



Habitat structure changes the relationships between predator behavior, prey behavior, and prey survival rates

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Abstract

The individual behavioral traits of predators and prey sometimes determine the outcome of their interactions. Here, we examine whether changes to habitat complexity alter the effects of predator and prey behavior on their survival rates. Specifically, we test whether behavioral traits (activity level, boldness, and perch height) measured in predators and prey or multivariate behavioral volumes best predict the survival rates of both trophic levels in staged mesocosms with contrasting structural complexity. Behavioral volumes and hypervolumes are a composite group-level behavioral diversity metric built from the individual-level behavioral traits we measured in predators and prey. We stocked mesocosms with a host plant and groups of cannibalistic predators ($n=5$ mantises/mesocosm) and their prey ($n=15$ katydids/mesocosm), and mesocosms varied in the presence/absence of additional non-living climbing structures. We found that mantis survival rates were unrelated to any behavioral metric considered here, but were higher in structurally complex mesocosms. Unexpectedly, katydids were more likely to survive when mantis groups occupied larger behavioral volumes, indicating that more behaviorally diverse predator groups are less lethal. Katydid mortality was also increased when both predators and prey exhibited higher average perch heights, but this effect was increased by the addition of supplemental structure. This is consistent with the expectation that structural complexity increases the effect of intraspecific behavioral variation on prey survival rates. Collectively, these results convey that the effects of predator and prey behavior on prey survival could depend highly on the environment in which they are evaluated.

Keywords Hypervolumes · Temperament · Behavioral syndromes · Mantidae · Tettigoniidae

Introduction

Intraspecific variation in behaviors like prey refuge use or predator foraging strategies can determine facets of individual's ecology, such as their ability to capture prey or evade

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We predict where and when predator behavior determines prey survival. Our results reveal that structurally complex habitats increase the effects of predator behavioral tendencies on prey survival.

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predators (Chang et al. 2017; DiRienzo et al. 2013; Sweeney et al. 2013). This conveys that the behavioral tendencies of individuals can at times predict the outcome of predator–prey interactions (Ballew et al. 2017; Finke and Snyder 2008; Hulthén et al. 2014; Sih et al. 2003; Smith and Blumstein 2008). However, in other cases, intraspecific behavioral variation is unrelated to predation outcomes (Keiser et al. 2015, 2017; Lichtenstein et al. 2017a, 2018). Bold (i.e., risk taking) sticklebacks are more likely to escape predation by pike (McGhee et al. 2012), for example, whereas stickleback boldness is unrelated to which macroinvertebrate prey they eat (Pearish et al. 2013). We therefore aim to determine when intraspecific behavioral variation predicts the outcome of predator–prey interactions and when it does not.

Variation among studies suggesting that intra-specific behavioral variation does and does not determine prey survival could be explained by heterogeneity in the habitat in which predator–prey interactions transpire. Several studies

have shown that predator–prey interaction outcomes depend on the habitat available to both trophic levels (Cook and Streams 1984; Crowder and Cooper 1982), and individuals' behavioral characteristics determine the kinds of habitats they use (Pearish et al. 2013; Wilson and McLaughlin 2007). For instance, bold and active sticklebacks tend to inhabit limnetic areas of ponds, whereas sedentary individuals occupy benthic depths (Pearish et al. 2013). These findings suggest that predator and prey behavior, the habitats they use, and the outcome of their interaction are likely to be closely linked. This leads us to predict that habitat characteristics may mediate whether and to what degree intraspecific behavior variation will determine predator–prey interaction outcomes (Keiser et al. 2017). Here, we evaluate whether the behavioral traits of predator and prey, when evaluated in isolation, can predict the performance of either trophic level in environments with contrasting structural features. We further compare the predictive value of univariate group-level behavioral metrics against a composite multidimensional trait diversity metric expressed by groups of predator and prey: behavioral volumes.

The behavioral volume concept was adapted for intraspecific behavioral variation by Pruitt et al. (2016). Behavioral volumes are defined as the multidimensional behavioral space occupied by an individual, group, or community. Volumes with more than three dimensions are called behavioral hypervolumes. The dimensions of behavioral space are animals' performance on three or more behavioral tests (Pruitt et al. 2016). Existing examples have used behavioral traits like activity level, boldness, and aggressiveness in their volumes (Lichtenstein et al. 2017b; Pruitt et al. 2016, 2017). Individual-level behavioral volumes are made up of multiple temporally clustered observations of an individual's behavior in three or more different assays. Thus, each cluster of observations on an individual becomes a point in behavioral trait space, and the individual-level volume is the trait volume captured by these points. In contrast, group-level volumes are composed of a cloud of points where each point is an individual's average behavioral response in three or more different assays. Thus, the group-level volume is estimated as the volume captured by that set of individuals in behavioral trait space. Here, we focus on group-level volumes. This volume is computed as the minimum convex polytope that captures these points. Greater behavioral dissimilarity among group constituents or groups that possess individuals with extreme behavioral types thus occupy larger behavioral volumes (Pruitt et al. 2017). This makes behavioral volumes a metric of behavioral diversity that is sensitive to extreme behavioral tendencies. Prior work has shown that behavioral volumes can determine habitat use and the outcome of species interactions. For example, large volumes are associated with decreased survival and conspecifics clustering in space, in competing mixed-species herbivore groups sharing a host

plant (Lichtenstein et al. 2017b). Groups of predators occupying larger volumes can prove more lethal to their prey, but this is particularly true in environments where predators can use space freely (Pruitt et al. 2017). This suggests that behaviorally diverse predator groups will decrease prey survival, but such effects may be sensitive to how individuals use space.

We consequently test whether a ubiquitous environmental variable, habitat structural complexity, determines the effect of behavioral volume on species interactions. Habitat structural complexity has many definitions (Amarasinghe and Balasubramaniam 1992; McElhinny et al. 2005; Moran 1980; Sugihara and May 1990), but typically refers to the presence of refuges, obstacles, or three-dimensional substrate (Attrill et al. 2000). For example, macroalgae in ponds and vegetation layers in forests offer structural complexity (Crowder and Cooper 1982; Diehl 1992; McElhinny et al. 2005). This increased habitat complexity tends to reduce predation, because it provides prey with refuges and avenues of escape (Cook and Streams 1984; Crowder and Cooper 1982; Diehl 1992; Keiser et al. 2017; Uetz 1991; Vince et al. 1976). By decreasing predation, these obstacles potentially allow the behavioral traits of predators and prey to shape interaction outcomes more so than structurally simple environments. For instance, even if shy prey that spend more time in refuges are less likely to be eaten by predators (Dall et al. 2004; Smith and Blumstein 2008), this tendency will not help them if there are no refuges. We therefore predict that structural complexity will accentuate the importance of single behavioral traits and behavioral volumes (measured before exposure to structural complexity) for predator–prey interactions. In contrast, when environments are more structurally simplistic, we expect weaker or no associations between predator and prey behavior and their interaction outcome.

In this study, we examine the effects of predator and prey behavioral volumes and habitat structural complexity on predator–prey interaction outcome using two old field insect species: Chinese mantises (*Tenodera sinensis*) and common meadow katydids (*Orchelimum vulgare*). We chose these species because mantises are common, cannibalistic, opportunistic predators that tend to reduce herbivore biomass (Hurd and Eisenberg 1984a, 1990; Prete et al. 1999) and increase plant biomass (Moran and Hurd 1997; Moran et al. 1996) in the eastern USA, and meadow katydids are some of the most commonly captured prey at our focal site (pers. obs. JLL, KAD, & JBW 2015–2018). Old fields vary widely in their structural complexity, notably in the amount of dead stalks from previous years' plants (McDonnell and Stiles 1983; Southwood et al. 1979). This system therefore allows us to test whether the presence of dead *Solidago* stalks increases predator and prey survival. Building on this prediction, we can test whether *Solidago* stalks strengthen

the relationships between the traits of predator or prey and the outcome of their interactions.

We use this system to evaluate the following hypotheses: (1) increased structural complexity in the form of added dead *Solidago* stalks increases the survival rates of prey or their cannibalistic predators; (2) greater predator behavioral volumes/diversity decreases cannibalism among predators or reduces prey survival, consistent with prior findings in other systems (Finke and Snyder 2008; Pruitt et al. 2017; Royauté and Pruitt 2015); (3) greater prey behavioral volumes increase prey survival, because behaviorally diversity is predicted to increase the odds that at least some individuals will survive predator encounters; (4) building on the first three predictions, we evaluated whether adding habitat structural complexity increases the effects of behavior on the outcome of predator–prey interactions. Then (5), we tested whether the predictive power of behavioral volumes exceeds that of the coefficient of variation of single traits, the range of single traits, the averages of single traits, or the average body size of predator and prey groups.

Materials and methods

Study organisms, collection, and maintenance

We collected our insects and performed our study at the Donald S. Wood field laboratory (DSW) of the Pymatuning Laboratory of Ecology. The DSW is located in northwest Pennsylvania (41°34′09.6″N, 80°27′51.4″W) on a property composed of deciduous forest and semi-annually mowed old fields. These fields are largely composed of the goldenrod species *Solidago canadensis*, *Solidago grandiflora*, and *Solidago rugosa* interspersed with *Rubus*, *Rosa*, and *Toxicodendron* species. We collected 1500 katydids (*Orchelimum vulgare*) and 500 mantises (*Tenodera sinensis*). Mantises had an average head to tip length of 42.00 ± 0.66 SE mm with a range 16.81–77.00 mm, and weighed on average 305 ± 15 SE mg with a range of 24–1701 mg. We collected mantises between their 4th and 7th instars haphazardly without regard to their sex. Katydids were on average 10.02 ± 0.12 SE mm in length ranging from 0.08 to 43.00 mm head to tip, and weighed on average 35 ± 7 SE mg ranging from 1 to 150 mg. These size ranges are large because they represent collection over ~40 days (06/25/2017–08/02/2017) of growth in these species. Chinese mantises consume a variety of insect prey, including other predators and mantises, thereby structuring prey and plant communities (Hurd and Eisenberg 1984a, 1990; Moran and Hurd 1997; Moran et al. 1996). These species' ranges overlap across the whole of the eastern USA and co-occur at a much finer scale in our collection site, often atop the same stems. *Tenodera sinensis* is a generalist insect predator and it readily consumes *O. vulgare* in captivity.

Both species are common at the DSW. Insects were collected via sweep netting. Immediately after collection, we stored katydids in 50 ml vials with a goldenrod leaf for moisture. We stored mantises in 300 ml plastic deli containers with moistened topsoil as substrate and four sticks for climbing. The laboratory was kept at 24 °C during the day and 20 °C at night. We began behavioral tests the day after collection at 800 h.

Behavioral assays

We ran 377 mantises and 1169 katydids through three assays once each in the following order: activity level, boldness, and perch height. These traits were then used to construct behavioral volumes occupied by groups of predator or prey in behavioral trait space, and test whether these volumes were predictive of the survival rates in either trophic level. Insects were provided a break of several hours between tests and were run through each assay only once before being assigned to a predator–prey interaction mesocosm. To evaluate the repeatability of these behavioral traits, we ran a separate cohort of mantises ($n = 24$) and katydids ($n = 20$) not used in the mesocosm experiment through repeated trials of each behavioral test once per day for 5 days, totaling five trials. To ensure that insects did not grow weak over the course of these 5 days, mantises were fed with a katydid every day, including the day prior to testing. Katydids were maintained in 300 ml containers filled with sections of planted grass.

Activity level

To assess activity level, we observed how much insects moved in open field tests. We placed insects in 11.8 cm-wide, 1.9 cm-long, and 11.1 cm-high plastic containers, with 1 cm graph paper attached to the outside. We used vertically oriented arenas because these insects occupy and climb through vertically stratified habitat. After a 30 s acclimation period, we counted how many squares the insects' heads crossed over the course of 300 s for mantises and 120 s for katydids. Mantises received longer trials because they were prone to remaining still for prolonged periods with sporadic bouts of movement. We cleaned the arenas with 70% isopropyl alcohol between each trial and dried them. Open field tests are commonly used metrics of activity level that are frequently associated with individual variation in foraging behavior (Dingemanse et al. 2002; Kurvers et al. 2009).

Boldness

To evaluate risk taking, we measured the latency of these insects to emerge from protective 300 ml plastic containers. We gently placed insects at the bottom of a new 300 ml plastic container. Immediately after, we placed a second

container on top to prevent insects from escaping. Trials began as soon as the second container was placed atop the first. We then measured the insects' latency to exit the bottom container, specifically when their heads crossed the border. We cleaned both containers with 70% isopropyl alcohol between each trial. This test closely resembles emergence tests used to assess boldness in other insects (Fisher et al. 2015; Hedrick and Kortet 2012; Müller and Müller 2015; Niemelä et al. 2012).

Perch height

To assess how these insects use space, we placed them in arenas and measured how high they perched within the enclosure. These arenas were mesh-collapsible field cage covers (bioquip 1451BC) attached to tomato cage frames (EmscoGroup 2328-1) by binder clips. We could adjust the height of these cages to our specifications. We set them up to be 30 cm wide, 30 cm long, and 45 cm tall. Arenas were wrapped around potted goldenrod plants, which we pruned to have exactly 40 leaves. We draped arenas at a height where the top of each plant would just touch the top of the enclosure. We placed the insects in arenas through the sealable opening at the base and then measured the height of their heads after a 10-min acclimation period. Ten minutes was enough time for over 90% of all insects to explore much of the cage and then cease movement for extended periods of time, implying an initial settlement decision. A test similar to this one predicted the outcome of an interaction between two different old field insect species (Lichtenstein et al. 2017b), although that study used different arenas. We designed this test to gauge how insects would use space in the specific arenas used for our experiment.

Predator–prey interactions

To test how the behavior traits of these insects might relate to the survival of both predators and prey, we stocked the same arenas used for the perch height test haphazardly with groups of mantises and katydids whose behavior traits had previously been evaluated. Katydid groups were added first to give them a chance to orient themselves before predator addition. Care was taken not to place predators immediately atop one another or atop prey, which could instigate unnatural cannibalism or predation. Mantis groups contained 5 individuals because this is just above the minimum number needed to calculate a behavioral volume, and katydid groups contained 15 because this is roughly twice the number we estimated 5 mantises could eat in a day. This is likely higher than natural mantis densities. Immediately before stocking the mesocosms, we weighed and measured the length of each insect. Any extra tested insects not put in mesocosms were used in mesocosms the next day. No insects were used in both the

predator–prey interaction trials and the repeatability trials. To manipulate structural complexity, we put eight 15–20 cm dead goldenrod stems in 35 mesocosms and left the other 39 bare ($N_{\text{mesocosms}} = 74$, $N_{\text{insects}} = 1480$). Eight is well within the natural range of dead stems present in these fields (JLL Pers Obs). The presence of dead goldenrod stems from previous years is a facet of habitat structural complexity that varies naturally in old fields (McDonnell and Stiles 1983; Southwood et al. 1979). We stocked and sealed the mesocosms between 1600 and 1800 h, and then left them for 23 h, allowing an hour for setup. After 23 h had elapsed, we opened the mesocosms and counted the number of surviving insects. We released all survivors in a small patch of goldenrod by a service road a few kilometers from where they were collected.

Statistical methods

We assessed the repeatability of all three behavioral traits for both species using the rptR package (Nakagawa and Schielzeth 2013) in R version 3.4.1 (R development team). We used rptR to fit generalized linear mixed models (GLMMs) fit with normal distributions, using behavioral test performance as the response variable, “trial number” as a predictor variable, and “individual ID” as a random effect. The package estimates repeatability as the proportion of variance explained by “individual ID”. To determine the significance of these estimates, rptR uses 95% confidence intervals created by subsetting data and re-running the models through bootstrap iterations (we chose 1000 iterations). Significant repeatability estimates have 95% confidence intervals that do not overlap zero.

We compared the performance of mantises on each of these behavioral tests to mantis mass and body condition using linear regressions. We calculated body condition as the residual distance of insect mass from a regression of mass upon length after Jakob et al. (1996). We also checked for associations between behavioral traits using linear regressions. We constructed these linear models in JMP version 13 (SAS), and used R for all repeatability analyses.

To calculate behavioral volumes, we Z-transformed the performance of each species on each test. This allows for more fluid comparisons of volumes across studies and across trait types. Next, we estimated volumes for each species group in each mesocosm replicate. We plotted the members of each group in three-dimensional behavioral space, where each dimension is an individual's performance on a behavioral test. The volume of each group was calculated as the smallest possible volume of a three-dimensional convex polytope bound by the individuals in behavioral space. We created the volumes in MATLAB (version 9.0, R2016a) by first computing separate 3-D Delaunay triangulations (using the delaunayTriangulation function) on the data points in each mesocosm group. We

subsequently fed these triangulation objects to MATLAB's convexHull function, whose output reports the volume occupied by the supplied polytope. Examples of these volumes can be found in Fig. 1. We used MATLAB for all behavioral volume calculations.

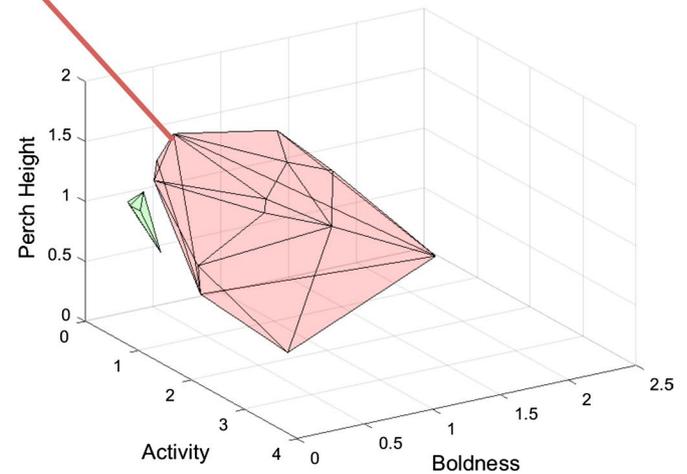
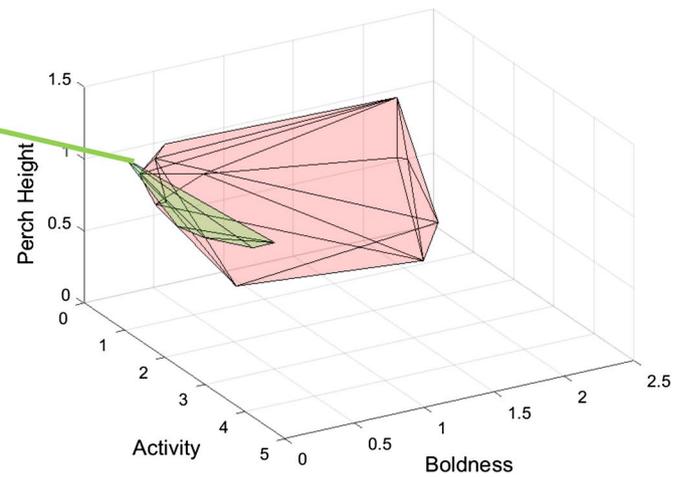
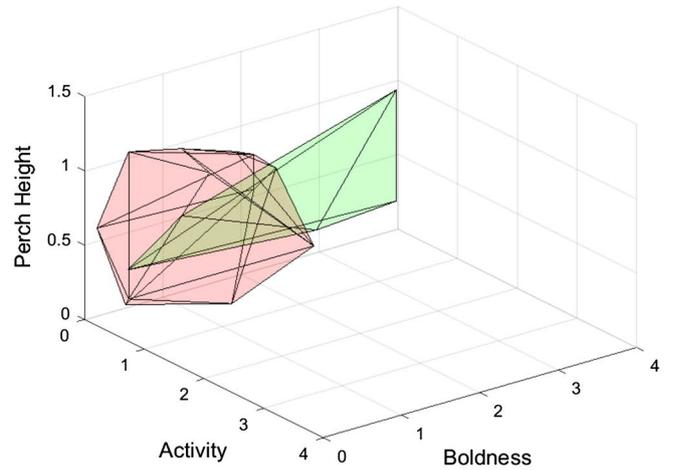
Next, to assess what factors predict mantis and katydid mortality, we made 24 GLMs fit with normal distributions. Each model had the same basic structure: mantis or katydid survival rate was used as the response variable, and the predictor variables were habitat structural treatment

Fig. 1 Examples of behavioral volumes. Green volumes represent mantises (group size = 5) and red volumes represent katydids (group size = 15) (color figure online)

Chinese mantis



Meadow katydid



(supplementary perches \pm), the mantis behavioral trait (varied by model), the katydid behavioral trait (varied by model), and associated interaction terms. The traits supplied for both species were (1) behavioral volumes, (2–4) the coefficient of variation (CV) of each behavioral trait, (5–7) the range of each behavioral trait, (9–10) the averages of each behavioral trait, and then average mass (11) and length (12). We assessed the fit of these 12 models for each insect species using two Akaike information weight comparisons, one comparing each of the model structures when predicting mantis survival rate and another set of comparisons for katydid survival. The Akaike weight comparison selects models with low AICc values and higher AICc weights (Akaike 1987; Burnham and Anderson 2003). We subsequently ran and interpreted the best models if they had more than double the Akaike weight of the next best model. If the best model did not have twice the weight of the second-best model, then we ran and interpreted both. We performed model comparison procedures and ran the best models in JMP Pro 13.

We implemented two post hoc analyses. First, to disentangle the causal relationships between average perch height, behavioral volumes, and katydid survival, we built three structural equation models with LAVAAN (Rosseele 2012) in R version 3.5.0. We specified the first model to compare mantis average perch height to mantis behavioral volume and then to compare mantis behavioral volume and mantis average perch height to katydid survival. By partitioning direct and indirect components of the model, we assessed whether behavioral volumes mediate the effect of average perch height on katydid survival. Next, we made two models with the same structure, but created one model for the low complexity mesocosm treatment and a second for the high complexity mesocosm treatment. Second, to look for effects of mantis cannibalism on prey survival we constructed a GLM with a normal distribution, mantis survival as the predictor variable, and katydid survival as the response variable in JMP Pro 13.

Results

Mantises had an average activity level of 36.03 ± 2.05 squares SE, an average boldness of 153.45 ± 10.63 s SE, and an average perch height of 40.79 ± 1.46 cm SE. Katydids had an average activity level of 38.09 ± 0.92 squares SE, an average boldness of 138.62 ± 3.42 s SE, and an average perch height of 29.09 ± 0.45 cm SE. The insects were significantly repeatable in their performance in each behavioral test (Supplementary Table S1).

Mantis mass was negatively associated with their activity level, explaining 1% of all activity level variation (Supplementary Table S2). Katydid mass positively associated with katydid activity level and perch height, and negatively

associated with boldness (Supplementary table S2). However, katydid mass explained only 0.6, 7 and 3% of the variation in these behavioral traits, respectively (Supplementary Table S2). Mantis body condition was positively associated with mantis boldness, katydid body condition was positively associated with katydid perch height, and katydid body condition was negatively associated with katydid boldness (Supplementary Table S2). Yet, body condition explained only 1% of mantis boldness, 1% of katydid boldness, and 2% of katydid perch height (Supplementary Table S2).

Mantis boldness was weakly associated with mantis perch height and mantis activity level, with R^2 values no higher than 0.04 (Supplementary Table S3). Katydid activity level, boldness, and perch height were all weakly associated with each other, with R^2 values no higher than 0.08 (Supplementary Table S3). These are much weaker correlations than those observed in other mantis species (Jones and DiRienzo 2018).

Predator–prey interactions

Mantis groups on average had a survival rate of $85 \pm 0.59\%$ SE. The length model (AICc = -73.671 , Akaike weight = 0.639) and the mass model (AICc = -72.493 , Akaike weight = 0.355) were roughly equal predictors of mantis survival rates, explaining 34.1% and 31.7% of all variation in mantis survival rates respectively and with Akaike weights over 77 times greater than the third-best model (Table 1). All mantises that died in these mesocosms were partially or entirely eaten, and we personally observed numerous instances of cannibalism. Thus, the mantis mortality observed here is likely attributable to cannibalism alone. Mantises were 8.7% more likely to survive in structurally complex mesocosms (Supplementary Figure S1; Table 2), and average katydid mass positively correlated with mantis survival (Table 2). There were significant mantis length by katydid length, mantis length by katydid length by treatment, and mantis mass by katydid mass interaction terms in the models predicting mantis survival (Table 2). However, mantis and katydid average length (linear regression: $R^2 = 0.728$, $F_{1,70} = 187.160$, $p < 0.001$), and mantis and katydid average mass (linear regression: $R^2 = 0.576$, $F_{1,70} = 96.354$, $p < 0.001$) turned out to be very strongly associated, so we disregarded these interaction terms, because we suspect them to be artifacts of multicollinearity.

On average, $34.13 \pm 1.7\%$ SE of katydids in a group survived mesocosm trials. The mantis behavioral volume model (AICc = -71.399 , Akaike weight = 0.375) and the mantis average perch height model (AICc = -72.147 , Akaike weight = 0.544) were roughly equal predictors of katydid survival, with Akaike weights over six times greater than the third best model (Table 1). We therefore have chosen to report both the volume and average perch height models.

Table 1 Model comparisons of models predicting katydid survival and mantis survival

Response variable	Personality metric	R^2	P	AICc	Relative AICc	Akaike weight
Katydid survival	Behavioral hypervolume	0.245	0.005	-71.399	0.990	0.369
	Activity level CV	0.059	0.730	-55.291	0.766	0.000
	Tube CV	0.073	0.595	-56.398	0.782	0.000
	Perch CV	0.207	0.018	-67.756	0.939	0.060
	Activity range	0.015	0.095	-61.637	0.854	0.003
	Boldness range	0.030	0.946	-51.697	0.717	0.000
	Perch range	0.074	0.576	-55.157	0.765	0.000
	Activity level average	0.181	0.043	-65.366	0.906	0.018
	Boldness average	0.112	0.280	-59.497	0.825	0.001
	Perch average	0.256	0.003	-72.147	1.000	0.537
	Average mass	0.109	0.300	-59.254	0.821	0.001
	Average length	0.192	0.032	-64.293	0.891	0.011
Mantis survival	Behavioral hypervolume	0.095	0.388	-52.048	0.718	0.000
	Activity level CV	0.133	0.166	-55.056	0.759	0.000
	Tube CV	0.120	0.230	-53.978	0.745	0.000
	Perch CV	0.109	0.296	-53.081	0.732	0.000
	Activity range	0.126	0.191	-56.444	0.779	0.000
	Boldness range	0.209	0.016	-63.799	0.880	0.005
	Perch range	0.065	0.661	-51.482	0.710	0.000
	Activity level average	0.118	0.250	-53.821	0.742	0.000
	Boldness average	0.169	0.060	-58.184	0.803	0.000
	Perch average	0.207	0.019	-59.514	0.821	0.001
	Average mass	0.317	0.000	-72.493	1.000	0.355
	Average length	0.341	0.000	-73.671	1.016	0.639

We used the Akaike weight information procedure to compare models that took into account behavioral volumes, the coefficient of variation (CV) of behavioral traits, average behavioral scores, and average mass and length. We ran separate analyses for mantis and katydid survival. Each model had the same basic structure. All had mantis or katydid survival as its response variable and the following predictor variables: structural complexity treatment, mantis trait, katydid trait, and all of their interaction terms

Mantis behavioral volume positively correlated with katydid survival (Fig. 2), seemingly more so in structurally complex environments, although this interaction term was only marginally significant (Table 2). Average mantis perch height was associated with decreased katydid survival (Table 2). However, katydid survival was lowest when both mantises and katydids had high average perch heights, conveying joint habitat overlap, but only in mesocosms with added habitat structural complexity (Table 2; Fig. 3).

Post hoc path analyses revealed that (1) average perch height negatively correlated with behavioral volumes and (2) behavioral volumes correlated with prey survival, but (3) average perch height did not directly predict prey survival (Fig. 4; Supplementary Table S2). This suggests that behavioral volumes mediate the effect of average perch height on katydid survival. These effects were seemingly stronger in mesocosms with added structural complexity (Fig. 4; Supplementary Table S4).

Finally, mantis survival was not significantly related to katydid survival (GLM: $R^2 = 0.029$, $\chi^2_{72} = 2.199$, $p = 0.138$), conveying that cannibalism did not increase prey survival.

Discussion

We examined here whether habitat structure and the multidimensional trait diversity present in predator and prey groups altered the survival of either interactor in a laboratory study. Mantis survival was not associated with any behavioral metric considered here (Table 1). Mantises were instead less likely to cannibalize each other in structurally complex environments and when katydids were larger (Table 2). Katydid survival was more likely to survive in mesocosms with more behaviorally diverse mantis groups, which together occupied a larger volume in behavioral trait space (Fig. 2). This was especially true when mesocosms were more structurally complex (Table 2). This means that the trait diversity present in the predator population can have risk-reducing effects for prey. Katydid survival was also more likely to survive when both they and mantises had low average perch heights, supporting evidence that individual variation in key behavior traits, like foraging mode or habitat use, can alter the outcome of species interactions (Chang et al. 2017; Preisser et al. 2007; Royauté and

Table 2 The outputs of the two best models explaining katydid survival and the best model explaining mantis survival

Response Variable	Predictor variable	R^2	$\beta \pm$ Standard error	df	χ^2	P
Katydid survival	Whole model	0.245	–	7	20.533	0.005
	Structural complexity		-0.012 ± 0.015 SE	1	0.594	0.441
	Mantis hypervolume		0.171 ± 0.046 SE	1	12.771	0.0004
	Katydid hypervolume		0.01 ± 0.014 SE	1	0.518	0.472
	Mantis hypervolume \times structural complexity		-0.088 ± 0.046 SE	1	3.647	0.056
	Katydid hypervolume \times structural complexity		-0.013 ± 0.014 SE	1	0.844	0.358
	Mantis hypervolume \times katydid hypervolume		0.015 ± 0.040 SE	1	0.147	0.701
	Mantis hypervolume \times katydid hypervolume \times structural complexity		0.008 ± 0.040 SE	1	0.036	0.849
Katydid survival	Whole model	0.256	–	7	21.243	0.003
	Structural complexity		-0.003 ± 0.015 SE	1	0.029	0.865
	Mantis average perch height		-0.013 ± 0.004 SE	1	9.523	0.002
	Katydid average perch height		-0.006 ± 0.003 SE	1	3.599	0.058
	Mantis perch height \times structural complexity		0.004 ± 0.004 SE	1	0.962	0.327
	Katydid perch height \times structural complexity		0.006 ± 0.003 SE	1	2.896	0.089
	Mantis perch height \times katydid perch height		0.001 ± 0.001 SE	1	0.069	0.793
	Mantis perch height \times katydid perch height \times structural complexity		-0.002 ± 0.001 SE	1	7.366	0.007
Mantis survival	Whole model	0.317	–	7	27.849	0.0002
	Structural complexity		-0.055 ± 0.020 SE	1	6.888	0.009
	Mantis average mass		-0.121 ± 0.127 SE	1	0.904	0.342
	Katydid average mass		5.621 ± 1.734 SE	1	9.813	0.002
	Mantis mass \times structural complexity		-0.005 ± 0.127 SE	1	0.002	0.967
	Katydid mass \times structural complexity		-0.748 ± 1.734 SE	1	0.186	0.667
	Mantis mass \times katydid mass		-10.613 ± 4.792 SE	1	4.747	0.029
	Mantis mass \times katydid mass \times structural complexity		6.256 ± 4.792 SE	1	1.684	0.1943
Mantis survival	Whole model	0.317	–	7	30.006	0.0001
	Structural complexity		-0.067 ± 0.020 SE	1	10.175	0.001
	Mantis average length		-0.001 ± 0.003 SE	1	0.075	0.784
	Katydid average length		0.022 ± 0.011 SE	1	3.777	0.052
	Mantis length \times structural complexity		-0.002 ± 0.003 SE	1	0.718	0.397
	Katydid length \times structural complexity		$0.008 \pm .011$ SE	1	0.474	0.492
	Mantis length \times katydid length		-0.002 ± 0.001 SE	1	9.967	0.002
	Mantis length \times katydid length \times structural complexity		$0.001 \pm .001$ SE	1	5.909	0.015

These models had the same basic structure: mantis or katydid survival as the response variable and for the predictor variables, structural complexity treatment, the mantis trait, the katydid trait, and all of their interaction terms. The length model (AICc = -73.671, Akaike weight = 0.639) and the mass model (AICc = -72.493, Akaike weight = 0.355) were similarly predictive of mantis survival. The behavioral volume model (AICc = -71.399, Akaike weight = 0.375) and the average perch height model (AICc = -72.147, Akaike weight = 0.544) were roughly equal predictors of katydid survival. Therefore, we report these four models here. P values in bold are significant at the $\alpha = 0.05$ level

Pruitt 2015; Schmitz 2007; Toscano et al. 2016; Toscano and Griffen 2014). However, behavioral volumes appear to mediate the effect of average perch height on katydid survival, suggesting that the effects of average perch height are indirect, but stronger in structurally complex mesocosms. Unfortunately, our design did not account for sex, thus we are unsure of the role mantis sex played in these results. These data taken together support our hypothesis that added structural complexity increases the survival of some interactors (mantises) and has the potential to change the functional relationships between predator behavior, prey behavior, and the outcomes of their interactions.

However, our data were inconsistent with many of our other directionally-explicit hypotheses.

Two factors appeared to predict mantis survival. First, structural complexity slightly reduced cannibalism in mantises (by less than 10%). This supports the claim that habitat complexity can reduce predation risk and suggests that our structural manipulations replicate findings from more intact nature systems (Crowder and Cooper 1982; Diehl 1992). Second, average katydid mass was strongly related to mantis survival. This may be because cannibalism decreases when heterospecific prey are larger and more profitable (Hironori and Katsuhiko 1997; Qin and Fast 1996), conveying that

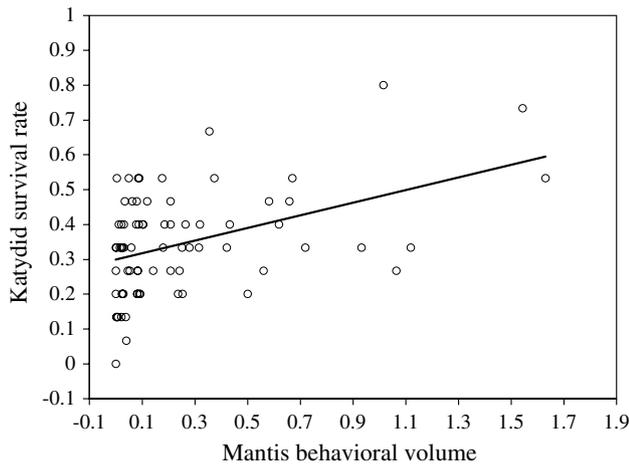


Fig. 2 Mantis behavioral volume is directly proportional to katydid survival (glm effect test: $\chi^2_1=12.771$, $p=0.004$). Line represents linear regression

conspecifics are potentially non-preferred prey (Hurd and Eisenberg 1984b). Alternatively, larger prey could satiate mantises reducing their appetites for conspecifics. We cannot presently distinguish between the effects of age and size within our experimental design, because larger katydids were collected at moments when mantises were both older and larger themselves. Nonetheless, these findings provide some evidence that predator and prey age and size are potentially important for determining the outcome of predator–prey interactions (Connell 1970; Cushing and Saleem 1982; Polis et al. 1989; Thompson 1975).

Multiple predator effects (MPEs) are cases where the presence of multiple predator species have non-additive

effects on prey survival (Sih et al. 1998; Soluk 1993), although the term has been borrowed to refer to non-additive interactions between individual predators of the same species (Royauté and Pruitt 2015). Existing evidence implies that the trait compositions present in predator populations can generate variation in MPEs (Royauté and Pruitt 2015). For instance, more behaviorally diverse populations of predators often prove more lethal to groups of prey (Finke and Snyder 2008; Pruitt et al. 2017; Royauté and Pruitt 2015). Our finding that mantis behavioral volumes actually decreased risk for katydids confirms that changes to the trait diversity present in predator populations can result in contrasting MPEs. However, the direction is the opposite of that observed in other studies to date, conveying that behaviorally diverse groups of predators are not always more lethal to their prey. The sensitivity of behavioral volumes to behaviorally extreme individuals could provide a clue as to why this is. In water striders, males with extreme aggressive phenotypes chase both males and females, dramatically reducing the mating success of all nearby individuals (Eldakar et al. 2009; Sih and Watters 2005). Similarly, behaviorally extreme mantises could disrupt conspecific hunting efforts, leading to increased prey survival, perhaps even more so if prey have numerous escape routes. Alternatively, there might be a particular behavioral phenotype in predators (e.g., a preference for high perch heights) that proves most lethal for all prey of a given species, resulting in situations where more diverse groups of predators have a smaller number of predators exhibiting the most lethal behavioral phenotype. This latter hypothesis is consistent with our finding that intraspecific variation in predator perching height is a predictor of prey survival. Future studies aimed at teasing apart the relationships between space use and intraspecific

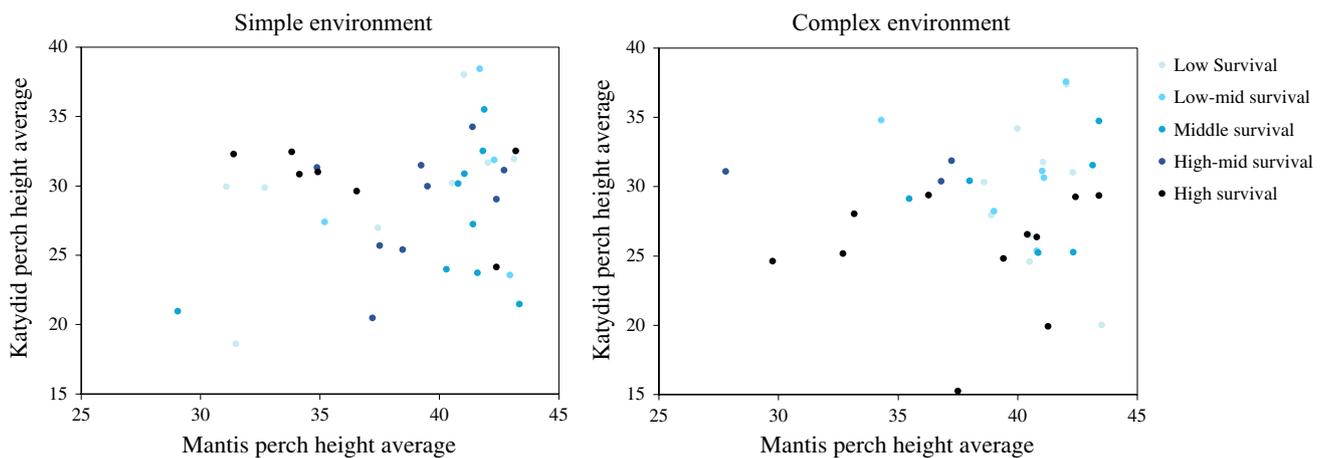


Fig. 3 In structurally complex environments, mantises eat more katydids when both species have high average perch heights (glm effect test: $\chi^2_1=7.366$, $p=0.007$). Low survival refers to katydid survival rates between 11 and 20%, mid-low refers to 21–30% katydid sur-

vival, middle survival refers to 31–35%, mid-high refers to 36–45%, and high survival refers to 46–100%. The boundaries of these categories were chosen to maximize group size evenness. We manipulated structural complexity by adding dried goldenrod stems to mesocosms

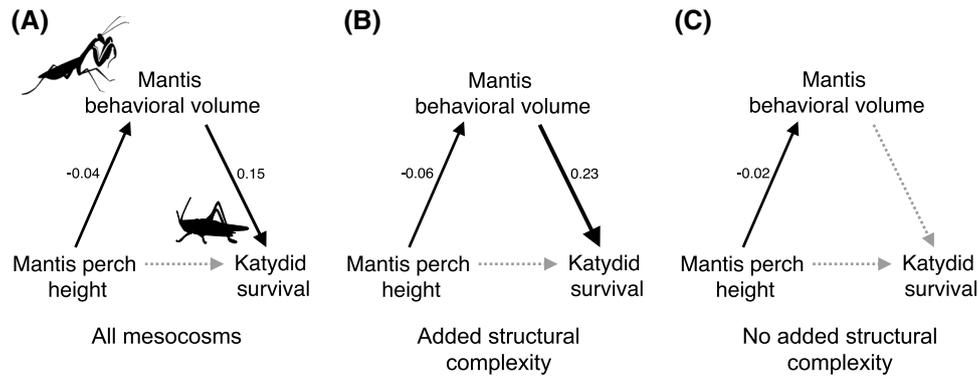


Fig. 4 Path diagrams showing relationships between mantis average perch height, mantis behavioral volume, and katydid survival in mesocosms. Diagram **a** was built using all mesocosms, diagram **b** was built with only mesocosms with added structural complexity, and dia-

gram **c** was built with mesocosm with no added structural complexity. Significant relationships are represented by black arrows with β estimates. Non-significant relationships are represented by dashed gray lines. Path analyses were performed with Lavaan in R

behavioral variation will help to resolve conflicting evidence suggesting that behavioral volumes or hypervolumes can enhance or reduce predator lethality.

Our perch height tests were designed to estimate how insects use space, and our boldness and activity level tests were designed to estimate what insects do in the space that they occupy. This makes our behavioral volumes a composite metric of the insects' behavioral repertoires, including how groups of insects use space and how they behave within that space. Despite this point, the average perch height of predators appeared to predict prey survival on its own. Katydid survival was predicted by perch height, or at around two-thirds up the height of the arena. Groups of mantises whose members tend to climb higher (i.e., just above the katydids' preferred perch height) consumed more katydids. This was especially true in structurally complex mesocosms (Table 2): in environments with added structural complexity, mantises did not eat more than 50% of katydids unless both species had high average perch heights (Fig. 3). This suggests that predation is most likely to occur when predator and prey overlap spatially, and when physical structure allows predator and prey to use that region of space. A handful of studies have linked individuals' behavioral tendencies to their space use (Boyer et al. 2010; Pearish et al. 2013; Spiegel et al. 2015; Wilson and McLaughlin 2007; Wilson et al. 1993), potentially conveying that findings like our own could hold in other systems.

However, post hoc path analysis revealed that behavioral volumes mediate the effect of predator perch height on katydid survival (Fig. 4; Supplementary Table S2). This suggests that high mantis perch height reduces katydid survival indirectly, because high mantis perch height reduces mantis behavioral volume. Importantly, this does not convey that mantis perch height has no influence on katydid survival. Our behavioral volumes are merely a more informative

composite measure that includes perch height. Instead, this conveys that mantis perch height determines katydid survival as a part of a trait ensemble that is more effectively summarized as a behavioral volume or hypervolume (Pruitt et al. 2016). This, in turn, reaffirms the importance of a multitrait approach when evaluating the effects of intraspecific behavioral variation on ecological outcomes (Sih et al. 2004, 2012).

Conclusions

We found that intraspecific variation in behavioral volumes and average perch height best predicted the survival of katydids, and that added habitat structure amplified some of these effects in staged lab interactions (Table 2; Fig. 3). Furthermore, structural complexity alone had no effect on katydid survival (Table 2), which is inconsistent with earlier research, which found that structural complexity increases prey survival (Cook and Streams 1984; Crowder and Cooper 1982). Instead, our data suggest that the benefit complex environments afford prey may depend on the behavioral traits of the individual predators involved. There is already compelling data showing that predator behavioral traits can foretell the outcome of species interactions (DiRienzo et al. 2013; Griffen et al. 2012; Keiser et al. 2015; Lichtenstein et al. 2017a; Pruitt and Ferrari 2011) and there is considerable evidence that behavioral traits determine how animals use their environments (Pearish et al. 2013; Wilson and McLaughlin 2007). We have found here that these processes are likely not independent. Work exploring the ecological consequences of intraspecific behavioral variation could therefore profit from considering how the behavioral tendencies of predators and prey relate to habitat use and how habitat use, in turn, relates to species interaction outcomes.

Such links may help to explain the contrasting results of an increasingly large number of ecologically minded animal personality studies.

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Author contribution statement JLLL designed the experiment, collected data, and wrote the manuscript. KAD and JBW contributed to data collection and writing. GND calculated behavioral volumes and contributed to writing. RCP performed path analyses and contributed to writing. CMW and JNP helped with experimental design and writing. All authors approved the manuscript in its current form.

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