


Habitat complexity dampens selection on prey activity level

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Abstract

Conspecific prey individuals often exhibit persistent differences in behavior (i.e., animal personality) and consequently vary in their susceptibility to predation. How this form of selection varies across environmental contexts is essential to predicting ecological and evolutionary dynamics, yet remains currently unresolved. Here, we use three separate predator–prey systems (sea star–snail, wolf spider–cricket, and jumping spider–cricket) to independently examine how habitat structural complexity influences the selection that predators impose on prey behavioral types. Prior to conducting staged predator–prey interaction encounters, we ran prey individuals through multiple behavioral assays to determine their average activity level. We then allowed individual predators to interact with groups of prey in either open or structurally complex habitats and recorded the number and individual identity of prey that were eaten. Habitat complexity had no effect on overall predation rates in any of the three predator–prey systems. Despite this, we detected a pervasive interaction between habitat structure and individual prey activity level in determining individual prey survival. In open habitats, all predators imposed strong selection on prey behavioral types: sea stars preferentially consumed sedentary snails, while spiders preferentially consumed active crickets. Habitat complexity dampened selection within all three systems, equalizing the predation risk that active and sedentary prey faced. These findings suggest a general effect of habitat complexity that reduces the importance of prey activity level in determining individual predation risk. We reason this occurs because activity level (i.e., movement) is paramount in determining risk within open environments, whereas in complex habitats, other behavioral traits (e.g., escape ability to a refuge) may take precedence.

KEYWORDS

activity, habitat complexity, individual variation, predator–prey interactions, selection

1 | INTRODUCTION

One of the goals of ecological research was to understand what factors determine the outcome of species interactions, and how these interactions produce larger-scale patterns of species abundance, distribution, and coexistence (Thompson, 1999). Over the last decade, an increasing number of studies have shown that the traits of individuals

can play a large role in determining the outcomes of species interactions (Bolnick et al., 2011; Crutsinger et al., 2006; Johnson & Agrawal, 2005; Pruitt & Ferrari, 2011). Individual variation can enhance biodiversity across multiple trophic levels (Crutsinger et al., 2006), cause populations to rebound more quickly from biotic disturbances (Randall Hughes & Stachowicz, 2011), or even accelerate the rate with which invasive species spread across landscapes (Brown, Phillips, & Shine,

2014; Fogarty, Cote, & Sih, 2011; Phillips, Brown, Webb, & Shine, 2006). Predator–prey interactions, which are our focus here, are known to play a large role in structuring prey population dynamics, community structure, and space use (Addicott, 1974; Hammill, Atwood, Corvalan, & Srivastava, 2015; Holt, 1977; Ingley & Johnson, 2016a,b), and several recent studies have shown that the traits of individual predators and prey can influence the outcome of their interaction (McGhee, Pintor, & Bell, 2013; Pruitt, Stachowicz, & Sih, 2012; Smith & Blumstein, 2010). However, predicting under what conditions individual variation will have its largest effects is still challenging. This is because there have been relatively few studies examining how the effects of individual variation on predator–prey dynamics change as a function of environmental context.

Individuals sampled from the same population, indistinguishable by physical characteristics, often occupy different points along a behavioral trait axis. Such among-individual behavioral differences can persist when measured repeatedly over time (Bell, Hankison, & Laskowski, 2009) and show moderate heritability (Dochtermann, Schwab, & Sih, 2015). In a predator–prey context, an individual prey's behavioral type (i.e., its value along a behavioral axis) often determines the predation risk it faces (Carter, Heinsohn, Goldizen, & Biro, 2012; Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Wilson, Clark, Coleman, & Dearstyne, 1994). For example, studies show that high activity in the presence of a predator can increase susceptibility to predation (Bell & Sih, 2007; Carter, Goldizen, & Tromp, 2010; Downes, 2002; Dugatkin, 1992), likely due to predators' increased detection and contact rate with prey. However, other studies show that activity can actually decrease (Godin & Davis, 1995; Réale & Festa-Bianchet, 2003; Smith & Blumstein, 2010) or have no effect (Blake & Gabor, 2014; Carlson & Langkilde, 2014) on individual prey susceptibility to predation. One potential reason for these contrasting outcomes is that the effect of consistent behavioral differences among prey on predation risk depends on environmental context.

Habitat structural complexity has long been known as an important factor in determining overall predation rates as prey in complex habitats have increased access to refugia, and predator sensory systems and searching behaviors can become obstructed (Kovalenko, Thomaz, & Warfe, 2012; Savino & Stein, 1982; Warfe & Barmuta, 2004). When a prey population exhibits consistent individual-level behavioral differences, as has been documented in an immensely diverse set of study systems (Bell et al., 2009; Mather & Logue, 2013), individual prey may utilize environmental refugia to different degrees, thus only providing protection for certain prey types with a specific set of phenotypic traits (Klecka & Boukal, 2014). For example, less bold or aggressive prey may be more likely to use habitat refugia (Kobler, Maes, Humblet, Volckaert, & Eens, 2011; Spiegel, Leu, Sih, Godfrey, & Bull, 2015) and thus experience higher survivorship in the presence of certain types of predators (Belgrad & Griffen, 2016). Thus, we reason that the effects of individual-level behavioral variation on predator–prey interactions will change based on the environment in which the interactions occur.

Here, we use parallel experimental designs across three different predator–prey systems (a sea star–snail system and two

spider–cricket systems) to test the joint effects of prey behavioral traits and habitat complexity in determining the predation risk that individuals face. These systems represent classic models of predator–prey interactions (Paine, 1966; Wise, 1995) where the predators differ in their foraging mode: these ground-dwelling spiders utilize movement-sensitive visual and vibrational systems to find prey (Barth, 1998; Persons & Uetz, 1997; Spano, Long, & Jakob, 2012), while sea stars forage largely via chemical cues. To examine evidence for prey behavioral types, we first test for the persistence of prey activity level over time and across the absence and presence of predation threat. We then assay individual prey activity level and subjected prey in groups to a single predator in both open and structurally complex habitats. We record overall prey consumption as well as individual prey survival. We view these parallel yet independent experimental designs as multiple tests of the hypothesis that environmental characteristics can alter the selection that predators impose on prey behavioral traits. Such studies will help illuminate whether or how the ecological effects of individual variation change as a function of the local environment and, in doing so, enhance our ability to predict when individual variation should have its largest (or weakest) effects.

2 | METHODS

2.1 | Experimental overview

We first tested whether individual-level differences in prey activity persisted over time and across the absence and presence of predation threat. Consistency over time and across contexts would suggest that among-individual activity level differences measured during behavioral assays were likely to persist during staged predator–prey encounters. For each prey species (black turban snails [*Chlorostoma funebris*] and domestic crickets [*Acheta domesticus*]), we assayed individual activity level twice in the absence of predation threat (hereafter referred to simply as “activity level” for brevity) and twice in the presence of predation threat, and then tested for relationships between these different behavioral measurements.

Next, we tested whether individual prey activity level influenced the likelihood of surviving predator exposure across structurally simple and structurally complex habitats. A similar experiment was performed for each of the three predator–prey systems (sea stars [*Pisaster ochraceus*]-snails, wolf spiders [*Tigrosa helluo*]-crickets, jumping spiders [*Phidippus clarus*]-crickets). Specifically, mesocosms in which predator–prey encounters took place were either “open” and contained no habitat structural complexity, or “complex” and contained artificial substrates that added structural complexity. We allowed predators and prey of known activity level to interact undisturbed within mesocosms, after which we recorded which prey individuals had survived predator exposure. These experiments further allowed us to test whether habitat complexity affected the overall number of prey consumed. Each predator was tested in both open and complex habitats separated by 1 week, and the order of habitats was randomized for each individual predator.

2.2 | Animal collection and husbandry

We collected snails and sea stars from mid-intertidal pools near Bodega Bay, California, and conducted experiments from August to October 2010. Animals were maintained in recirculating seawater systems prior to experiments (see Pruitt et al., 2012 for details). Snails were housed in the laboratory in groups of 15 individuals in 590-ml plastic containers. Containers were fitted with plastic grates over the lids and sides to allow water flow. Sea stars were housed individually in outdoor flow-through seawater systems and provided an ad libitum diet of mussels (*Mytilus californianus*).

We obtained domestic crickets from a commercial supplier (Ghann's Cricket Farm) and held them in large plastic tubs containing ad libitum potato slices. We collected female wolf spiders from Riechert Farm, Powell, TN, in the summer of 2009 and conducted experiments within a 1-month period. These spiders were housed individually in plastic containers (36 × 36 × 14 cm) containing a cotton ball soaked with water. We collected mature female jumping spiders from Riechert Farm, Powell, TN, in summer of 2010 and 2009 and conducted experiments within a 1-month period. Jumping spiders were housed individually in clear plastic containers (diameter = 11 cm, height = 10 cm). We placed a single cardboard bridge in each container to provide a retreat and further provided each jumping spider with water via a cotton ball soaked with water. Both spider species were fed a maintenance diet of four 2-week-old crickets weekly.

2.3 | Measuring repeatability of prey activity level

To test whether prey activity level was repeatable, we assayed individual activity level twice in the absence of predation threat and once in the presence of predation threat ($n = 35$ snails; $n = 20$ crickets). We randomized the order in which individuals were subjected to each condition (predation threat absent vs. present threat present). Activity level assays were separated by 24 hr.

To measure snail activity level, we placed individually marked snails in groups of 15 in outdoor circular arenas (diameter = 45 cm, height = 43 cm) filled with 15 L of seawater. Each group of 15 snails was assayed together within a single mesocosm. Snails were marked individually by painting a unique sequence of colored dots atop their shell. Arenas were demarcated every 2 cm on the side of the enclosure. We estimated individuals' activity level by measuring the distance they traveled out of the water every 2 min for 20 min and recorded the peak height obtained out of the water during that time. That is, more active snails travel farther out of the water. We are unsure as to whether snail activity levels change in the presence of conspecifics (i.e., if their activity levels would have been different if measured in isolation). However, we tested snails in groups because that is the context in which they would experience the predator threat in the predation experiment. To measure snail activity level in the presence of predation threat, we conducted the same behavioral assay with a caged sea star placed in the arena.

To measure cricket activity level, we placed individual crickets into individual housing containers and applied a unique acrylic paint

mark atop their thorax. We quantified activity level by placing a single cricket in a clear plastic container (18 × 18 × 2.5 cm) atop a 1 × 1 cm grid paper. We provided crickets with a 3-min acclimation period beneath a black dish (diameter = 7 cm, height = 3 cm) before the start of observations. We then removed the black dish and counted the number of lines an individual cricket crossed in this open field over a 10 min period. To measure cricket activity level in the presence of predation threat, we performed the same assay as above, but lined the plastic containers with filter paper on which a wolf spider had been placed for 10 min directly beforehand (similar to methods in Hlivko & Rypstra, 2003). Thus, we were able to test the behavior of crickets in the presence of cues deposited by the spider (e.g., silk and feces) which have previously been shown to alter prey behavior (Hlivko & Rypstra, 2003; Rypstra & Buddle, 2013).

2.4 | Sea star–snail predation experiment

Next, we subjected snails of known activity level (measured once in the absence of predator cues) to sea star predators to test how individual activity level influenced predation susceptibility in open vs. structurally complex habitats. Snails used in this experiment were different than those used to test for the repeatability of snail activity level, to minimize the amount of handling each snail experienced before the predation experiment and to test individuals that had not previously experienced experimental predator cues. We followed the methods of Pruitt et al. (2012). In short, we staged encounters between snails and sea stars in rectangular mesocosms (54 × 34 × 29 cm). Complex habitat mesocosms contained four standpipes (height = 10 cm tall, diameter = 6.35 cm) glued to the bottom of the enclosure, while open environments were lacking standpipes. Individually marked snails were placed within mesocosms ($n = 15$ snails per mesocosm) and given 15 min to acclimate before a randomly selected female sea star was added to the mesocosm. Sea stars were starved for 5 days prior to predation trials. The lids of the mesocosms were then closed and left undisturbed for a 14-day period, after which we recorded the number of snails consumed and their identities. In total, we conducted six replicate mesocosms for each habitat treatment (i.e., open vs. complex) with a total of six sea stars (each sea star was used twice, once in each habitat treatment separated by 7 days). At the end of the experiment, we recorded the number of snails consumed and the identities of the surviving snails. Snails that survived the experiment and sea stars were released back to their site of origin.

2.5 | Wolf spider–cricket predation experiment

The wolf spider–cricket predation experiment occurred 5 days after a routine feeding of wolf spiders. Cricket activity level was measured once in the absence of predator cues, and crickets were individually marked using the same methods described above. Crickets used in this experiment were different than those used to test for the repeatability of activity level, to reduce the amount of handling each cricket experienced before the predation experiment. Wolf spider–cricket predation trials were conducted in plastic shoeboxes (30 × 64 × 18 cm).

Mesocosms with a complex environment contained a 6 cm deep layer of artificial leaves along the base of the tank, while open environments were empty and thus devoid of any structural complexity. We added raw potato slices to both environments to provide crickets with a source of food and water during the trials. For each mesocosm (open environment: $n = 7$; complex environment: $n = 7$), we placed 15 crickets into the mesocosm and allowed them to acclimate for 20 min before adding a single mature female wolf spider. Spiders were allowed to interact freely with crickets for the next 48 hr. We tested each individual spider in both open and complex environments separated by 7 days. At the end of the experiment, we recorded the number of crickets consumed and the identities of the surviving crickets.

2.6 | Jumping spider–cricket predation experiment

For the jumping spider–cricket predation experiment, we followed the methods of Sweeney, Cusack, Armagost, O'Brien, Keiser, & Pruitt, (2013). In short, for each mesocosm (open environment: $n = 4$; complex environment: $n = 4$), we placed an individual spider and 20 randomly selected crickets of known activity levels (measured once in the absence of predator cues) into $30 \times 30 \times 30$ cm mesocosm chambers. Crickets used in this experiment were different than those used to test for the repeatability of activity level, to reduce the amount of handling each cricket experienced before the predation experiment. The mesocosms consisted of a cube which was metal on the bottom, one of the side walls was composed of cloth, while two of the sides and the top were composed of a chiffon screen, and the last side was composed of a clear plastic screen (product catalog #: Bioquip 1450 BC). Crickets were allowed to acclimate for a period of 10 min, after which time we introduced the jumping spider and sealed the mesocosms for a period of 7 days. Mesocosms with a complex environment contained a 6 cm deep layer of artificial leaves along the base of the tank, while open environments were empty. Both mesocosms contained small cubes of raw potato for the crickets to consume over the course of the week. Each spider was tested in both open and complex environments separated by 7 days. At the termination of each mesocosm, we recorded the number of crickets consumed and the identities of the surviving crickets.

2.7 | Statistical analyses

2.7.1 | Repeatability of activity measurements

We used linear regression to test for the persistence of individual activity level over time and across contexts. Specifically, for each prey species, we tested for a relationship between the first activity level measurement and the second activity level measurement (both in the absence of predation threat), and a relationship between activity level measured in the absence of predators and activity level measured in the presence of predators (two models per species). Model residuals were normally distributed (Shapiro–Wilk normality tests: $p > .069$) justifying Gaussian error distributions. All statistical analyses were conducted in the statistical software R (Team, 2012).

2.7.2 | Predation experiments

We used ANOVA to verify that the prey individuals separated into open vs. complex habitats did not differ in their average activity levels. We first tested whether habitat complexity influenced the proportion of prey consumed. To do this, we used three separate generalized linear mixed models (one for each of the three predator–prey systems) with proportional prey consumption as the response variable and habitat complexity as a fixed factor (binomial error distribution and logit link; lme4 package in the statistical software R; Team, 2012). Individual predators were used once in each habitat complexity treatment, and so predator individual was modeled as a random effect. We tested the significance of habitat complexity by dropping this factor and comparing nested models using likelihood ratio tests. The random effect of predator individual was retained in model comparisons.

Next, we tested the effects of individual prey activity level and habitat complexity on individual prey survival. We used generalized linear mixed models (one for each of the three predator–prey systems) with a binomial error distribution and logit link to model the binary response (survived = 0, eaten = 1). Each model included prey activity level and habitat complexity as fixed effects along with their interaction to test whether predator selection depended on environmental context. We also included mesocosm ID as a random effect to account for the non-independence of prey within the same mesocosm. We tested the significance of the prey activity level \times habitat complexity interaction by dropping this term and comparing nested models using likelihood ratio tests. The random effect of mesocosm ID was retained in model comparisons.

3 | RESULTS

3.1 | Repeatability of prey activity level

Individual activity level persisted over time and across contexts for both prey species. Specifically, individual-level differences in snail activity in the absence of predator cues persisted over time (linear regression: adjusted $R^2 = 0.46$, $F_{1,33} = 29.77$, $p < .001$; Figure 1A), as well as across the absence and presence of sea star predation threat (linear regression: adjusted $R^2 = 0.64$, $F_{1,33} = 62.2$, $p < .001$; Figure 1B). Similarly, individual-level differences in cricket activity persisted over time (linear regression: adjusted $R^2 = 0.64$, $F_{1,18} = 35.37$, $p < .001$; Figure 1C), as well as across the absence and presence of wolf spider predation threat (linear regression: adjusted $R^2 = 0.44$, $F_{1,18} = 16.01$, $p < .001$; Figure 1D). Thus, active prey individuals remained active over time and across contexts, and the same was true for sedentary individuals.

3.2 | Predation experiments

Across all three systems, prey individuals separated into open and complex habitats did not differ in their average activity levels (Sea stars: $p = .10$; wolf spiders: $p = .40$; jumping spider: $p = .14$). Habitat complexity had no effect on the proportion of prey consumed in any of the three predator–prey systems (GLMM, likelihood ratio test: $p > .41$; Figure 2). Habitat complexity did, however, interact strongly with prey

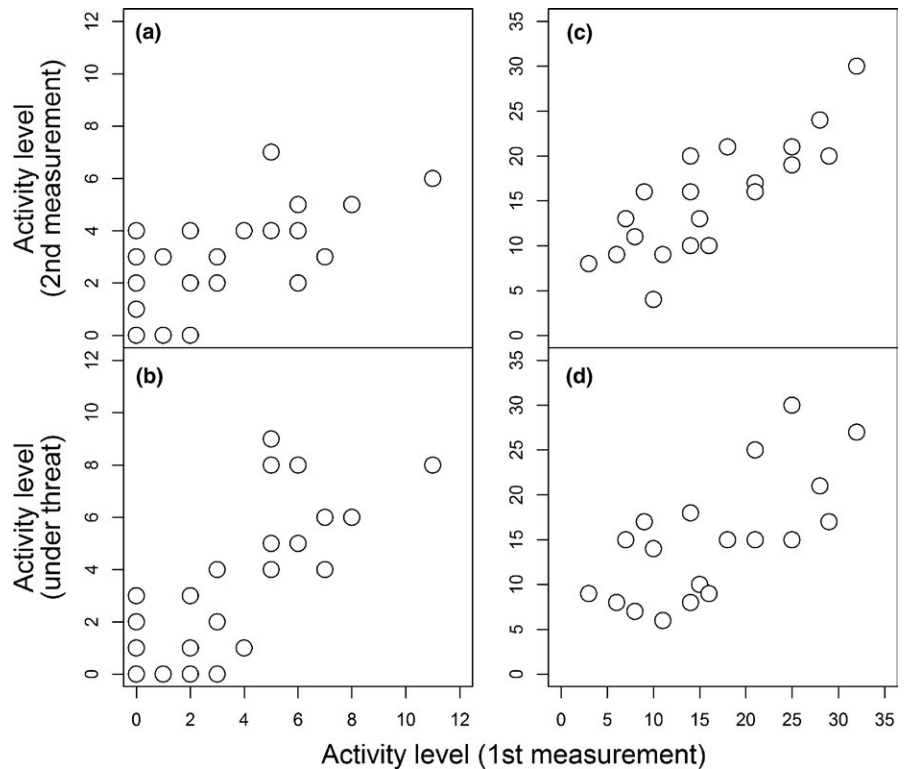


FIGURE 1 Persistence of prey activity level over time and across contexts (predation threat absence and presence) for snails (panels A, B) and crickets (panels C, D). Repeated activity level measurements were separated by 24 hr. Activity level under predation threat was measured for these same prey individuals

activity level to determine individual prey survival. Specifically, we detected a significant interaction between prey activity level and habitat complexity for both the sea star–snail (GLMM, likelihood test: $p = .02$) and wolf spider–cricket predator–prey systems (GLMM, likelihood ratio test: $p = .02$). While this interaction was visually apparent in the jumping spider–cricket system, the effect was not significant (GLMM, likelihood ratio test: $p = .35$). Specifically, in open habitats, both sea stars and spiders imposed strong selection on prey activity level: sea stars preferentially consumed sedentary snails (Figure 3A), while wolf spiders preferentially consumed active crickets (Figure 3B). In all three systems, habitat complexity dampened selection, equalizing the predation risk that active and sedentary prey faced (Figure 3).

4 | DISCUSSION

Here, we sought to evaluate how habitat complexity mediates the selection that predators impose on individual prey activity level using three different predator–prey systems (sea stars–snails, wolf spiders–crickets, and jumping spiders–crickets) with contrasting ecologies. While habitat complexity had no effect on the total number of prey consumed, it did strongly influence the identity of prey consumed within each predator–prey system. In open habitats, sea stars imposed strong selection on snail behavioral types, preferentially consuming sedentary snails. Wolf spiders, in contrast, preferentially consumed active crickets within open habitats. Interestingly, habitat complexity eliminated both these effects, equalizing the predation risk that active and sedentary snail and crickets faced. These findings suggest a general (i.e., system-independent) effect of habitat complexity that reduces the importance of prey activity level in determining individual predation risk.

Similar relationships were uncovered in all three study systems despite wildly differing ecologies (e.g., marine vs. terrestrial, chemosensory predators vs. visual predators), suggesting that such effects may hold in other systems. One potential reason for this general effect of habitat complexity is that activity level is paramount in determining risk within open environments, whereas in complex habitats, additional behavioral traits that were unmeasured in the present study may take precedence. Within open habitats, prey activity entails movement which should in theory increase encounter rates with predators (although this likely depends on predator hunting mode, as explained below). Within complex habitats, other behavioral traits such as refuge use and escape ability into nearby refugia could become important (Heithaus, Wirsing, Burkholder, Thomson, & Dill, 2009)—this may be especially important for prey like the snails studied here that can entirely escape predation via refuge use. That is, when refugia are available, differences in open-field activity alone may become less important in determining individual susceptible predation. This explanation could be tested in future studies by measuring a wider range of individual prey behavioral traits beyond activity level (e.g., refuge use) and comparing the effects of these traits on individual predation risk across different environmental contexts.

The majority of laboratory studies of prey behavioral selection by predators are conducted in simplified environments. We caution that such studies (including some of our own) could overestimate selection on prey traits that would be dampened (or just absent) in more complex environments. This issue is particularly important when attempting to extrapolate laboratory results to field situations in which predators and prey likely interact within a range of different habitats as well as single habitat types that differ in their level of structural complexity. Thus, selection studies conducted in simplified laboratory environments may

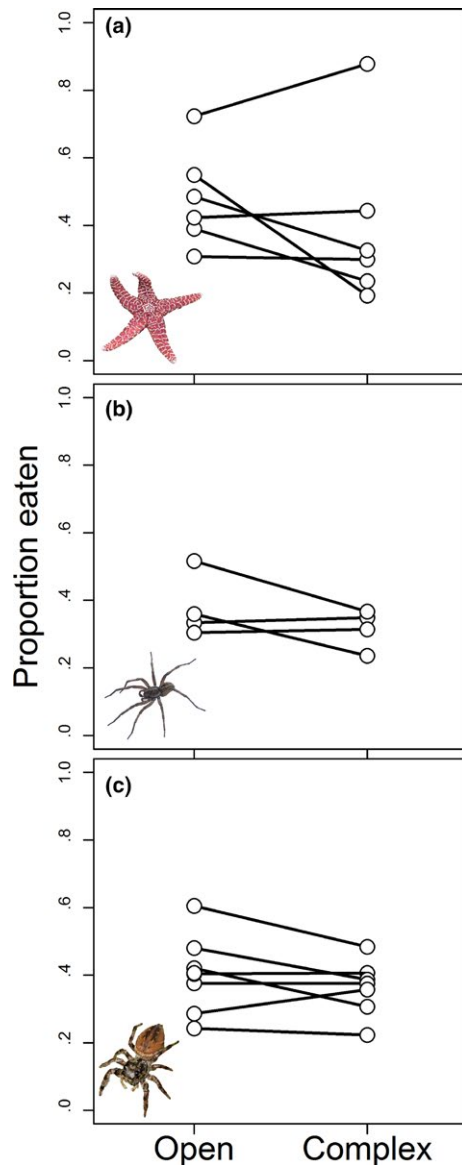


FIGURE 2 Proportion of prey consumed by sea star (panel A), wolf spider (panel B), and jumping spider (panel C) predator individuals across open and complex habitats. Points connected by lines indicate the consumption rate of each individual predator used in the study across habitat contexts. A small amount of vertical displacement (jitter) was added to points for clarity. [Colour figure can be viewed at wileyonlinelibrary.com]

yield inaccurate predictions in field situations. Although we are unsure of the degree to which prey activity levels differed across open and complex habitats, previous studies have shown reductions in activity level in more complex environments (Folsom & Collins, 1984; Stoner, 2009; Sundbaum & Näslund, 1998). Future studies might further probe how individuals vary in their response to changes in habitat complexity (e.g., via a “behavioral reaction norms” approach), and how these differences alter the dynamics of predator–prey interactions. Furthermore, our study suggests that studies conducted in structurally simple vs. structurally complex environments are not directly comparable, and thus environmental context must be accounted for in any

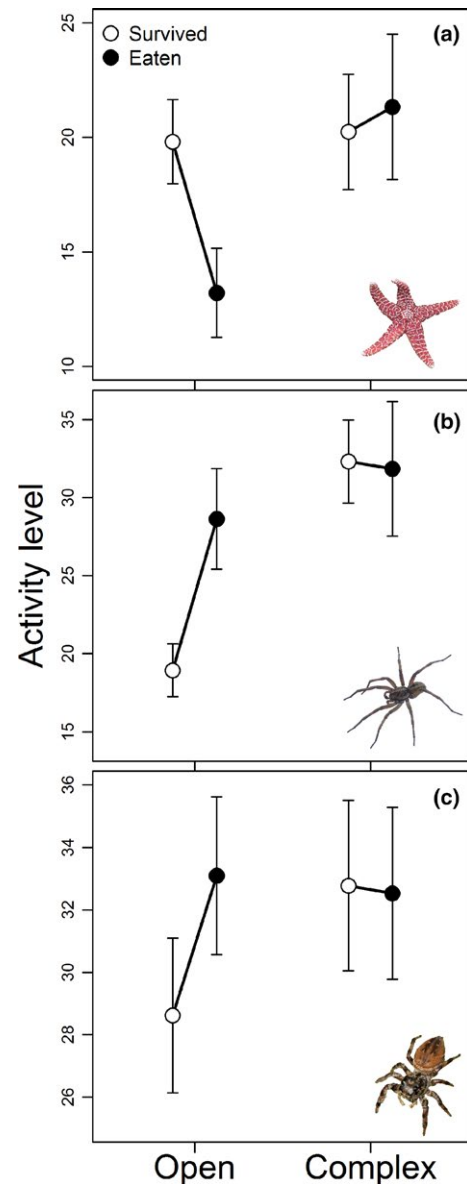


FIGURE 3 Mean activity level (± 1 standard error) of prey that survived (white circles) and were eaten (black circles) during the predation experiments across open and structurally complex habitats. [Colour figure can be viewed at wileyonlinelibrary.com]

future meta-analysis that attempts to yield a general understanding of how prey behavioral types influence individual predation risk.

Interestingly, we showed that within open habitats, on average, sea stars preferentially consumed sedentary prey individuals, while spiders preferentially consumed active prey individuals. Because these results emerged from independent experiments, we do not aim to draw species-level contrasts as in a comparative study. However, we provide potential explanations for these patterns that should be tested in a more direct experimental design. For example, these opposing effects may be attributable to interspecific differences in predator foraging mode (Huey & Pianka, 1981; Miller, Ament, & Schmitz, 2014; Scharf, Nulman, Ovadia, & Bouskila, 2006), where the kinds of prey captured by predators often depends on their hunting strategies and escape strategies of their prey. Foraging modes are usually defined in terms of predator

movement behavior: active predators tend to capture sedentary prey, and sit-and-wait predators tend to capture active prey (Huey & Pianka, 1981). Active prey is likely more apparent to the movement-sensitive visual systems of these ground-dwelling spiders (Persons & Uetz, 1997; Spano et al., 2012). Sea stars, however, forage predominantly via chemical cues (Moore & Lepper, 1997; Sloan & Campbell, 1982), which is less likely to be influenced by prey activity level. However, the presence of multiple predators that vary in their foraging mode, which prey most likely encounter in nature, may negate the effects of habitat complexity on differential prey survivorship (Wilby, Villareal, Lan, Heong, & Thomas, 2005). Lastly, individual predators also likely differed in their foraging mode from one another (i.e., intraspecific variation in foraging mode) and thus differed in the number and types of prey they consumed (e.g., Pruitt et al., 2012; Smith & Blumstein, 2010; Sweeney, Gadd, 2013). Although we did not account for individual variation in predator traits, it is almost certain that differences in body size and behavioral tendencies contribute to their individual effects on prey selection. Thus, future studies should identify the degree to which predator and prey behavioral types interact differently across habitats.

Taken together, our results suggest that the behavioral traits that are advantageous for prey survival differ based on the environmental context in which interactions occur. Structured habitats dampened patterns of selection on prey traits relative to open habitats within all three predator-prey systems. Our results suggest that in habitats that experience rapid shifts in their structural complexity trait-mediated predator-prey dynamics are likely to be altered (Sih, 2013; Tuomainen & Candolin, 2011; Wong & Candolin, 2015). Many forms of human-induced rapid environmental change have the potential to reduce the structural complexity of habitats in a diversity of ecosystems, including valuable biodiversity hotspots like coral reefs (Loya et al., 2001), mangroves (Hoegh-Guldberg & Bruno, 2010), and tropical forests (Harvey et al., 2008). Understanding how these alterations change predator-prey dynamics remains a significant challenge. This challenge can only be addressed once we expand the environmental contexts in which predator-prey interactions are studied.

5 | DATA ACCESSIBILITY

Upon acceptance, the data associated with this manuscript will be deposited at Dryad Digital Repository (DOI).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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