

# Fear on the move: predator hunting mode predicts variation in prey mortality and plasticity in prey spatial response

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## Summary

**1.** Ecologists have long searched for a framework of *a priori* species traits to help predict predator–prey interactions in food webs. Empirical evidence has shown that predator hunting mode and predator and prey habitat domain are useful traits for explaining predator–prey interactions. Yet, individual experiments have yet to replicate predator hunting mode, calling into question whether predator impacts can be attributed to hunting mode or merely species identity.

**2.** We tested the effects of spider predators with sit-and-wait, sit-and-pursue and active hunting modes on grasshopper habitat domain, activity and mortality in a grassland system. We replicated hunting mode by testing two spider predator species of each hunting mode on the same grasshopper prey species. We observed grasshoppers with and without each spider species in behavioural cages and measured their mortality rates, movements and habitat domains. We likewise measured the movements and habitat domains of spiders to characterize hunting modes.

**3.** We found that predator hunting mode explained grasshopper mortality and spider and grasshopper movement activity and habitat domain size. Sit-and-wait spider predators covered small distances over a narrow domain space and killed fewer grasshoppers than sit-and-pursue and active predators, which ranged farther distances across broader domains and killed more grasshoppers, respectively. Prey adjusted their activity levels and horizontal habitat domains in response to predator presence and hunting mode: sedentary sit-and-wait predators with narrow domains caused grasshoppers to reduce activity in the same-sized domain space; more mobile sit-and-pursue predators with broader domains caused prey to reduce their activity within a contracted horizontal (but not vertical) domain space; and highly mobile active spiders led grasshoppers to increase their activity across the same domain area. All predators impacted prey activity, and sit-and-pursue predators generated strong effects on domain size.

**4.** This study demonstrates the validity of utilizing hunting mode and habitat domain for predicting predator–prey interactions. Results also highlight the importance of accounting for flexibility in prey movement ranges as an anti-predator response rather than treating the domain as a static attribute.

**Key-words:** food web, grasshopper, grassland, habitat domain, predator effects, predator–prey interaction, prey strategy, spider

## Introduction

An emerging priority in community ecology is to identify species traits that enable prediction of context dependency in predator–prey interactions and facilitate the incorporation of biotic interactions into models of food web dynamics and ecosystem functioning (Ings *et al.* 2009; Beckerman, Petchey & Morin 2010; Schmitz 2010).

Predator–prey interactions are typically classified into two main types: (i) consumptive interactions, in which predators kill and consume prey, and (ii) non-consumptive interactions, in which the threat of predation generates behavioural, morphological or physiological defence responses in prey (Schmitz 1998; Werner & Peacor 2003; Schmitz, Krivan & Ovadia 2004; Abrams 2008; Laundré, Hernandez & Ripple 2010). However, rather than operate as dichotomous alternatives, these mechanisms seem to operate in a graded manner that depends on two

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trait-based features of predators and prey: predator hunting mode and predator and prey habitat domains (Schmitz, Kaivan & Ovadia 2004; Schmitz 2005; Preisser, Orrock & Schmitz 2007; Woodcock & Heard 2011).

Predator hunting modes can be described by three main categories (McLaughlin 1989): (i) sit-and-wait or ambush, when a predator remains primarily motionless and attacks a prey only when it moves within immediate catching distance (e.g. egrets, horned lizards, praying mantis), (ii) sit-and-pursue, when a predator remains motionless until a prey moves within chasing distance (e.g. owls, tigers, wolf spiders), and (iii) active hunting, when a predator continuously moves through its environment to find, follow and chase down prey (e.g. kites, wolves, dragonfly adults). A species' hunting mode is complemented by its habitat domain, which can be either narrow or broad (Schmitz, Krivan & Ovadia 2004; Schmitz 2005) and differs from conventional ways of defining habitat use (e.g. microhabitat choice) in that it considers a species' use in terms of both microhabitat choice and the extent of spatial movement within the chosen microhabitat. Habitat domain can be quantified by measuring the vertical and horizontal spatial movement of prey and predator individuals during replicate daily activity cycles (Schmitz 2007).

Hunting mode can generate distinct consumptive and non-consumptive effects in prey. Less active predators (sit-and-wait and sit-and-pursue hunters) often evoke larger magnitudes of anti-predator response because their cues are more persistent in the local environment than more active predators (Schmitz 2007). The lasting influence of fear from less active predators has been observed to influence traits such as prey physiology and metabolism, growth, fecundity and density, thereby spanning from individual to population-level processes (Preisser, Orrock & Schmitz 2007; Creel, Winnie & Christianson 2009; Hawlena & Schmitz 2010a; Ramirez *et al.* 2010; Romero & Srivastava 2010). In contrast, more active predators can generate substantial shifts in prey activity levels, such as movement (Schmitz 2007). Less active predators thus tend to induce non-consumptive effects and largely have compensatory mortality effects on prey, whereas active predators tend to have consumptive effects that generate greater additive mortality on prey populations (Schmitz 2007).

The 'hunting mode-habitat domain' concept holds promise for conceptualizing and predicting predator-prey interactions in a variety of systems, including terrestrial (Barton & Schmitz 2009; Griffin *et al.* 2011; Romero & Koricheva 2011; Woodcock & Heard 2011), freshwater (Nilsson *et al.* 2008; Rehage, Dunlop & Loftus 2009; Yee 2010; Flynn & Moon 2011), marine (Gerald & Powers 2011) and across ecosystem boundaries (Wesner 2012). Although these studies examine multiple species of predators and prey, a specific kind of hunting mode or habitat domain is often only represented by a single predator species. This lack of replication of predator hunting mode or habitat domain leads to the appropriate criticism that

these studies cannot fully discount the hypothesis that one is observing a species identity, rather than a species trait, effect (Newman 2008).

We report here on an experimental study that addresses this problem. We examined how several species of sit-and-wait, sit-and-pursue and active hunting predator species interact with the same species of insect herbivore prey, thereby allowing an assessment of the trait-based, rather than species identity, effects on predator-prey interactions. Our work also advances the 'hunting mode-habitat domain' concept in two important ways. First, the original idea (Schmitz 2005) treats both hunting mode and habitat domain as static properties, when in nature these traits can be flexible and dependent on surrounding conditions (McLaughlin 1989). Indeed, hunting mode can depend on a variety of biotic and abiotic factors, including prey availability, habitat structure, time of day and temperature (Sih 2005; Barton & Schmitz 2009; Michel & Adams 2009). Yet, it remains uncertain whether this plasticity also exists for habitat domains (Tylianakis & Romo 2010). Our study reveals the graded responses displayed by prey species to predators with different movement activity within a hunting mode class, thereby offering quantitative insight into the trait-based effect. Secondly, the original 'hunting mode-habitat domain' concept (Schmitz 2005) assumes that the habitat domain of species is a fixed species attribute. We show here that prey species may exhibit plasticity in components of habitat domain that varies with the degree of predator hunting activity. Together, these insights provide a nuanced understanding of spatial predator-prey interactions that advances understanding of the evolutionary ecological interplay between predators and prey that drives food web dynamics.

## Materials and methods

### STUDY SYSTEM

Previous experimentation in our grassland system in north-eastern Connecticut, USA, motivated us to explore the idea of using hunting mode and habitat domain contingency to explain the different non-consumptive and consumptive effects of hunting spider predator species on grasshopper (*Melanoplus femurrubrum*) prey (Schmitz & Suttle 2001). In the system, grasshoppers utilize a broad habitat domain throughout the entire vertical canopy space. The sit-and-wait hunter *Pisaurina mira* generates the weakest consumptive predator effects on prey and causes the strongest non-consumptive anti-predator response – a refuge-seeking habitat shift by grasshoppers. The active hunter *Phidippus rimator* generates the strongest consumptive mortality effects and causes the weakest non-consumptive anti-predator responses. The sit-and-pursue predator *Hogna rabida* causes both refuge-seeking habitat shift and strong consumptive mortality. The predators avoid interspecific interactions with each other by segregating spatially in the vegetation canopy, with the sit-and-wait predator utilizing a narrow habitat domain in the upper vertical canopy, the sit-and-pursue predator residing across a broad domain in the mid-canopy and lower canopy and the active hunter dominating

a broad domain in the middle of the canopy (Schmitz & Suttle 2001; Barton & Schmitz 2009).

We expanded our evaluation of the hunting mode-habitat domain concept here by investigating the effects of six spider predators: sit-and-wait nursery web spiders *P. mira* and *Pisaurina brevipes*, sit-and-pursue slender crab spiders *Tibellus maritimus* and *Tibellus oblongus* and active jumping spiders *P. rimator* and *Phidippus audax*. The sit-and-pursue predators *T. maritimus* and *T. oblongus* were selected because they displayed intermediate levels of activity compared with the two other extreme hunting modes, exhibiting infrequent bursts of rapid motion. We expected *Tibellus* sit-and-wait predators to produce a combination of consumptive and non-consumptive effects on prey similar to the sit-and-wait *H. rabida* explored previously (Schmitz & Suttle 2001) and in essence serve as an 'intermediate' hunting mode to more effectively test a gradient of predator strategies and effects. Predator hunting mode in our species is clearly not phylogenetically independent. However, the natural history of our field sites and the broader landscape around the field sites precluded us from having a large enough regional pool of predator species to draw phylogenetically independent replicates that were also known to interact with the grasshopper prey in the study area. Moreover, distinctions between hunting modes in our study system are typically enabled by differences in predator morphology, which is phylogenetically linked. For example, the sit-and-wait predator genus *Pisaurina* is characterized by long, thin, brown-coloured abdomen and legs that enable the spiders to remain camouflaged when perched with their middle legs extended on plant stems and leaf axils until they ambush prey with an infrequent yet rapid flurry of movement; the sit-and-pursue genus *Tibellus* features thicker abdomen and legs, allowing them to pursue prey more frequently with vigorous bursts of activity; and active hunting predators have small and compact bodies with bulky legs that enable them to jump and move quickly and continuously. Therefore, for a given hunting mode, we selected species belonging to the same genus to standardize predator size, behaviour and location in the environment. This challenge represents the innate difficulty in field-based community ecology in teasing apart hunting mode effects from species identity effects, yet replicating within a taxonomic group, nonetheless, strengthens evidence for hunting mode effects by broadening the taxonomic level in focus. We excluded the previously used sit-and-pursue wolf spider predator *H. rabida* (Schmitz & Suttle 2001) because other species within the genus that were capable of subduing grasshopper prey were not obtainable in the field.

#### STUDY DESIGN

We experimentally evaluated the consumptive and non-consumptive effects emerging from grasshopper interactions with different predator species using behavioural observations in terraria. For two summers in July 2011 and 2012, we observed 2nd and 3rd instar grasshoppers and adults of each spider species in terraria placed on outdoor benches in a grass field and exposed to ambient light, temperature and moisture. Each terrarium consisted of a 30 × 50 cm rectangular plywood base enclosed by 50 cm (2011) or 75 cm (2012) tall fibreglass insect screen stapled to a wooden support beam attached to the base to prevent arthropods from escaping. Terraria size was based on previous field observations of spider movement (Schmitz & Suttle 2001) and designed small enough to observe spiders and grasshoppers yet

large enough for grasshoppers to escape predators using any natural tactic (e.g. crawling, hopping or flying). Terraria were filled with sod of natural grasses, and herbs cut from the same fields where grasshoppers and spiders reside naturally. Sod was cut to include natural growth distributions of grasses and herbs and feature one to three 40–50 cm high stalks of the dominant herb *Solidago rugosa*, which was previously identified as an important source of protective cover (Schmitz 2003) and nutrition (Hawlena & Schmitz 2010b) for grasshoppers under stress from spider predators. Vertical habitat structure was naturally divided into two habitat types: the lower half was dominated by grasses, short herbs and *S. rugosa* bare stalks and the upper half consisted of *S. rugosa* stalks and leaves. A grid was drawn on each side of the terraria to quantify spatial location and hence measure movement in three-dimensional space. A 4 × 3 grid of squares measuring 12.5 × 15 cm was used in 2011 and subsequently adapted to a 30 × 20 grid of squares measuring 2.5 × 2.5 cm in 2012 for finer-scale resolution of interaction. Results were scaled, analysed and compared in centimetres for consistency between years.

Terraria were stocked each with one spider and one grasshopper for spider treatments and with one grasshopper only (no predator) for a control. Spiders and grasshoppers were collected from the field 24–72 h prior to stocking, and new individuals were placed into the cages each day to obtain independent estimates. Spiders were starved for 24 h prior to release into terraria to ensure that individuals would hunt. Because arthropod prey responds strongly to predator chemical cues (Dicke & Grostal 2001), each cage was restricted to a single spider species to avoid confounding effects from multiple predators.

The horizontal and vertical positions of spiders and grasshoppers were recorded with respect to the observation grid. Spiders and grasshoppers were observed from 07:00 to 17:00, when most activity occurs (Schmitz & Suttle 2001), at 3-min intervals for 1–2 h sessions and 20-min intervals for the remaining observation period. These two time-scales enabled analysis of both fine- and broad-scale interactions between predators and prey. Spider and grasshopper individuals were stocked simultaneously the morning of observation and given 30 min to acclimate to the terrarium before observations began. If a spider succeeded in killing a grasshopper, we recorded the mortality event, and observations were concluded for the day.

Up to eight terraria were observed at a time for 9 days in 2011 and 22 days in 2012 during ambient temperatures and cloud cover; observations were stopped when rainfall was too heavy to observe individuals. One terrarium of each treatment and additional replicates were run each day depending on the spider species available from the field. In total, we observed grasshopper prey and spider predators in 22 control (no predator), 28 *P. mira*, 30 *P. brevipes*, 7 *T. oblongus*, 8 *T. maritimus*, 22 *P. rimator* and 16 *P. audax* treatment cages during 2011 and 2012 combined. Sample sizes of sit-and-pursue predators were low due to their natural rarity in the study area and the difficulty of catching these species.

#### DATA ANALYSIS

We characterized spider predator hunting mode by quantifying each spider species' activity and grasshopper consumption rates. Spider activity was calculated as the mean Euclidean distance moved between an individual's location at time  $t$  and  $t + 1$  at 20-min intervals observed through the day (2011 and 2012) and

3-min intervals observed during rapid observation sessions (2012). In 2011, due to the coarser cage grid, we measured the spider's two-dimensional horizontal and vertical distance moved in the field using a ruler aligned with the spider outside of the cage. For 2012 data, we calculated Euclidean distance moved based on fine-scale grid locations of spiders. Data from both years, analysed in cm, showed similar trends of activity by hunting mode; thus, we combined the data sets to generate a more robust sample size. Furthermore, *T. maritimus* was sampled only during 2011 and *T. oblongus* sampled only during 2012 due to field availability, making the combination of both year's data sets essential for comparing the two sit-and-pursue predators. Grasshopper kill rates were calculated as the number of grasshoppers killed per spider of each species during behavioural observations. Finally, we calculated the location of spider predators in the canopy by taking the median vertical and horizontal locations.

We tested for plasticity in grasshopper prey response to predator presence and hunting mode in two ways. First, we examined changes in domain size by examining the overall area of movement across predator treatments. Previous studies (Schmitz & Suttle 2001; Schmitz 2007) calculated habitat domain as the 95% confidence interval area around a mean location. However, in this study, we observed notable variation in the vertical locations of spider and grasshopper individuals within a single species or treatment, respectively, with some individuals remaining high and others low in the canopy. To avoid a skewed mean, we therefore calculated an individual's habitat domain centre as the median location and habitat domain size as the difference between the 3rd and 1st quartiles (box plot whiskers), or the middle 50% of locations, in the vertical and horizontal directions (Zar 1999). We analysed vertical and horizontal dimensions separately rather than multiplying to calculate domain area because some individuals periodically remained motionless in either direction, thus negating the value of an area. Furthermore, as predators segregate spatially in the vertical canopy in nature (Schmitz & Suttle 2001), we thus expected predators, and likely prey responses, to differ by hunting mode primarily in their vertical movements.

Secondly, we tested for plasticity in prey response by examining the mean distance moved by prey and predators per observation interval to determine how prey movement varied with predator hunting mode. To test prey response, we calculated mean Euclidean distance moved using fine-scale 2012 observation data for both spiders and grasshoppers. Because limited field availability prevented the use of *T. maritimus* in 2012, data for this sit-and-pursue predator were not available for this part of the analysis. Both habitat domain size and mean distance moved were based on data from 20-min observation intervals throughout the day to capture a broad temporal scale of activity. We obtained species averages by calculating the mean for all individuals in the species.

Understanding the mechanisms driving predator-prey spatial encounters requires a fine-scale grasp of which individual – predator or prey – drives interactions. We were particularly curious whether movement by predators in pursuit of prey or prey in avoidance of predators drove the spatial interaction between individuals. We investigated this question in two ways. First, we assessed the distance between prey and predators by hunting mode. Using 3-min observation interval data from 2012, we calculated the mean Euclidean distance between each grasshopper and its accompanying spider in a cage. We obtained species

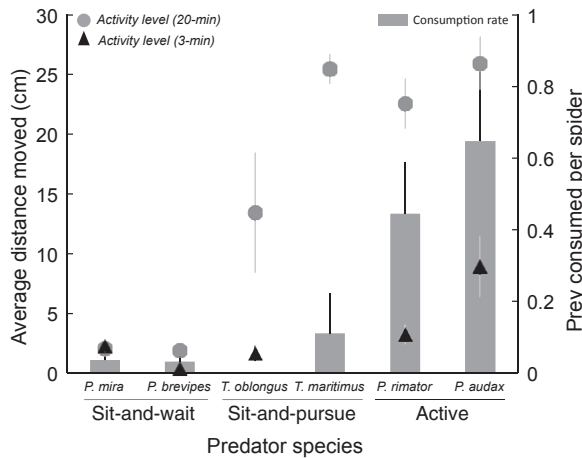
averages by calculating the mean for all individuals in the species. Secondly, we analysed the cross-correlation between the grasshopper or spider's movement at time  $t$  and the subsequent predator-prey distance at time  $t + 1$ . We examined data over an hour of sequential 3-min interval observations, because 1 h was the maximum time period for which we could continuously observe both grasshoppers and spiders in the cage during every observation interval. We recorded whether the cross-correlation coefficient was significant or insignificant and positive or negative and then tallied all records. Analysis was not possible for individuals that did not move during the observation period; these pairs were excluded from analysis. We calculated the proportion of grasshopper or spider individuals in each predator treatment that exhibited a significant correlation to procure a coarse indicator of whether spider or grasshopper movement most influenced the individuals' interactions.

We statistically tested for differences between predator hunting modes and effects on prey response by running one-way ANOVAs by hunting mode followed by *post hoc* Tukey's tests. We also tested for consistency in response between predator species within a hunting mode by running one-way ANOVAs by hunting mode with spider species as an interaction. Significance of cross-correlation was calculated as 95% confidence intervals. All analyses were run using the program R v.2.15.3 (The R Project for Statistical Computing, <http://www.r-project.org/>).

## Results

### CHARACTERIZING HUNTING MODES

As expected, more active hunting modes were characterized by increases in both spider activity level and grasshopper kill rate. An ANOVA by hunting mode revealed that hunting mode was a significant determinant of spider activity at the 20-min observation scale ( $F_{2,89} = 124.292$ ,  $P < 0.001$ ) but not the 3-min scale ( $F_{2,18} = 2.235$ ,  $P = 0.136$ ). At the 20-min observation scale, sit-and-wait predators rarely moved and covered short distances, moving an average of 1–2 cm between intervals, while active hunters roamed more continuously and extensively through the vegetation, covering 22–25 cm (Fig. 1). The sit-and-pursue predators, categorized as such because of their infrequent bursts of rapid movement, were less consistent between species, with *T. oblongus* moving on average 10 cm and *T. maritimus* 25 cm per interval. A Tukey's test indicated differences between sit-and-wait and sit-and-pursue as well as sit-and-wait and active predators (Tukey  $P < 0.001$ ), but no difference between sit-and-pursue and active predators ( $P = 0.411$ ). An ANOVA on hunting mode nested by species found differences between species activity levels with a hunting mode ( $F_{3,89} = 3.591$ ,  $P = 0.167$ ). In particular, the differences between sit-and-pursue predators *T. oblongus* and *T. maritimus*, the latter of which covered distances comparable with active hunters (Fig. 1), emphasize the nature of the sit-and-pursue hunting strategy as a mixture of sit-and-wait and active modes and the continuous gradient of hunting modes in general.

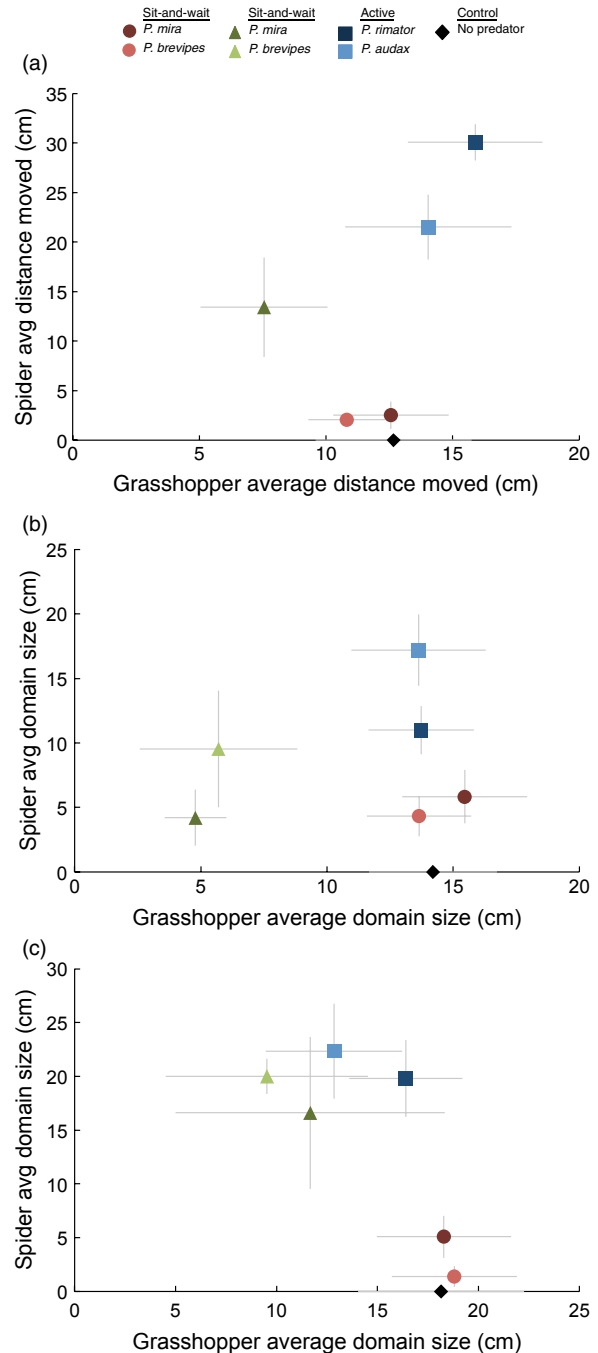


**Fig. 1.** Spider predator hunting modes characterized by activity level (primary y-axis; grey dots represent 20-min observations; black triangles represent 3-min observations) and consumption rate of grasshopper prey (secondary y-axis; grey bars). Bars represent standard error. Predator species are categorized as sit-and-wait, sit-and-pursue or active hunters as indicated beneath spider species names. Predator mortality effects strengthen with the activity level of the spider, increasing from sit-and-wait to active hunting predators. Activity level was significant by hunting mode at the 20-min ( $F_{2,89} = 124.292$ ,  $P < 0.001$ ) but not the 3-min observation scale ( $F_{2,18} = 2.235$ ,  $P = 0.136$ ), although both show an increasing trend from sit-and-wait to active predators.

Grasshopper mortality likewise increased with predator activity across hunting modes ( $F_{2,112} = 11.476$ ,  $P < 0.001$ ): kill rates were lowest for sit-and-wait predators, moderate for the sit-and-pursue predator *T. maritimus* and highest for active hunters (Fig. 1). A Tukey's test revealed significant differences in mortality rates between active hunters and sit-and-wait as well as sit-and-pursue predators ( $P < 0.001$  and  $P < 0.05$ , respectively) but not sit-and-wait and sit-and-pursue predators ( $P = 0.975$ ). The sit-and-pursue predator *T. oblongus* did not kill during formal behaviour observations but did kill and consume grasshoppers outside of the sampling period, indicating that the species was capable of capturing and subduing the grasshopper prey. An ANOVA by hunting mode with species as an interaction revealed consistency between species within each hunting mode ( $F_{3,112} = 0.563$ ,  $P = 0.641$ ).

Spider median location in the vegetation canopy did not spatially cluster by hunting mode in the vertical dimension as expected (Fig. S1, Supporting Information). Sit-and-wait and active predators positioned themselves widely through the canopy in terraria rather than favouring the upper and lower vertical strata, respectively. Sit-and-pursue predators limited themselves to the middle level of the vertical canopy.

Spider habitat domain size varied significantly across the gradient of hunting mode in both the horizontal ( $F_{2,108} = 8.691$ ,  $P < 0.001$ ; Fig. 2b) and vertical dimensions ( $F_{2,108} = 23.852$ ,  $P < 0.001$ ; Fig. 2c). Sit-and-wait spiders utilized narrow habitat domains, occupying a small fraction (<12%) of the available horizontal and vertical space, while



**Fig. 2.** Grasshopper prey and spider predator (a) average distance moved in 20-min observation intervals and (b) average horizontal domain size and (c) vertical domain size. Symbols represent predator treatments according to spider hunting mode; circles represent sit-and-wait predators *Pisaurina mira* (dark red) and *Pisaurina brevipes* (light red); triangles represent sit-and-pursue predators *Tibellus oblongus* (dark green) and *Tibellus maritimus* (light green); squares represent active predators *Phidippus rimator* (dark blue) and *Phidippus audax* (light blue); the black diamond represents the 'no-predator' control (spider domain size shown as 0). For colour distinctions, please refer to the electronic version of the article.

active predators roamed across broader habitat domains and utilized nearly 30% of the cage. This difference between sit-and-wait and active hunters remained consis-

tent across the horizontal and vertical dimensions of the canopy (Tukey  $P < 0.001$ ). Sit-and-pursue spiders exhibited a mixture of domain sizes depending on the dimension, moving widely along the vertical strata like an active predator (Tukey  $P = 0.827$ ) and unlike a sit-and-wait predator (Tukey  $P < 0.001$ ), but ranging across a more moderate domain in the horizontal direction that overlapped both sit-and-wait (Tukey  $P = 0.766$ ) and active hunters (Tukey  $P = 0.090$ ). Thus, with sit-and-pursue predators in the mix, spiders clustered into two functional hunting modes across the vertical dimension: more mobile predators that utilized a broad domain space and less mobile predators that utilized a narrow domain space. In the horizontal dimension, predators demonstrated a more continuous gradient of overlapping domain sizes. Spider species responses were consistent within hunting modes in both the horizontal ( $F_{3,108} = 1.772$ ,  $P = 0.157$ ) and vertical dimensions ( $F_{3,108} = 0.586$ ,  $P < 0.001$ ).

PREY RESPONSE

Grasshopper prey changed their activity levels significantly in the presence of predators, moving less with sedentary predators and more with active predators (Fig. 2a). Activity shifts were apparent at the 20-min observation scale ( $F_{3,49} = 7.869$ ,  $P < 0.001$ ), where they were also consistent between species within hunting modes ( $F_{2,49} = 0.125$ ,  $P = 0.883$ ), but not at the 3-min scale ( $F_{3,25} = 1.440$ ,  $P = 0.255$ ). Tukey's tests at the 20-min scale revealed significance between treatments with and without predators ( $P < 0.01$ ) but not between hunting modes ( $P > 0.05$ ), although weak trends in average movement are visible (Fig. 2a). Grasshoppers covered larger distances per 20-min interval (14–16 cm) in the presence of active hunters than they did without predators (13 cm; Fig. 2a). Grasshoppers moved slightly shorter distances (11–13 cm) in response to sit-and-wait predators and showed notably less movement (8 cm) with sit-and-pursue predators.

Grasshopper prey adjusted the size of their habitat domain by hunting mode in the horizontal ( $F_{3,129} = 2.628$ ,  $P = 0.053$ ; Fig. 2b) but not vertical dimension ( $F_{3,129} = 1.110$ ,  $P = 0.348$ ; Fig. 2c). Grasshoppers utilized large horizontal domains (14–15 cm) without predators and with sit-and-wait and active predators and covered smaller areas (5–6 cm) in the presence of sit-and-pursue predators. Horizontal domains differed significantly between sit-and-wait and sit-and-pursue ( $P = 0.035$ ) and marginally significantly between sit-and-pursue and active hunters ( $P = 0.079$ ), and species effects were consistent within hunting modes ( $F_{3,129} = 0.131$ ,  $P = 0.942$ ). Grasshopper domains with predators did not differ in size from the no predator control treatment ( $P > 0.05$ ), although sit-and-wait predator effects were weakly insignificant ( $P = 0.101$ ). Prey domain size was not significant by hunting mode in the vertical dimension. Grasshoppers occupied the largest domains (18–19 cm) without a preda-

tor or in the presence of sit-and-wait spiders, covered moderately sized domains (13–16 cm) with active hunters and moved within the narrowest domains (10–12 cm) when situated with sit-and-pursue predators.

In examining fine-scale interactions between grasshoppers and spiders, we found that the distance between prey and predator was not significantly different between hunting modes ( $F_{2,18} = 1.587$ ,  $P = 0.232$ ; Fig. 3). Cross-correlation analysis revealed significant correlations between predator–prey distance and grasshopper movement in the *P. brevipes* and *P. rimator* treatments and spider movement for the *P. mira* treatment; all other treatments had no significant effect (Tables S1 and S2, Supporting Information). Overall, 25% of grasshopper ( $n = 20$ ) and only 8% of spider ( $n = 12$ ) cross-correlations were significant, indicating that predator–prey distance was more strongly controlled by grasshopper movement than spider movement. Results did not vary by hunting mode.

Discussion

We tested the utility of the 'hunting mode-habitat domain' concept to explain contingent consumptive and non-consumptive mechanisms of predator effects on prey by replicating predator hunting mode and examining effects on the behaviour and mortality of the same prey species. We specifically assessed effects along a gradient of predator activity ranging from sit-and-wait ambush to sit-and-pursue to actively coursing hunting spider predators.

As expected, the sit-and-wait predators *P. mira* and *P. brevipes* infrequently moved, the sit-and-pursue *T. ob-*

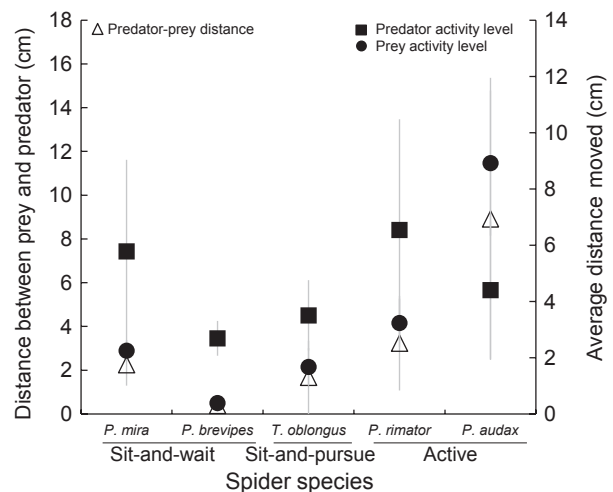


Fig. 3. Average distance between grasshopper prey and its spider predator per 3-min observation interval by predator treatment (primary y-axis; open triangles) vs. activity levels (secondary y-axis) shown as the average distance moved by prey (filled squares) and predators (filled circles). Predator species are categorized as sit-and-wait, sit-and-pursue or active hunters as indicated beneath spider species names. Bars represent standard error. Prey–predator distance is insignificant by hunting mode yet parallels trends in predator but not prey activity.

*longus* and *T. maritimus* occasionally moved longer distances and the active hunting *P. rimator* and *P. audax* roamed constantly across the farthest distances (Fig. 1). Grasshopper mortality rate due to predator consumptive effects increased with hunting mode activity, reflecting the potentially higher metabolic demands of more mobile predators (Fig. 1). Sit-and-pursue kill rates were intermediate to sit-and-wait and actively hunting predators, consistent with previous observations of the sit-and-pursue wolf spider *H. rabida* (Schmitz & Suttle 2001).

Predators similarly differed in habitat domain size. Sit-and-wait predators used substantially narrower domains than the broad domains of active hunters, which were 3–4 times larger in both the horizontal and vertical dimensions (Fig. 2). The sit-and-pursue predator *T. oblongus* utilized a combination of these two movement strategies by covering a narrow horizontal and broad vertical area. These differences in activity level and habitat domain size aptly reflect distinctions between hunting mode characteristics: sit-and-wait predators attack only when prey are very close, sit-and-pursue predators chase prey when they are nearby and active hunters roam to locate and run down prey.

Prior to interacting with a predator, grasshoppers were moderately mobile across broad horizontal and vertical habitat domains (Fig. 2). In the presence of predators, grasshoppers reduced their activity levels with less mobile predators and increased their movement with more active predators (Fig. 2a). While changes in vertical domain size with predators were not statistically significant (Fig. 2c), domain sizes did significantly differ by hunting mode in the horizontal domain (Fig. 2b). Grasshoppers reacted strongly in the horizontal canopy to sit-and-pursue predators, reducing the size of their domains as much as 50–60% (Fig. 2b) and moving smaller distances (Fig. 2a). Active predators increased prey movement but did not substantially impact domain size; this result supports the previous finding that cues from sit-and-pursue predators decrease activity more than cues from active predators (Preisser, Orrock & Schmitz 2007). The fact that sit-and-wait predators did not evoke a response in prey habitat domain echoes the general understanding that these stationary predators generate the greatest non-consumptive effects on prey life history (e.g. fecundity, growth and density) but do not strongly impact activity (Preisser, Orrock & Schmitz 2007; Schmitz 2007).

The disparity between low prey movements with less mobile sit-and-wait and sit-and-pursue predators and larger movements with active predators resembles the spider hunting mode characteristics themselves and indicates that grasshoppers adjust their activity levels relative to spider activity patterns. Furthermore, the sit-and-wait hunting ‘ambush-when-near’ strategy is aimed at catching highly mobile prey, whereas the more active hunting ‘find-and-destroy’ strategies target sedentary prey (Huey & Pianka 1981). The prey response of decreasing activity with sit-and-wait predators and increasing activity with active

hunters could reflect a prey anti-predation strategy tuned to different encounter rates and risk imposed by predators with different hunting modes. Likewise, the strategy of narrowing a prey’s area of movement in the presence of widely roaming sit-and-pursue predators points to a reactionary mechanism to focus movement within an area of greater structural protection from an attack and could reduce the probability of a spatial encounter and thus potentially improve prey survivorship.

The distance between grasshoppers and spiders simultaneously offers insight and raises deeper questions about the fine-scale mechanisms behind predator–prey interactions. Our ability to interpret these distances is constrained by the feedback that defines the hunt; whether predator chasing prey or prey escaping predator, it is challenging to determine from behaviour alone which individual most ‘controls’ an encounter. Yet, considering the restricted movement of sit-and-wait predators, it seems logical to deduce that grasshoppers willingly remained closest to these predators (Fig. 3). This is particularly interesting in the light of the strong non-consumptive stress effects that sit-and-wait spider can have on grasshoppers (Hawlena & Schmitz 2010a,b) and suggests that grasshoppers, at least in terraria, may prefer to follow the anti-predation strategy of ‘keeping one’s predators close’ to avoid consumption. The fact that the distance between prey and predators increases linearly with spider activity and grasshopper mortality rates makes it impossible to tease apart these predator characteristics as drivers of anti-predator distances. Larger distances between grasshoppers and sit-and-pursue and active predators (excluding *P. audax*) suggest that grasshoppers may alternatively respond to diffuse predator chemical or aromatic cues (Dicke & Grostal 2001; Eiben & Persons 2007; Casas, Steinmann & Dangles 2008) and that widely roaming, frequently moving predators may prompt prey to maintain more cautionary distances with respect to predator locations. Combined with the low success rate we observed during spider attacks on prey, these results provide rudimentary evidence that grasshoppers may command greater ‘control’ in interactions with predators. This finding is further supported by our fine-scale cross-correlation analysis of predator–prey distance, which suggests that grasshopper movement is more often significantly correlated with this distance than is spider movement. We recognize, however, that predator–prey interactions are complex and require a more detailed analysis of temporal and spatial feedbacks to properly understand. In addition, the active hunter *P. audax*, which demonstrates the highest levels of activity and mortality, shows a dampened distance response in grasshoppers, further highlighting the complicated nature of the question.

Because our study treatments featured single predators, spiders did not spatially segregate by hunting mode into distinct zones within the vertical canopy as they do when they coexist with other predators to reduce intraguild

interactions (Schmitz & Suttle 2001; Barton & Schmitz 2009). This enabled spiders to more freely pursue prey across the entire vertical canopy. Nevertheless, the sit-and-wait, sit-and-pursue and active hunting predators in our study still utilized narrow, moderate and broad habitat domains, respectively, consistent with previous studies (Schmitz & Suttle 2001; Schmitz 2005; Preisser, Orrock & Schmitz 2007; Barton & Schmitz 2009). The fact that grasshopper prey in our study responded to hunting mode despite the lack of distinct predator spatial segregation indicates that prey could be responding to predator presence cues other than, or in addition to, visual location. Many arthropod prey sense predator presence more strongly from chemical cues than visual or vibratory signs (Eiben & Persons 2007), and grasshoppers in our study may have used spider chemical cues to guide their anti-predation response.

This study demonstrates the validity in utilizing hunting mode and habitat domain for predicting predator-prey interactions. Our study found consistent differences in predator effect attributable to hunting mode rather than merely species identity. The study also highlights the importance of considering plasticity in prey movement ranges as an anti-predator response rather than treating the domain as a static attribute as has been performed in the past. The effects of both hunting mode and habitat domain can be substantial and valuable as a management tool for adapting and even predicting prey responses to predators.

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### Data accessibility

Behavioural observations: Dryad data package DOI: 10.5061/dryad.n5d15.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Fig. S1.** Median locations of spider predators in the vertical and horizontal dimensions of the vegetation canopy.

**Table S1.** Results of cross-correlation analysis for grasshopper movement and predator–prey distance.

**Table S2.** Results of cross-correlation analysis for spider movement and predator–prey distance.