats perceived as being of intermediate risk between shrub and open microhabitats. Despite the presumed benefits of the protective cover of downed woody debris, small mammals may perceive downed woody debris as a relatively risky foraging site in southeastern pine forests where the high diversity and abundance of rodent-eating snakes may provide a primary predatory threat.

Introduction

The threat of predation is often the largest cost associated with foraging (Brown & Kotler 2004; Preisser et al. 2005; Creel & Christianson 2008). Foragers primarily assess the threat of predation based on indirect cues of risk, such as microhabitat features and environmental conditions (Orrock et al. 2004; Verdolin 2006). For example, small mammals often respond to the threat of predation by biasing their foraging activity to areas of shrub cover and by increasing foraging on rainy, overcast nights (Brown & Kotler 2004; Verdolin 2006). Although it is well known that small mammals lower the cost of predation by altering their behavior in response to shrubs (e.g., Brown & Kotler 2004; Orrock et al. 2004; Matos & Orrock 2010), much less is known about how

other microhabitat features (e.g., rocks and downed woody debris) alter the anti-predator behavior of small mammals in the field (but see Wywiałowski 1987 for a lab-based study of habitat structure). Understanding how microhabitat features affect anti-predator behavior is important not only for understanding one of the primary costs for foraging small mammals, but also because forest management practices can have significant effects on the composition of microhabitat features.

Downed woody debris is an important microhabitat feature for numerous species of terrestrial animals, including small mammals (Loeb 1996). Small mammals use cavities in downed woody debris as daytime refuges (McCay 2000; Hinkelman & Loeb 2007) and the surface of downed woody debris as travel routes (Barnum et al. 1992; Planz & Kirkland

1992; McMillan & Kaufman 1995; McCay 2000; Zollner & Crane 2003), but it is unknown whether small mammals perceive downed woody debris as low-risk foraging sites. Understanding the behavioral implications of downed woody debris is important because small mammal foraging influences seedling establishment (Ostfeld et al. 1997; Schnurr et al. 2004), insect outbreaks (Jones et al. 1998), songbird nesting success (Schmidt et al. 2001), and biological invasions (Orrock et al. 2008). Despite the importance of small mammal foraging for forest ecosystems and the dramatic changes in downed woody debris often caused by forest management (McMinn & Hardt 1996; Duvall & Grigal 1999), the role of downed woody debris in affecting the risk perceived by foraging small mammals has not been examined.

We quantified how downed woody debris alters perceived predation risk by using foraging trays (Brown 1988) to assess small mammal foraging behavior in a field setting. Our approach explicitly compared the value of downed woody debris relative to other common foraging environments experienced by woodland small mammals, that is, protected foraging microhabitats below shrubs and exposed foraging microhabitats without any protective cover. We predicted that the protective cover of downed woody debris and shrubs would result in small mammals exhibiting less risk-averse foraging behavior in trays next to downed woody debris and beneath shrubs than trays in the open. We also predicted that there would be a microhabitat-by-moonlight interaction. In particular, we expected that the difference between use of trays associated with cover (downed woody debris and shrubs) and open trays should be greatest on bright nights when the threat of predation is the strongest (Kotler et al. 1991; Longland & Price 1991; Orrock et al. 2004).

Methods

The study was conducted on the Savannah River Site (SRS), a 78 000-ha National Environmental Research Park in South Carolina, from September 10 to 21, 2003, in three 9.3-ha plots situated in 50-yr-old *Pinus taeda* stands. The SRS is located in the upper coastal plain and Sandhills physiographic regions where soils are sandy and well drained (Workman & McLeod 1990). *Pinus taeda* was the dominant overstory species, but *Quercus* spp., *Carya* spp., *Liquidambar styraciflua*, and *Morella cerifera* were found throughout the plots in the overstory and midstory. Numerically dominant understory species included *Toxicodendron pubescens*, *Anthemis cotula*, and

Lespedeza spp. In August 2001, trees were felled to increase downed woody debris volumes; felling trees yielded open stands with well-developed understory vegetation and abundant downed woody debris in an early stage of decay. Downed woody debris volumes in these stands ($\sim 55 \text{ m}^3/\text{ha}$) were approximately three times greater than those found in natural pine stands in South Carolina and Georgia and 8–12 times greater than volumes found in pine plantations (McMinn & Hardt 1996).

We used giving-up densities as a measure of the forager's perceived predation risk because the amount of food remaining in an artificial food patch after a foraging bout (i.e., giving-up density) reveals how a forager assesses the costs (e.g., predation risk) and benefits (e.g., harvest rate) of remaining in a patch (Brown & Kotler 2004). By placing patches with the same properties (e.g., food density, substrate volume) in different microhabitats, the differences in giving-up densities among patches can be attributed to differences in predation risk associated with microhabitat (e.g., shrub and downed woody debris) rather than other costs of foraging (Brown 1988). Similarly, by collecting giving-up densities from the same microhabitat over time, the differences in giving-up densities can be attributed to environmental conditions, such as moonlight (Brown & Kotler 2004; Orrock et al. 2004; Mattos & Orrock 2010) and temperature (Meyer & Valone 1999; Kilpatrick 2003; Orrock 2009).

Fourteen experimental foraging stations were established in the three study plots with stations separated by at least 40 m. Each station consisted of three foraging trays with one tray placed next to each of the three microhabitats (open, downed woody debris, and shrub). We placed trays no more than 5 m apart within a station to minimize differences in metabolic costs (e.g., temperature effects) and missed opportunity costs (e.g., encounters with potential mates) between trays. We placed foraging trays next to large pieces of downed woody debris ($>10 \text{ cm}$ diam.) in an early stage of decay, which was the most abundant type of downed woody debris on the plots. Because of the abundance of downed woody debris in the study plots, there were numerous sites where all three microhabitats were in close proximity.

Foraging trays were plastic storage containers ($11 \times 27 \times 27 \text{ cm}$) with 4-cm diameter holes in adjacent sides and contained 3 g of millet seed thoroughly mixed into 1 l of sand. These trays have been successfully used to quantify rodent anti-predator behavior in previous studies in this area (Orrock

& Danielson 2004; Orrock et al. 2004). Foraging trays were accessible 24 hr/d, but a cover was used to exclude avian granivores from the patches. The cover also excluded rain, but only trace amounts of precipitation fell during the course of the study. We established 14 foraging stations, but ants were repeatedly found in six of the stations. Although changes in rodent behavior caused by ants are of general interest (Orrock et al. 2004), we omitted stations with ants from our analyses because we lacked the statistical power to resolve potential ant effects. Our approach maximized the power to resolve the role of microhabitat, which was our primary research goal. We measured giving-up densities from the remaining eight stations for 6–12 consecutive nights; this duration of data collection is consistent with other studies of small mammal foraging (Morgan & Brown 1996; Davidson & Morris 2001; Schmidt & Ostfeld 2003; Orrock & Danielson 2004; Orrock 2009).

Each morning, the remaining seeds were sifted from the sand and signs of small mammal foraging (i.e., tracks, tail drags, and feces) were noted. Seed samples were cleaned of debris, dried at 60°C for 5 h, and then weighed. The 1st d of data collection for each station ranged from September 10 to 16, 2003, because we started collecting giving-up densities only after observing signs of small mammal foraging in at least one tray at a station for three consecutive days to allow animals to acclimate to foraging in the food patches (Gutman & Dayan 2005). Cotton mice (*Peromyscus gossypinus*) represent approximately 80% of terrestrial small mammals captured in pine forests at the SRS (Loeb et al. 2001); live-trapping data collected after our study affirm that species on our study plots were almost exclusively cotton mice (see Results).

We analyzed the perceived predation risk (response variable: giving-up density) with a linear mixed model with a normal error distribution (PROC MIXED in SAS, Cary, NC, USA). We used the arcsine square-root transformation of the giving-up density (proportion of seeds remaining) to meet the assumption of normality in the linear mixed model. Microhabitat was treated as a fixed effect, and the fraction of the moon illuminated was a covariate. We treated the foraging tray as the subject of repeated measures, used compound symmetry to model the covariance structure, and estimated the denominator degrees of freedom with the Satterthwaite approximation. We obtained data on the proportion of the moon that was illuminated each night from the US Naval Observatory in Washington, DC.

Results

We collected 204 foraging observations from eight foraging stations over 12 nights; on an average, 8.5 nights of foraging observations were obtained from each station (three patches/station over 68 station-nights). Small mammal trapping was conducted on these plots from September 24 to 30 (i.e., 3 d after the end of foraging experiment). Eighteen individuals were captured during trapping; 17 were cotton mice (S.C. Loeb, unpubl. data).

The proportion of seeds remaining in a tray, a measure of giving-up density, was significantly affected by microhabitat ($F_{1,21.1} = 4.65$, $p = 0.021$) and the amount of moonlight ($F_{1,11.7} = 9.65$, $p = 0.009$); because there was no interaction between moonlight and microhabitat ($p > 0.15$), we did not include this interaction in our final model. We measured significantly lower giving-up densities (i.e., fewer seeds remaining) from trays on nights with less moonlight (Fig. 1a) and significantly lower giving-up densities from shrub trays (mean proportion seeds remaining = 0.81) than open trays ($\bar{x} = 0.87$; $t = 3.04$, $df = 21.1$, $p = 0.006$; Fig. 1b). There was no significant difference in giving-up densities from downed woody debris patches ($\bar{x} = 0.84$) compared with either open ($t = -1.28$, $df = 21.1$, $p = 0.214$) or shrub patches ($t = 1.76$, $df = 21.1$, $p = 0.094$).

Discussion

Changes in foraging activity are a fundamental component of anti-predator behavior. Our work suggests that downed woody debris, a key feature of temperate forest understories, is not perceived by cotton mice as a refuge from predation relative to sheltered microhabitats below shrubs. Rather, downed woody debris is perceived as an area of intermediate risk that is not significantly different from open or shrub microhabitats. In addition to supporting previous findings that rodent foraging is greater on nights with little moon illumination (Wolfe & Summerlin 1989; Orrock et al. 2004; Kotler et al. 2010) and that rodent foraging is greater in shrub microhabitats (Morris & Davidson 2000; Brown & Kotler 2004; Orrock et al. 2004; Verdolin 2006), our work illustrates that downed woody debris is not a low-risk foraging area for cotton mice.

Our finding that cotton mice did not exhibit greater foraging near downed woody debris appears counterintuitive based on the known importance of downed woody debris as a refuge site for cotton

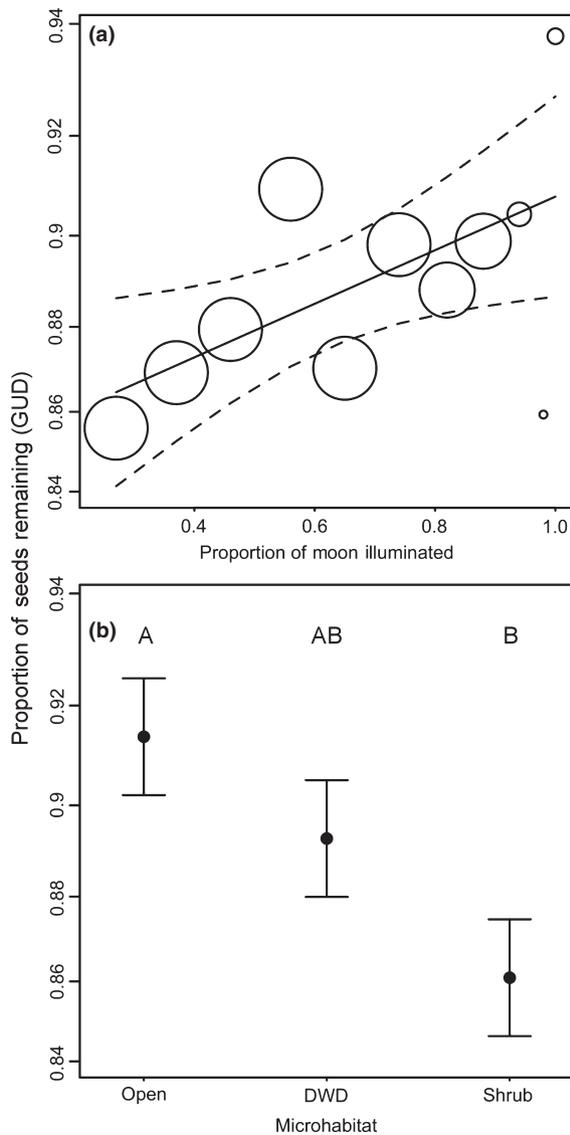


Fig. 1: Effect of moon illumination and microhabitat on giving-up densities for foraging trays visited by nocturnal small mammals in a southeastern pine forest. (a) Mean giving-up density as a function of the proportion of the moon illuminated. Size of circle represents the number of observations with the same moonlight measurement. For illustration purposes, we fitted a weighted least squares regression ($t = 2.66$, $df = 9$, $p = 0.026$, $R^2 = 0.38$; solid line) with 95% confidence intervals (dashed lines). (b) Mean giving-up density as a function of microhabitat. Error bars represent standard error of the mean. Different letters indicate significant differences in the least squares means from the mixed-model analysis. In both panels, the y-axis was scaled to present results obtained on the transformed scale in terms of the proportion of seeds remaining.

mice (McCay 2000; Hinkelman & Loeb 2007) and evidence that traveling along downed woody debris may limit detection of rodents by auditory predators (Fitzgerald & Wolff 1988; Roche et al. 1999). How-

ever, our findings may reflect a greater predation risk posed by terrestrial predators, particularly snakes, near downed woody debris. For example, timber rattlesnakes (*Crotalus horridus*) use downed woody debris as ambush sites (Reinert et al. 1984). Because snake diversity and abundance is high in southeastern pine forests relative to other forest ecosystems (Gibbons & Dorcas 2005), small mammals may perceive downed woody debris as safe foraging sites in ecosystems where snakes are not the primary predatory threat. However, mammalian predators, such as the American marten (*Martes americana*), are also known to hunt near downed woody debris (Andruskiw et al. 2008). Thus, the hunting tactics and activity patterns (both daily and seasonal) of the main terrestrial predators in a habitat may alter whether small mammals perceive downed woody debris as safe or risky foraging sites. Downed woody debris may also attract ants (Hill et al. 2008; Todd et al. 2008), which can reduce foraging activity of small mammals (Orrock & Danielson 2004). We excluded the direct effect of ants on cotton mouse foraging by omitting stations with ants, but if cotton mice in southeastern pine forests have learned to associate downed woody debris with ants, particularly red-imported fire ants (*Solenopsis invicta*), then our findings might indicate an indirect effect of ants on foraging by cotton mice. In southeastern pine forests, where fire ants and snakes are both abundant, avoidance of ants by small mammals could reduce the success of snakes hunting near downed woody debris (i.e., behavioral resource depression, Charnov et al. 1976).

The amount of illumination from the moon provides an environmental context for shifts in predation risk in our study, a pattern that supports other studies of rodent foraging (Wolfe & Summerlin 1989; Orrock et al. 2004; Kotler et al. 2010). We expected that cotton mice would shift their foraging efforts away from open microhabitats to sheltered microhabitats (downed woody debris and shrubs) on bright nights, but our prediction was not supported. At least two potential explanations, which are not mutually exclusive, may account for this observation. First, our study did not include the darkest part of the lunar cycle (new moon–0% illuminated) when the threat of predation should be weakest and the difference between open and sheltered giving-up densities should be the smallest (Bowers 1988; Brown & Kotler 2004; Orrock et al. 2004). Second, although nights with little moon illumination may reduce detection of small mammals by predators, there may be differences in probability of escape

among microhabitats (Wywiałowski 1987; Schooley et al. 1996). Differences in detection would lead to an overall reduction in risk at all microhabitats during periods of low moonlight, but differences in escape probability could maintain the differences in giving-up densities among foraging environments if small mammals are more adept at escaping from predators when under a shrub or when near downed woody debris. Our work highlights that studies of risk-sensitive foraging may be particularly informative when coupled with studies that evaluate how escape probability affects foraging (e.g., Thorson et al. 1998), especially because the same habitat characteristics (e.g., downed woody debris) that affect the likelihood of a predator attack are also likely to affect the probability of prey escape once an attack is underway (Lima 1992; Caro 2005).

In addition to illustrating the role of downed woody debris in affecting anti-predator behavior, our findings highlight how management of downed woody debris requires consideration of the multiple contexts in which it is used by small mammals: downed woody debris plays an equivocal role in anti-predator behavior but serves as a refuge site (McCay 2000; Hinkelman & Loeb 2007) and provides familiar pathways for navigation and orientation (Joslin 1977; Barry & Francq 1980; Drickamer & Stuart 1984). Although invertebrates and fungi found in downed woody debris may provide a food source for small mammals (Loeb 1996, 1999), no studies have documented granivorous rodents using downed woody debris as a source of alternative, but valuable, food resources such as fungi.

Southeastern pine forests are characterized by the relative scarcity of forest floor structure, but the sites in our study contained experimentally increased volumes of downed woody debris. Future work should address how the abundance of downed woody debris, which is greatly affected by forest management practices (McMinn & Hardt 1996; Duvall & Grigal 1999), influences the value of downed woody debris as protective cover for foraging small mammals. Additionally, the importance of downed woody debris to small mammals not only depends on the context of use, but also the characteristics of downed woody debris (e.g., size, decay stage). In this study, we controlled for these characteristics by placing foraging trays next to large pieces of downed woody debris in an early stage of decay. Future work should explore how predation risk changes with downed woody debris size and decay stage because effective management of downed woody debris depends on understanding how the character-

istics of downed woody debris affect small mammals (Loeb 1996).

Acknowledgements

Funding was provided by the Department of Energy-Savannah River Operations Office through the USDA Forest Service Savannah River under Interagency Agreement DE-IA09-00SR22188 and the USDA Forest Service, Southern Research Station.

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