

UNIVERSITY OF CALIFORNIA SANTA BARBARA

Animal personality shapes the outcome of species interactions and thereby the structure of
ecosystems

A Dissertation submitted in partial satisfaction of the requirements for the degree Doctor of
Philosophy in Ecology, Evolution, and Marine Biology

by

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- 2020 DN Fisher, **JLL Lichtenstein**, R Costa-Pereira, J Yeager, JN Pruitt. "Assessing the repeatability, robustness to disturbance, and parent-offspring colony resemblance of collective behaviour." Journal of Evolutionary Biology (33) 4, 410-421. <https://doi.org/10.1111/jeb.13576>
- 2020 BL McEwen, **JLL Lichtenstein**, DN Fisher, CM Wright, GT Chism, N Pinter-Wolman, JN Pruitt. "Predictors of colony extinction vary by habitat type in social spiders." Behavioral Ecology and Sociobiology 74 (1), 2. <https://doi.org/10.1007/s00265-019-2781-x>
- 2019 **JLL Lichtenstein**, DN Fisher, *BL McEwen, *DT Nondorf, E Calvache, C Schmitz, J Elässer, JN Pruitt. "Collective aggressiveness limits colony persistence in high but not low elevations sites in Amazonian social spiders." Journal of Evolutionary Biology 33 (1), 1362-1367. <https://doi.org/10.1111/jeb.13532>

- 2019 CM Wright, **JLL Lichtenstein**, *LP Luscuskie, *GA Montgomery, *S Geary, JN Pruitt, N Pinter-Wollman, CN Keiser "Spatial proximity and prey vibratory cues influence collective hunting in social spiders" Israel Journal of Ecology and Evolution. <https://doi.org/10.1163/22244662-20191062>
- 2019 G Navid Doering, KA Sheehy, **JLL Lichtenstein**, B Drawert, LR Petzold, JN Pruitt. "Sources of intraspecific variation in the collective tempo and synchrony of ant societies." Behavior Ecology 30 (6), 1682-1690. <https://doi.org/10.1093/beheco/arz135>
- 2019 *JD Pretorius, **JLL Lichtenstein**, EJ Eliason, AC Stier, JN Pruitt. "Predator-induced selection on urchin activity level depends on urchin body size." Ethology 125 (10), 716-723. <https://doi.org/10.1111/eth.12924>
- 2019 CM Wright, *BL McEwen, DN Fisher, **JLL Lichtenstein**, *A Antoun, EA Tibbets, JN Pruitt. "Egg discrimination is mediated by individual differences in queen associative learning and boldness." Behavioral Ecology 30 (5), 1306-1313. <https://doi.org/10.1093/beheco/arz078>
- 2019 **JLL Lichtenstein**, CM Wright, JN Pruitt. "Repeatability of between-group differences in collective foraging is shaped by group composition in social spiders." Journal of Arachnology 47 (2), 276-279. <https://doi.org/10.1636/JoA-S-18-046>
- 2019 CM Wright, **JLL Lichtenstein**, EA Tibbets, JN Pruitt. "Individual variation in queen morphology and behavior predicts colony performance in the wild." Behavioral Ecology and Sociobiology 73 (9), 122. <https://doi.org/10.1007/s00265-019-2739-z>
- 2019 CM Wright, **JLL Lichtenstein**, *LP Luscuskie, *GA Montgomery, N Pinter-Wollman, JN Pruitt. "Better safe than sorry: spider societies mitigate risk by prioritizing caution." Behavioral Ecology 30 (5), 1234-1241. <https://doi.org/10.1093/beheco/arz069>
- 2019 CM Wright, DN Fisher, *WV Nerone, **JLL Lichtenstein**, EA Tibbets, JN Pruitt. "Foundress number but not queen size or boldness, predicts colony life-history in wild paper wasps." Biological Journal of the Linnean society 128 (1), 20-29. <https://doi.org/10.1093/biolinnean/blz080>
- 2019 **JLL Lichtenstein**, *KA Daniel, *JB Wong, CM Wright, G Navid Doering, R Costa-Pereira, JN Pruitt. "Habitat structure changes the relationship between predator behavior, prey behavior, and prey survival rate." Oecologia 190(2), 298-308. <https://doi.org/10.1007/s00442-019-04344-w>

- 2019 CM Wright, **JLL Lichtenstein**, G Navid Doering, JD Pretorius, J Munier, JN Pruitt. "Collective personalities: present knowledge and new frontiers." *Behavioral Ecology & Sociobiology* 73 (3), 31. <https://doi.org/10.1007/s00265-019-2639-2>
- 2018 **JLL Lichtenstein**, A Kamath, SE Bengston, L Avilés, JN Pruitt. "Female-biased sex ratios increase colony survival and reproductive output in the spider *Anelosimus studiosus*." *The American Naturalist*, 192 (5), 552-663. <https://doi.org/10.1086/699838>
- 2018 CN Keiser, **JLL Lichtenstein**, CM Wright, *GT Chism, JN Pruitt. "Personality and behavioral syndromes in insects and spiders." From *Insect Behavior: From Mechanisms to Ecological and Evolutionary consequences*. Oxford University Press, 237-257. <https://doi.org/10.1086/705087>
- 2018 **JLL Lichtenstein**, *HK Rice, JN Pruitt. "Personality variation in two predator species does not predict survival of multiple prey and plant damage in a multitrophic system." *Behavioral Ecology & Sociobiology* 72 (4), 70. <https://doi.org/10.1007/s00265-018-2487-5>
- 2018 JN Pruitt, CM Wright, **JLL Lichtenstein**, *GT Chism, *BL McEwen, A Kamath, Noa Pinter-Wollman. "Selection for collective aggressiveness favors social susceptibility in social spiders." *Current Biology* 28 (1), 100-105. <https://doi.org/10.1016/j.cub.2017.11.038>
- 2017 **JLL Lichtenstein**, *GT Chism, A Kamath, JN Pruitt. "Intraindividual behavioral variability predicts foraging outcome in a beach-dwelling jumping spider." *Scientific Reports* 7(1), 18063. <https://doi.org/10.1038/s41598-017-18359-x>
- 2017 **JLL Lichtenstein**, CM Wright, *BL McEwen, N Pinter-Wollman, JN Pruitt. "The multidimensional behavioural hypervolumes of two interacting species predict their space use and survival." *Animal Behaviour* 132, 129-136. <https://doi.org/10.1016/j.anbehav.2017.08.010>
- 2017 **JLL Lichtenstein**, CM Wright, *LP Luscuskie, *GA Montgomery, JN Pruitt. "Bold spiders and participation in collective foraging augment weight gain in social spider colonies." *Current Zoology* 63 (5), 561-567. <https://doi.org/10.1093/cz/zow097>
- 2017 CM Wright, **JLL Lichtenstein**, *GA Montgomery, *LP Luscuskie, N Pinter-Wollman, JN Pruitt. "Exposure to predators reduces collective foraging aggressiveness and eliminates its relationship with colony personality composition." *Behavioral Ecology and Sociobiology* 71 (8), 126. <https://doi.org/10.1007/s00265-017-2356-7>

- 2017 JN Pruitt, KA Howell, SJ Gladney, Y Yang, **JLL Lichtenstein**, ME Spicer, SA Echeverri, & N Pinter-Wollman. “Behavioral Hypervolumes of Predator Groups and Predator-Predator Interactions Shape Prey Survival Rates and Selection on Prey Behavior.” *The American Naturalist* 189 (3), 254-266. <https://doi.org/10.1086/690292>
- 2016 **JLL Lichtenstein**, *K Knutson, *C Kuo, *KC Zhao, *HA Brittingham, *SE Geary, *S Ministero, *HK Rice, *Z David, I Scharf, JN Pruitt. Behavioral Ecology and Sociobiology. “Prolonged food restriction decreases body condition and reduces repeatability in individual personalities in web-building spiders.” *Behavioral Ecology & Sociobiology* 70 (11), 1793-1803. <https://doi.org/10.1007/s00265-016-2184-1>
- 2015 **JLL Lichtenstein**, JN Pruitt, AP Modlmeier. “Intraspecific variation in collective behaviors drives interspecific contests in ants.” *Behavioral Ecology* 27 (2), 553-556. <https://doi.org/10.1093/beheco/arv188>
- 2015 **JLL Lichtenstein**, JN Pruitt. “Similar patterns of frequency dependent selection on animal personalities emerge in three species of social spider.” *Journal of Evolutionary Biology* 28 (6), 1248-1256. <https://doi.org/10.1111/jeb.12651>
- 2015 AP Modlmeier, KN Kieser, CM Wright, **JLL Lichtenstein**, JN Pruitt. “Integrating animal personality into insect population ecology.” *Current Opinion in Insect Science* 9, 77-85. <https://doi.org/10.1016/j.cois.2015.03.008>

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ABSTRACT

ANIMAL PERSONALITY SHAPES THE OUTCOME OF SPECIES INTERACTIONS AND THEREBY THE STRUCTURE OF ECOSYSTEMS

By

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Most animals on the planet seem to exhibit some form of consistent individual variation in behavior. For instance, one goose might be exceptionally aggressive towards joggers its entire life, whereas another goose never harasses a jogger until the day it dies. These kinds of consistent patterns are called animal personality and they affect how individuals interact with members of their own species and other species. Aggressive water striders attack males and females so ferociously they prevent entire ponds of striders from mating. Active dragonfly larvae reduce the abundance of their prey, increasing the abundance of algae. Animal personality traits are thus functional traits with the potential to shape ecosystems. However, it remains unknown how animal personality affects complex ecosystems with numerous interacting populations. Here, I answer three key questions that reveal how and why animal personality shapes species interactions and ecosystem structure.

First, I asked whether the effect of animal personality on interactions between species depends on interactions between members of the same species. I tested whether behaviorally diverse katydids would be more likely to associate with members of their own species but reduce the survival of a potential competitor, froghoppers. Indeed, behaviorally diverse katydids tended to cluster together spatially and resulted in greater froghopper

mortality. This suggests that the effect of animal personality on the interaction between these species may depend on how they interact with members of their own species.

Second, I asked whether habitat structure and predator cannibalism determine the effect of predator and prey personality on prey survival. We filled mesocosms with predators (mantis) and prey (katydid) groups and observed how their behavioral variability affected katydid survival, while half of the mesocosms were filled with additional habitat structure in the form of climbing sticks. Mantis behavioral diversity correlated with katydid survival, likely because diverse groups contained the fewest of highly lethal phenotype. However, this was only true when we added habitat structure. The effects of animal personality on interactions between these two species depend on the habitat structure available to them.

In ecosystems with hundreds of interacting species, the signal of individual behavioral traits from any one species could easily be lost. Third, I tested whether mantis behavioral diversity could affect the structure of wild ecosystems. I cut 4m^2 squares into a meadow and added mantises with high and low levels of behavioral variability to the plots. After 40 days, I measured the biomass of plants and prey taxa in these plots. High mantis behaviorally diversity increased the biomass of the most dominant plant species (goldenrod), seemingly by reducing the prevalence of herbivores and predators. This demonstrates for the first time that animal personality can shape the structure of wild ecological communities.

Ecosystem processes occur at the scale of populations with numerous interacting species. These studies show how and why animal personality can affect species interactions and thereby ecosystems at a population level, whereas previous work focuses on the individual level. I thus show that animal personality can affect population-level processes in nature for the first time, opening the door to endless new questions.

TABLE OF CONTENTS

Chapter 1. Introduction to the ecology of animal personality.....	1
Animal personality.....	1
Animal personality and species interactions.....	4
References.....	7
Chapter 2. The multidimensional behavioral hypervolumes of two interacting species predict their space use and survival	13
Introduction.....	14
Materials and methods.....	17
Results.....	25
Discussion.....	28
References.....	33
Chapter 3. Habitat structure changes the relationships between predator behavior, prey behavior, and prey survival rates.....	37
Introduction.....	38
Materials and methods.....	42
Results.....	51
Discussion.....	58
References.....	63
Chapter 4. Top-down effects of intraspecific predator behavioral variation	68
Introduction.....	69
Materials and methods.....	72
Results.....	83

Discussion.....	88
References.....	91
Chapter 5: After all that what is the role of personality in ecology.....	98
The role of between-population variation in species interactions.....	99
Possibilities of personality eco-evo dynamics.....	102
Future directions and potential uses.....	104
Concluding thoughts.....	107
References.....	108

CHAPTER 1. INTRODUCTION TO THE ECOLOGY OF PERSONALITY

The central goal of this work is to see how individual trait variation shapes species interactions and thereby ecosystem structure. I will do this by combining two trait ecology approaches. Functional ecology focuses on the idea that species' traits, more than species identities, can predict species interaction outcomes and ecosystem structure (McGill, Enquist, Weiher, & Westoby, 2006; Schmitz, 2007). However, focusing on average trait levels for species can overlook critical information carried by within-species trait variation (Bolnick et al., 2003; Violle et al., 2012; Williams, 2007). Individual niche theory predicted that that individual identity drives ecological processes and is potentially more important than species identity (Van Valen, 1965). Individuals of the same species tend to be more similar to each other than they are to members of other species, so this variation was often discounted (Taper & Chase, 1985). Further, because niche can encompass endless traits, many studies lacked a mechanistic trait focus, instead considering the phenomenological actions of niche variation (Schreiber, Bürger, & Bolnick, 2011; Violle et al., 2012). These ideas can be bridged by evaluating the ecological consequences of individual variation in a functional trait with extensive background research. I will do this with animal personality.

ANIMAL PERSONALITY:

Individual animals often vary between each other and within themselves in how they behave (Bell, Hankison, & Laskowski, 2009; Stamps, Briffa, & Biro, 2012). For instance, all lizards may hide more and forage less after they sense a predator, but one lizard on average tends to

forage more despite risk of predation, whereas another prefers to hide and save energy (Rodríguez-Prieto, Martín, & Fernández-Juricic, 2011). When this kind of within-population variation between individuals can be distinguished from random variation, it is called animal personality (Bell et al., 2009; Gosling, 2001). The strength of personality variation is quantified by estimating repeatability, the ratio of variation between individuals to total variation (Nakagawa & Schielzeth, 2010). Greater variation between individuals and less variation within individuals increases repeatability estimates (Nakagawa & Schielzeth, 2010). Although personality refers to individuals' traits it is thus measured by assessing behavioral differences between members of a population, making it both an individual- and group-level phenomenon.

Virtually every animal species on the planet appears to exhibit some amount of this facet of behavioral variation (Bell et al., 2009; Kralj-Fišer & Schuett, 2014), from ants (Modlmeier & Foitzik, 2011) to lizards (Highcock & Carter, 2014), to geese (Kurvers et al., 2009), to sea anemones (Briffa & Greenaway, 2011). This is surprising, because natural selection generally erodes behavioral variation by eliminating non-adaptive phenotypes (Dingemanse & Réale, 2005). The question of why so much variation exists spawned thousands of papers probing the causes and consequences of animal personality (Beekman & Jordan, 2017; Bell et al., 2009). Because researchers aimed to relate behavioral variation to fitness (Smith & Blumstein, 2008), they picked traits that reflected how they interacted with their environment, like aggressiveness towards conspecifics (Eldakar, Dlugos, Wilcox, & Wilson, 2009), risk averseness (Carter, Heinsohn, Goldizen, & Biro, 2012; Laskowski & Bell, 2013), and metrics of habitat use (Drent, Verbeek, & Boon, 1996; Wilson, Coleman, Clark, & Biederman, 1993). For instance, if a researcher wanted to see how risk-taking

behavior (often called boldness) affected predation risk, they would measure how prey respond to a sham predator, and see how it relates to how they fare with a real predator (McGhee, Pintor, Suhr, & Bell, 2012). Consequently many studies revealed that individuals' personality traits can predict their fitness (Dingemanse, Both, Drent, & Tinbergen, 2004; Smith & Blumstein, 2008). Along the way, all this work found something else. Consistent individual behavior related to virtually every facet of animals' lives from prey choice (Nakayama, Rapp, & Arlinghaus, 2017; Oudman et al., 2016; Wilson et al., 1993) to parental behavior (Schuett, Dall, & Royle, 2011; Stein & Bell, 2012) to dispersal behavior (Badyaev et al., 2002; Cote, Clobert, Brodin, Fogarty, & Sih, 2010; Spiegel, Leu, Sih, Godfrey, & Bull, 2015) to the ticks on a squirrel (Boyer, Réale, Marmet, Pisanu, & Chapuis, 2010).

This litany of evidence suggests that animal personality traits are the strategies individuals use to eat, avoid being eaten, and reproduce, as well as the product of natural selection. For instance, the willingness of a fish to take risks might allow them to spend time in the open areas of their pond, so they consume more zooplankton than benthic invertebrates (Wilson et al., 1993). Their behavioral traits affect how they interact with predators and which prey they consume (Wilson et al., 1993), so having numerous bold fish in a population would deplete zooplankton and allow benthic invertebrates to survive, until herons deplete the pond of bold fish by eating them. Populations of the same species vary widely like this in the behavioral traits they contain (Bell et al., 2009). Animal personality is thus a widespread and widely variable class of functional traits that can potentially determine how animals interact with members of other species and their own species (Toscano, Gownaris, Heerhartz, & Monaco, 2016).

ANIMAL PERSONALITY AND SPECIES INTERACTIONS:

The effects of individual personality, much less personality variability, on ecological processes have barely been explored. There is evidence that individuals' personality traits can affect which species they interact with, and how they interact with them (Sih, Cote, Evans, Fogarty, & Pruitt, 2012; Toscano et al., 2016; Wolf & Weissing, 2012). Individuals' personalities predict how they escape predators (Godin & Davis, 1995; Pretorius, Lichtenstein, Eliason, Stier, & Pruitt, 2019), catch prey (Belgrad & Griffen, 2016; Nannini, Parkos III, & Wahl, 2012), compete with other species (Webster, Ward, & Hart, 2009), and acquire parasites (Boyer et al., 2010; Wilson et al., 1993). For instance, the functional response of highly active individual crabs eating mussels leveled off at higher mussel densities (more mussels eaten) compared to crabs that spent more time hiding (Toscano & Griffen, 2014). However, all this work looks at how the behavior of an individual affects interactions between individuals. Although there is literature to suggest that single individuals can have disproportionate impacts on conspecifics (Modlmeier, Keiser, Watters, Sih, & Pruitt, 2014), the behavioral traits of individuals rarely affect the outcome of ecosystems. To assess the effects of personality on ecosystems then, requires considering the population-level aspect of personality (i.e. between-population variation in between-individual variability).

Already, functional ecology provides much evidence for how between-population variation in trait averages can affect ecological processes (McGill et al., 2006; Schmitz, 2007). Individual niche theory, conversely, provides clues to how between-population variation in between-individual variation might affect ecological processes (Bolnick et al.,

2011; Violle et al., 2012). Take that a behavioral trait x affects an ecological outcome by the function $f(x)$. For instance, the activity level of ants might affect how they compete with another species along $f(x)$. According to Jensen's inequality, when this function is non-linear, then the average of $f(x)$, the actual ecological outcome, will not equal $f(\text{average of } x)$, the predicted outcome using the average trait value (Figure 1.1). So, if the effect of individual ant activity on competition between nests is not linear, the cumulative effect of the ants behavior will not equal the predicted effect of the average of all the ants' activities. In these cases, changing the variance of x , while holding the average constant can affect the ecological outcome, meaning that nonlinear effects of traits on ecological outcomes lead to trait variability affecting outcomes (Dyer, Croft, Morrell, & Krause, 2009).

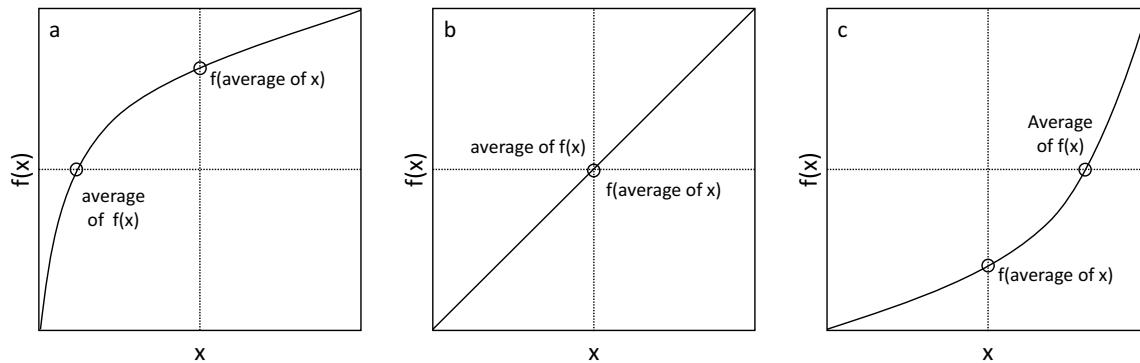


Figure 1.1 Graphical illustration of Jensen's inequality. In these plots, a trait x predicts an ecological outcome along function $f(x)$, represented by solid lines. Vertical dashed lines represent the average of x , and horizontal dashed lines represent the average of $f(x)$. If (a) $f(x)$ is non-linear and concave, then $f(\text{average of } x)$ will be greater than the average of $f(x)$. If (b) $f(x)$ is linear and then $f(\text{average of } x)$ will equal the average of $f(x)$. If (c) $f(x)$ is non-linear and convex, then $f(\text{average of } x)$ will be less than the average of $f(x)$.

Put in terms of personality traits, when the effect of individual behaviors on an ecological outcome do not combine additively, the effect of behavior will be non-linear. For

instance, while active ants perform various colony tasks readily (Charbonneau & Dornhaus, 2015), active ants do not always combine to form active ant colonies (Modlmeier, Keiser, Shearer, & Pruitt, 2014), and the activity of colonies nonlinearly determines how they fare in contests over resources with other species (Lichtenstein, Pruitt, & Modlmeier, 2015). The traits of individuals non-additively affect ecological outcomes like this, because individuals' behaviors also affect how they interact with members of their own species (David, Cézilly, & Giraldeau, 2011; Kurvers et al., 2009; Lichtenstein et al., 2016; Schuett, Godin, & Dall, 2011), increasing positive or negative interactions between individuals. Individuals' personality traits shape interactions between conspecifics very often. Based on this, I predict that between-population variation in personality variability often determines how species interact with each other.

Intraspecific interactions relate closely to one of two potential mechanisms behind the effects of trait diversity on ecological outcomes: sampling effects and complementarity/interference (Stachowicz, Best, Bracken, & Graham, 2008; Tilman, 1997). Sampling effects entail diverse groups being more likely to have individuals with some key phenotype that drives ecological processes (Huston, 1997; Stachowicz et al., 2008). For instance, a population of organisms with diversity in immune traits is more likely to survive a bad infectious disease outbreak (A. R. Hughes & Stachowicz, 2004; W. O. Hughes & Boomsma, 2004; Spielman, Brook, Briscoe, & Frankham, 2004). Sampling effects are hard to differentiate from the effects of trait averages on ecological outcomes, because diverse groups containing key phenotypes have higher average levels of those traits, but it is nonetheless very important to consider. The effects of complementarity depend on whether animals with different traits tend to compete and interfere with each other less or more (Sih,

Englund, & Wooster, 1998). If animals with different traits use different resources, like refuges from predators or food, then trait diverse populations should compete with each other less and avoid predators and find food more readily (Sih et al., 1998). There is some evidence that both of these mechanisms work in plant traits (Crutsinger et al., 2006; Lankau & Strauss, 2007), but they have only been pondered in behavioral traits (Pruitt et al., 2017). It remains largely untested whether, how, and when animal personality affects ecological processes at the scale of populations.

Here, I will address key questions that reveal how and when personality affects population-scale ecological processes. First, it is not known how the effects of animal personality on species interactions relates to intraspecific interactions. I will answer this, by testing how group-level behavioral metrics affects the outcome of interactions between members of the same species and members of two species (Chapter 2). Animal personality varies widely across space, so personality will affect species interactions across many habitats. I therefore tested how behavioral diversity can affect species interactions across variable environments (Chapter 3). Finally, it is very possible that the effects of one species' behavioral traits are lost in communities with hundreds of species, with hundreds of species traits affecting interactions (Lichtenstein, Rice, & Pruitt, 2018). I will therefore test whether behavioral diversity can shape the structure of wild unenclosed ecosystems with hundreds of interacting species (Chapter 4). After this experimental treatment of these subjects, I will synthesize these results and what they tell us about what animal personality does in ecosystems (Chapter 5).

REFERENCES:

- Badyaev, A. V., Hill, G. E., Beck, M. L., Dervan, A. A., Duckworth, R. A., McGraw, K. J., . . . Whittingham, L. A. (2002). Sex-biased hatching order and adaptive population divergence in a passerine bird. *Science*, 295(5553), 316-318.
- Beekman, M., & Jordan, L. A. (2017). Does the field of animal personality provide any new insights for behavioral ecology? *Behavioral Ecology*, 28(3), 617-623.
- Belgrad, B. A., & Griffen, B. D. (2016). Predator-prey interactions mediated by prey personality and predator hunting mode. *Proceedings of the Royal Society of London B: Biological Sciences*, 283(1828), 20160408. doi: 10.1098/rspb.2016.0408
- Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, 77(4), 771-783. doi: 10.1016/j.anbehav.2008.12.022
- Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., . . . Vasseur, D. A. (2011). Why intraspecific trait variation matters in community ecology. *Trends in ecology & evolution*, 26(4), 183-192. doi: 10.1016/j.tree.2011.01.009
- Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist*, 161(1), 1-28. doi: doi:10.1086/343878
- Boyer, N., Réale, D., Marmet, J., Pisanu, B., & Chapuis, J. L. (2010). Personality, space use and tick load in an introduced population of Siberian chipmunks *Tamias sibiricus*. *Journal of Animal Ecology*, 79(3), 538-547.
- Briffa, M., & Greenaway, J. (2011). High in situ repeatability of behaviour indicates animal personality in the beadlet anemone *Actinia equina* (Cnidaria). *PLoS One*, 6(7), e21963.
- Carter, A. J., Heinsohn, R., Goldizen, A. W., & Biro, P. A. (2012). Boldness, trappability and sampling bias in wild lizards. *Animal Behaviour*, 83(4), 1051-1058.
- Charbonneau, D., & Dornhaus, A. (2015). Workers ‘specialized’ on inactivity: behavioral consistency of inactive workers and their role in task allocation. *Behavioral Ecology and Sociobiology*, 69(9), 1459-1472.
- Cote, J., Clobert, J., Brodin, T., Fogarty, S., & Sih, A. (2010). Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 4065-4076.
- Crutsinger, G. M., Collins, M. D., Fordyce, J. A., Gompert, Z., Nice, C. C., & Sanders, N. J. (2006). Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science*, 313(5789), 966-968. doi: 10.1126/science.1128326
- David, M., Cézilly, F., & Giraldeau, L.-A. (2011). Personality affects zebra finch feeding success in a producer-scrounger game. *Animal Behaviour*, 82(1), 61-67.
- Dingemanse, N. J., Both, C., Drent, P. J., & Tinbergen, J. M. (2004). Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 271(1541), 847-852.
- Dingemanse, N. J., & Réale, D. (2005). Natural selection and animal personality. *Behaviour*, 142(9-10), 1159-1184.

- Drent, P. J., Verbeek, M. E., & Boon, A. (1996). Exploration, aggressive behaviour and dominance in pair-wise confrontations of juvenile male great tits. *Behaviour*, 133(11-12), 945-963.
- Dyer, J. R., Croft, D. P., Morrell, L. J., & Krause, J. (2009). Shoal composition determines foraging success in the guppy. *Behavioral Ecology*, 20(1), 165-171.
- Eldakar, O. T., Dlugos, M. J., Wilcox, R. S., & Wilson, D. S. (2009). Aggressive mating as a tragedy of the commons in the water strider *Aquarius remigis*. *Behavioral Ecology and Sociobiology*, 64(1), 25.
- Godin, J.-G. J., & Davis, S. A. (1995). Who dares, benefits: predator approach behaviour in the guppy (*Poecilia reticulata*) deters predator pursuit. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 259(1355), 193-200.
- Gosling, S. D. (2001). From mice to men: what can we learn about personality from animal research? *Psychological Bulletin*, 127(1), 45. doi: 10.1037//0033-2909.127.1.45
- Highcock, L., & Carter, A. J. (2014). Intraindividual variability of boldness is repeatable across contexts in a wild lizard. *PLoS One*, 9(4), e95179.
- Hughes, A. R., & Stachowicz, J. J. (2004). Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. *Proceedings of the National Academy of Sciences of the United States of America*, 101(24), 8998-9002. doi: 10.1073/pnas.0402642101
- Hughes, W. O., & Boomsma, J. J. (2004). Genetic diversity and disease resistance in leaf-cutting ant societies. *Evolution*, 58(6), 1251-1260.
- Huston, M. A. (1997). Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia*, 110(4), 449-460.
- Kralj-Fišer, S., & Schuett, W. (2014). Studying personality variation in invertebrates: why bother? *Animal Behaviour*, 91, 41-52.
- Kurvers, R. H., Eijkelenkamp, B., van Oers, K., van Lith, B., van Wieren, S. E., Ydenberg, R. C., & Prins, H. H. (2009). Personality differences explain leadership in barnacle geese. *Animal Behaviour*, 78(2), 447-453.
- Lankau, R. A., & Strauss, S. Y. (2007). Mutual Feedbacks Maintain Both Genetic and Species Diversity in a Plant Community. *Science*, 317(5844), 1561-1563. doi: 10.1126/science.1147455
- Laskowski, K. L., & Bell, A. M. (2013). Competition avoidance drives individual differences in response to a changing food resource in sticklebacks. *Ecology Letters*, 16(6), 746-753.
- Lichtenstein, J. L., Pruitt, J. N., & Modlmeier, A. P. (2015). Intraspecific variation in collective behaviors drives interspecific contests in acorn ants. *Behavioral Ecology*, arv188.
- Lichtenstein, J. L., Rice, H. K., & Pruitt, J. N. (2018). Personality variation in two predator species does not impact prey species survival or plant damage in staged mesocosms. *Behavioral Ecology and Sociobiology*, 72(4), 70.
- Lichtenstein, J. L., Wright, C. M., Luscuskie, L. P., Montgomery, G. A., Pinter-Wollman, N., & Pruitt, J. N. (2016). Participation in cooperative prey capture and the benefits gained from it are associated with individual personality. *Current Zoology*, 63(5), 561-567.
- McGhee, K. E., Pintor, L. M., Suhr, E. L., & Bell, A. M. (2012). Maternal exposure to predation risk decreases offspring antipredator behaviour and survival in threespined

- stickleback. *Functional Ecology*, 26(4), 932-940. doi: 10.1111/j.1365-2435.2012.02008.x
- McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in ecology & evolution*, 21(4), 178-185.
- Modlmeier, A. P., & Foitzik, S. (2011). Productivity increases with variation in aggression among group members in Temnothorax ants. *Behavioral Ecology*, arr086.
- Modlmeier, A. P., Keiser, C. N., Shearer, T. A., & Pruitt, J. N. (2014). Species-specific influence of group composition on collective behaviors in ants. *Behavioral Ecology and Sociobiology*, 68(12), 1929-1937.
- Modlmeier, A. P., Keiser, C. N., Watters, J. V., Sih, A., & Pruitt, J. N. (2014). The keystone individual concept: an ecological and evolutionary overview. *Animal Behaviour*, 89, 53-62.
- Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biological Reviews*, 85(4), 935-956.
- Nakayama, S., Rapp, T., & Arlinghaus, R. (2017). Fast–slow life history is correlated with individual differences in movements and prey selection in an aquatic predator in the wild. *Journal of Animal Ecology*, 86(2), 192-201.
- Nannini, M. A., Parkos III, J., & Wahl, D. H. (2012). Do Behavioral Syndromes Affect Foraging Strategy and Risk-Taking in a Juvenile Fish Predator? *Transactions of the American Fisheries Society*, 141(1), 26-33. doi: 10.1080/00028487.2011.639268
- Oudman, T., Bijleveld, A. I., Kavelaars, M. M., Dekkinga, A., Cluderay, J., Piersma, T., & van Gils, J. A. (2016). Diet preferences as the cause of individual differences rather than the consequence. *Journal of Animal Ecology*, 85(5), 1378-1388.
- Pretorius, J. D., Lichtenstein, J. L. L., Eliason, E. J., Stier, A. C., & Pruitt, J. N. (2019). Predator-induced selection on urchin activity level depends on urchin body size. *Ethology*, 125(10), 716-723. doi: 10.1111/eth.12924
- Pruitt, J. N., Howell, K. A., Gladney, S. J., Yang, Y., Lichtenstein, J. L., Spicer, M. E., . . . Pinter-Wollman, N. (2017). Behavioral Hypervolumes of Predator Groups and Predator-Predator Interactions Shape Prey Survival Rates and Selection on Prey Behavior. *The American Naturalist*, 189(3), 254-266.
- Rodríguez-Prieto, I., Martín, J., & Fernández-Juricic, E. (2011). Individual variation in behavioural plasticity: direct and indirect effects of boldness, exploration and sociability on habituation to predators in lizards. *Proceedings of the Royal Society B: Biological Sciences*, 278(1703), 266-273.
- Schmitz, O. J. (2007). Predator diversity and trophic interactions. *Ecology*, 88(10), 2415-2426.
- Schreiber, S. J., Bürger, R., & Bolnick, D. I. (2011). The community effects of phenotypic and genetic variation within a predator population. *Ecology*, 92(8), 1582-1593.
- Schuett, W., Dall, S. R., & Royle, N. J. (2011). Pairs of zebra finches with similar ‘personalities’ make better parents. *Animal Behaviour*, 81(3), 609-618.
- Schuett, W., Godin, J. G. J., & Dall, S. R. (2011). Do female zebra finches, *Taeniopygia guttata*, choose their mates based on their ‘personality’? *Ethology*, 117(10), 908-917.
- Sih, A., Cote, J., Evans, M., Fogarty, S., & Pruitt, J. (2012). Ecological implications of behavioural syndromes. *Ecology Letters*, 15(3), 278-289. doi: 10.1111/j.1461-0248.2011.01731.x

- Sih, A., Englund, G., & Wooster, D. (1998). Emergent impacts of multiple predators on prey. *Trends in Ecology & Evolution*, 13(9), 350-355.
- Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: a meta-analysis. *Behavioral Ecology*, 19(2), 448-455.
- Spiegel, O., Leu, S. T., Sih, A., Godfrey, S. S., & Bull, C. M. (2015). When the going gets tough: behavioural type-dependent space use in the sleepy lizard changes as the season dries. *Proceedings of the Royal Society of London B: Biological Sciences*, 282(1819), 20151768.
- Spielman, D., Brook, B. W., Briscoe, D. A., & Frankham, R. (2004). Does inbreeding and loss of genetic diversity decrease disease resistance? *Conservation Genetics*, 5(4), 439-448.
- Stachowicz, J. J., Best, R. J., Bracken, M. E., & Graham, M. H. (2008). Complementarity in marine biodiversity manipulations: reconciling divergent evidence from field and mesocosm experiments. *Proceedings of the national Academy of Sciences*, 105(48), 18842-18847.
- Stamps, J. A., Briffa, M., & Biro, P. A. (2012). Unpredictable animals: individual differences in intraindividual variability (IIV). *Animal Behaviour*, 83(6), 1325-1334.
- Stein, L. R., & Bell, A. M. (2012). Consistent individual differences in fathering in threespined stickleback *Gasterosteus aculeatus*. *Current Zoology*, 58(1), 45-52.
- Taper, M. L., & Chase, T. J. (1985). Quantitative genetic models for the coevolution of character displacement. *Ecology*, 66(2), 355-371.
- Tilman, D. (1997). Distinguishing between the Effects of Species Diversity and Species Composition. *Oikos*, 80(1), 185-185. doi: 10.2307/3546532
- Toscano, B. J., Gownaris, N. J., Heerhartz, S. M., & Monaco, C. J. (2016). Personality, foraging behavior and specialization: integrating behavioral and food web ecology at the individual level. *Oecologia*, 182(1), 55-69.
- Toscano, B. J., & Griffen, B. D. (2014). Trait-mediated functional responses: predator behavioural type mediates prey consumption. *Journal of Animal Ecology*, 83(6), 1469-1477.
- Van Valen, L. (1965). Morphological variation and width of ecological niche. *The American Naturalist*, 99(908), 377-390.
- Violle, C., Enquist, B. J., McGill, B. J., Jiang, L., Albert, C. H., Hulshof, C., . . . Messier, J. (2012). The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution*, 27(4), 244-252.
- Webster, M., Ward, A., & Hart, P. (2009). Individual boldness affects interspecific interactions in sticklebacks. *Behavioral Ecology and Sociobiology*, 63(4), 511-520.
- Williams, T. D. (2007). Individual variation in endocrine systems: moving beyond the 'tyranny of the Golden Mean'. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1497), 1687-1698.
- Wilson, D. S., Coleman, K., Clark, A. B., & Biederman, L. (1993). Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): An ecological study of a psychological trait. *Journal of Comparative Psychology*, 107(3), 250. doi: 10.1037/0735-7036.107.3.250
- Wolf, M., & Weissing, F. J. (2012). Animal personalities: consequences for ecology and evolution. *Trends in Ecology & Evolution*, 27(8), 452-461. doi: 10.1016/j.tree.2012.05.001

CHAPTER 2. THE MULTIDIMENSIONAL BEHAVIORAL HYPERVOLUMES OF TWO INTERACTING SPECIES PREDICT THEIR SPACE USE AND SURVIVAL

ABSTRACT:

Individual animals differ consistently in their behaviour, thus impacting a wide variety of ecological outcomes. Recent advances in animal personality research have established the ecological importance of the multidimensional behavioural volume occupied by individuals and by multi-species communities. Here, we examine the degree to which the multidimensional behavioural volume of a group predicts the outcome of both intra- and interspecific interactions. In particular, we test the hypothesis that a population of conspecifics will experience low intraspecific competition when the population occupies a large volume in behavioural space. We further hypothesize that populations of interacting species will exhibit greater interspecific competition when one or both species occupy large volumes in behavioural space. We evaluate these hypotheses by studying groups of katydids (*Scudderia* nymphs) and froghoppers (*Philaenus spumarius*), which compete for space on, and food from their shared host plant, *Solidago canadensis*. We found that individuals in single-species groups of katydids positioned themselves closer to one another, suggesting reduced competition, when groups occupied a large behavioural volume. When both species were placed together, we found that the survival of froghoppers was greatest when both froghoppers and katydids occupied a small volume in behavioural space, particularly at high froghopper densities. These results suggest that groups that occupy large behavioural volumes can have low intraspecific competition but high interspecific competition. Thus, behavioural hypervolumes appear to have ecological consequences at both the level of the

population and community and may help to predict the intensity of competition both within and across species.

INTRODUCTION:

Consistent individual differences in behaviour, known as animal personality, appear to be ubiquitous throughout the animal kingdom (Gosling, 2001; Kralj-Fišer & Schuett, 2014).

Animal personality determines aspects of individuals' ecology such as individual variation in social behaviour (Lichtenstein et al., 2016; Wright, Holbrook, & Pruitt, 2014) space use (Pearish, Hostert, & Bell, 2013; A. D. Wilson & McLaughlin, 2007), and diet (D. S. Wilson, Coleman, Clark, & Biederman, 1993). The personality literature has long argued that a comprehensive understanding of an individual's behaviour requires a multi-trait approach (Sih, Bell, & Johnson, 2004; Sih, Cote, Evans, Fogarty, & Pruitt, 2012). Despite this early emphasis on a multi-trait approach and the availability of statistical approaches to evaluate multiple behaviours simultaneously, many studies that relate personality to ecological outcomes continue to examine only one trait at a time (Wolf & Weissing, 2012). Here we examine multiple behaviours simultaneously using a recently developed multivariate measure, the behavioural hypervolume (Pruitt, Bolnick, Sih, DiRienzo, & Pinter-Wollman, 2016; Pruitt et al., 2017).

We define a behavioural hypervolume as the volume of an irregular convex polygon in multidimensional behavioural space occupied by an individual, group, population, or even community. Multidimensional behavioural space refers to a space in which each dimension represents standardized performance in a different personality test. In other words,

behavioural hypervolumes are a metric of behavioural diversity that incorporates three or more personality traits. Behavioural hypervolumes emphasize behavioural extremes, because observations on the boundaries of these shapes in behavioural space dictate their hypervolume (Pruitt et al., 2016; Pruitt et al., 2017). Consequently, individuals in convex polygons that occupy more behavioural space at the group or population level tend to be more behaviourally dissimilar to each other, at least, when one considers the most extreme individuals. This dissimilarity may, in turn, map to individuals' ecological niche, including the degree to which they compete with conspecifics and heterospecifics. There is considerable evidence to suggest that this is true: individual variation in personality often predicts how individuals interact with conspecifics (Kurvers et al., 2009; Laskowski & Bell, 2013) and heterospecifics (Chang, Teo, Norma-Rashid, & Li, 2017; DiRienzo, Pruitt, & Hedrick, 2013; Webster, Ward, & Hart, 2009). Thus, behavioural hypervolumes may impact ecological processes.

For instance, recent work has shown that the behavioural hypervolume of a group can influence the outcome of predator-prey interactions (Pruitt et al., 2017), and the behavioural hypervolume of a mixed-species community can determine their stability (Pruitt et al., 2016). Here we examine whether the behavioural hypervolumes of groups of interacting species can predict the outcome of both intra- and interspecific interactions. We evaluate this possibility by examining two insect species that inhabit and feed on the Canada Goldenrod (*Solidago canadensis*). We chose these two species because they are two of the most common insects in old fields, they share a resource, and they are found on the same plant parts, especially leaves near the crown, which suggests that they may compete for access to the most preferred regions of their host plant (Lichtenstein & McEwen, pers. obs.). Katydid nymphs from the

genus *Scudderia* and the Meadow Froghopper (*Philaenus spumarius*) both feed on the Canada Goldenrod (Weaver & King, 1954). Notably, *Scudderia* nymphs are leaf chewers native to our study site, whereas the froghoppers, *P. spumarius*, are sap-suckers that are wildly successful invaders across the Nearctic. These froghoppers are in some areas the second most abundant herbivore on Goldenrods (Root & Cappuccino, 1992), and have more deleterious effects on Goldenrod growth and reproduction than other herbivores (Meyer, 1993; Meyer & Root, 1993). Both species reach high densities on goldenrod leaves over large geographic ranges, thus creating ample opportunities for both species to interact with both conspecifics and each other.

Here, we ask whether behavioural hypervolumes shape how each species interacts with conspecifics (intraspecific interaction) and with other species (interspecific interaction). Specifically, we evaluated two predictions: First, we predict that single-species groups of katydids with greater behavioural hypervolumes will cluster together in space more than groups with small behavioural hypervolumes. We reason that individuals in single species groups occupying larger hypervolumes will differ from each other more in their niches, thus reducing intraspecific competition. This is based on the assertion that personality traits relate to the ecological niche that individuals occupy, such as differences among individuals in diet (D. S. Wilson et al., 1993) and space use (Pearish et al., 2013; A. D. Wilson & McLaughlin, 2007).

Second, we predict that greater behavioural hypervolumes in katydids, froghoppers, or both, will decrease the survival of froghoppers due to interspecific competition. There is considerable evidence showing that individual's personality scores relate to the strategies that animals use when interacting with other species (Belgrad & Griffen, 2016; Chang et al.,

2017; DiRienzo et al., 2013; Webster et al., 2009). Therefore, we reason that behaviourally diverse groups will contain a greater diversity of these interaction strategies, thus causing them to interact with other species more frequently and intensely. Addressing these hypotheses will allow us to further evaluate the ecological consequences of behavioural hypervolumes and potentially extend the ecological niche concept to behavioural or personality ‘niches’.

MATERIALS & METHODS:

Collection Site and Study Organisms

We performed our experiments at the Donald S. Wood Field Laboratory (DSW) of the Pymatuning Laboratory of Ecology in June, July, and August 2016. The DSW is located in Northwest Pennsylvania ($41^{\circ}34'09.6''N$ $80^{\circ}27'51.4''W$). The property is composed of mixed forest and semi-annually mowed old field. The old field portion is dominated by the goldenrod species *Solidago canadensis*, *Solidago grandiflora*, and *Solidago rugosa*, in order of relative abundance. At our collection site, these species tend to form dense monospecific stands comprising hundreds or thousands of stems with a few lone stems scattered around (Lichtenstein & McEwen, per obs). We collected roughly 1000 froghoppers, *Philaenus spumarius* (Aphrophoridae), and approximately 400 3rd -7th instar katydid nymphs from the genus *Scudderia* (Tettigoniidae) from a 40m by 60m section of the old field via sweep-netting. *Philaenus spumarius* are an invasive insect native to the Palearctic that has spread over the entire Nearctic and feeds on hundreds of plant species, including *S. canadensis* (Weaver & King, 1954). At an average length of 6mm, froghoppers, are much smaller than

katydid nymphs but they are the longest and fastest jumping insect species relative to body size yet measured, surpassing even fleas (Burrows, 2003). They reach densities of more than 15 individuals per host plant at our site (Lichtenstein & McEwen, per obs). Katydid nymphs of the two species that occur at our site (*S. curvicauda* and *S. furcata*) are indistinguishable as nymphs and preferentially inhabit moist and poorly drained old field areas (Cantrall, 1943). We found both of these insects frequently in *S. canadensis* stands and observed them feeding on *S. canadensis* leaves in the lab and *in situ*. After we captured the insects, we kept each individual in a 50 ml tube (12 cm tall, 3 cm diameter) with an *S. canadensis* leaf. Aside from the insects we used for our personality repeatability trials described below, we did not keep insects in tubes for more than 24 hours.

Behavioural assays

To acquire behavioural hypervolumes, we ran our insects through three behavioural tests: (i) perch height (i.e., habitat use), (ii) activity level, and (iii) boldness. We performed these tests in the same sequence for each individual before returning them to their home containers, with 2h between tests of different behaviours. To assess the repeatability of these traits, we performed each behavioural assay on each individual once a day for four consecutive days on 13 froghoppers and 12 katydid nymphs. After establishing the repeatability of these behaviours, we concluded that our behavioural assays quantified temporally consistent personality traits in these species. This allowed us to run individuals in each behavioural assay only once for the mesocosm and space-use studies (described below).

Perch height: To quantify an individual's perch height, we measured the height at which an individual perched in a novel 50 ml storage tube containing a single leaf of their

host plant. We made sure that each tube had a leaf of a similar size (between 6-7 cm length). This species spends much of their time on goldenrod leaves, particularly near the crown of the plant. Therefore, we measured the specific location on leaves where they might spend most of their time. The trial was initiated by setting an individual at the bottom of a clean tube and then gently placing a leaf so that it extended up the side of the tube, with the stem facing downward. We then permitted the insects 30 minutes to climb their leaves and to select a site on which to settle and initiate feeding. Most insects ascended to the top of the container within 10-15 minutes and then settled at a lower point. After 30 minutes, we measured their height above the ground. For the repeatability trials, we changed each insect's leaf and container between consecutive trials. Height was measured to the millimeter using digital calipers.

Activity level: Activity level was assessed by placing an individual insect at the bottom of a clean 50 ml tube. The 50 ml tube was placed at a 15° angle to the ground to instigate the insects' tendency to climb up the surface of the container. We then measured the time in seconds each individual spent active (walking, climbing) over the next five minutes. Activity was quantified as the number of seconds during which an individual moved in the 5-minute observation, with more active individuals moving for longer durations.

Boldness: To measure the boldness of individual insects we placed each individual in a clean 700 ml container and allowed it to settle for 15 minutes. We then gently prodded the insects repeatedly on the head from the front with a toothpick until they jumped or until we reached 50 prods. We quantified boldness as the number of prods required to elicit a flight response. A value of 50 was given if we could not elicit a jump response after 50 prods. This happened for 10.4 % of froghoppers, and 42.5% of katydids. The rationale here is that bold

individuals remain longer on their host plant despite being disturbed by an unknown competitor or predator, whereas shy individuals flee more quickly when disturbed.

Space use experiment

We focused on the effects of behavioural hypervolumes on space use in katydids because of the difficulty of visually tracking froghopper groups. To test our prediction that groups of katydids that occupy greater behavioural hypervolumes tend to cluster spatially (potentially indicative of lower competition) we placed groups of five katydids whose behaviour had previously been tested in all three behavioural assays, in 60 cm x 60 cm steel and mesh cages (1450DSV: BioQuip Products Inc.) with five non-focal froghoppers. The presence of froghoppers mimics the conditions that katydids experience in the wild and the context in which these species interact during our staged survival experiments. The cages were kept indoors and contained only a single potted *S. canadensis* stem. We evaluated the effects of behavioural hypervolumes on space use in a mixed-species situation to mimic the conditions of our survival studies (described below) and because these are the conditions that we most commonly observe these insects *in situ*. Around 17:00 the day before we recorded, we placed the insects in mesocosms. The next day, we recorded the spatial position of all individuals in the cage over the course of eight hours. We drew axes along the outside of the cages running between 0 cm and 60 cm, to create a 3-dimensional grid at the resolution of 1cm³ that allowed us to note the position of each individual every hour between 9:00 and 16:00 on the day after establishing the mesocosm. We computed the average distance between each of the katydids using the pdist function in Matlab to obtain an average interindividual distance for each time point.

Survival experiment

To test the effects of behavioural hypervolumes on species interaction outcomes, we observed froghopper survival in mesocosms (1450DSV: BioQuip Products Inc.) containing katydids, under two conditions: high and low froghopper density. This design allowed us to evaluate possible density-dependent effects of behavioural hypervolumes. Low froghopper density mesocosms contained 10 froghoppers and 10 katydids ($n = 16$) and high froghopper density mesocosms contained 20 froghoppers and 10 katydids ($n = 16$). No katydids were used in both the space use and survival experiments. Three weeks prior to initiating our mesocosm trials we transplanted a single goldenrod (*S. canadensis*) stem into patches of manicured lawn immediately adjacent to our old field site. The day before we deployed the mesocosms, we cut all the plants within a meter of the stem to 6cm in height to help ensure that all mesocosms had similar structural environments. The single goldenrod in each mesocosm was 45-55cm tall at the start of the survival study. We placed one mesocosm of each froghopper density treatment on the ground every other day during the months of June, July, and the first week of August. This procedure resulted in 20 mesocosms being deployed at any given time. Mesocosm enclosures were deployed with detached bottom panels to allow placing them on the ground in the field around living stems. We then lined the bottom edges of the inside and outside of each mesocosm with commercial topsoil to prevent animals from escaping.

Once the mesocosms were prepared, we assembled treatment groups haphazardly using pools of insects that we tested behaviourally the day before, blind to their performance on behavioural tests. Ten days later, we harvested the insects by hand until we could no

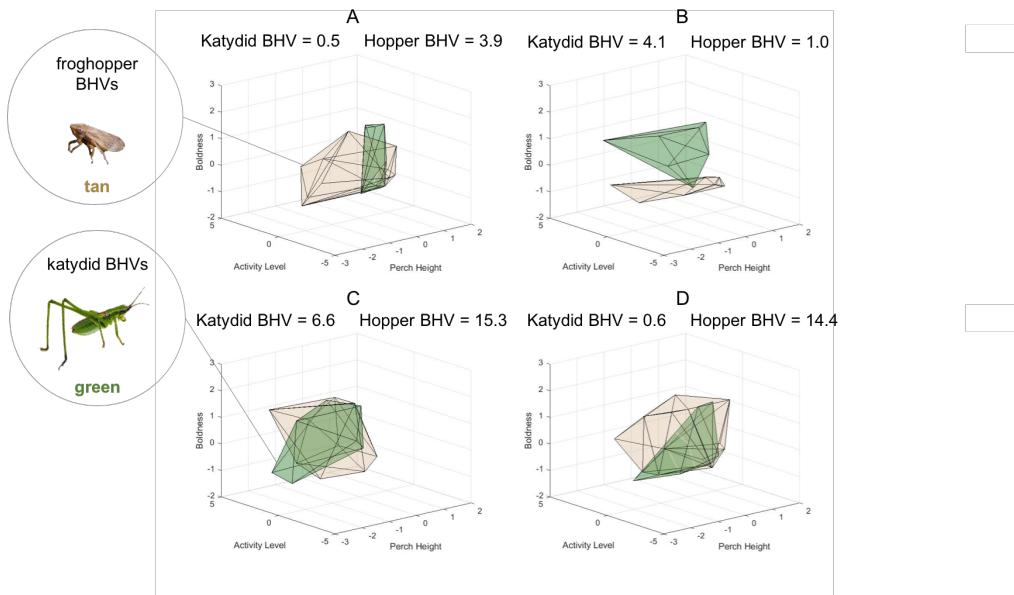
longer find insects and recorded the number of individuals that had disappeared. We assumed that insects that had gone missing during this time had perished, as opposed to escaped. This assumption is anecdotally supported by the number of froghopper carcasses recovered at the bottom of each mesocosm. The harvesting process required approximately one hour per mesocosms to ensure all were collected, although most insects were recovered in the first fifteen minutes.

Statistical Methods

We first calculated the repeatability of each behavioural trait for each species. We did this using the rptR package (Nakagawa & Schielzeth, 2013) in R (version 3.3.1). This package fits GLMMs with “individual ID” designated as a random factor, trial number as a fixed effect, and individuals’ performance on the test as the response variable. The proportion of variation explained by individual ID was used as our estimate of repeatability. Next the package establishes confidence intervals for the data using a bootstrapping procedure, and the estimate was deemed to be significant if its 95% CI did not overlap with zero. Our bootstraps used 1000 iterations. We fit both species’ boldness with a Poisson distribution, because this distribution best fit our data for both species, as determined by examining q-q plots comparing our data with other distributions. Froghopper perch height and activity level did not conform to a normal distribution, even after log transformation, however, they did fit a Poisson distribution which was used as the link function in their analysis as well. Katydid

perch height conformed to a normal distribution after log transformation and fits this model well.

Figure 2.1. Example behavioural hypervolume (BHV) pairs from four mesocosms in the ‘survival’ experiment. Green hypervolumes represent katydids, and tan hypervolumes represent froghoppers in each mesocosm. These behavioural hypervolumes represent the behavioural 3-dimentional space that the individuals in each species occupy. Each dimension in this space is defined by performance on one of the three behavioural tests. Pairs A and B are examples where both species had relatively low hypervolumes, and pairs C and D are examples where both species had relatively high hypervolumes.



To calculate behavioural hypervolumes, we first scaled each of the three behavioural measures using a Z-transformation, relative to all conspecifics. Then, we plotted each individual insect as a point in a 3-dimentional behavioural space in which each dimension represents performance in one of our behavioural tests. The hypervolume was then calculated as the volume of the smallest possible convex polyhedron defined by a group of individuals of the same species. We calculated the behavioural hypervolume for each species in every space use and survival assessment replicate. We computed all hypervolume calculations using the convhulln function in Matlab. Examples of these volumes can be found in Figure 2.1. We also compared the average hypervolume of the froghopper groups in the high versus

low-density treatments to test whether our density treatments confounded density with behavioural hypervolume, because larger groups may occupy larger behavioural hypervolumes by chance alone.

Because in the space use experiment we tracked the position of insects hourly over the course of eight hours, we first examined if interindividual distances changed over time. Using the rptR package in R, we found that katydid groups were consistent in their interindividual distance across hourly observations in their space use trials. We therefore proceeded to use the average interindividual distance (IID) across all time points in subsequent analysis. Specifically, we used a normally distributed GLM with katydid average IID as a response variable and katydid behavioural hypervolume as a predictor variable. The model's residuals did not deviate significantly from a normal distribution (Shapiro-Wilk W test: $W = 0.943$, $p = 0.619$).

To test the effects of behavioural hypervolumes on froghopper survival, we used a normally distributed GLM with the proportion of froghoppers that survived as our response variable and froghopper density treatment, froghopper *hypervolumes*, katydid *hypervolume*, and all possible interaction terms as predictor variables. These interaction terms allowed us to examine whether the hypervolumes of either or both species predicted froghopper survival. This model's residuals also did not deviate significantly from a normal distribution (Shapiro-Wilk W test: $W = 0.965$, $p = 0.348$), once again suggesting that it is a good fit for the model.

We further evaluated the predictive power of behavioural hypervolumes against univariate metrics of personality (the average personality scores of each species) using the Akaike weight criterion. This model selection procedure selects for models with low AICc and high Akaike weights (Akaike, 1987; Burnham & Anderson, 2003). We performed this

procedure separately for models predicting froghopper and katydid survival. We used JMP version 13.0 for these analyses, with the exception of our repeatability and behavioural hypervolume calculations.

Results

Both insects ranged in perch height from 0.1 cm to 12 cm. Froghoppers perched at an average height of 8.07 ± 0.10 SE cm, and katydids perched at 7.94 ± 0.15 SE cm. Froghoppers and katydids both ranged in time spent moving from 0 to 300 seconds, froghoppers moved for an average of 50.14 ± 1.82 SE seconds and katydids moved for 25.19 ± 1.88 SE seconds. Froghoppers moved after an average of 12.55 ± 0.57 SE pokes, and katydids after an average of 30.44 ± 1.16 SE pokes.

Hypervolumes

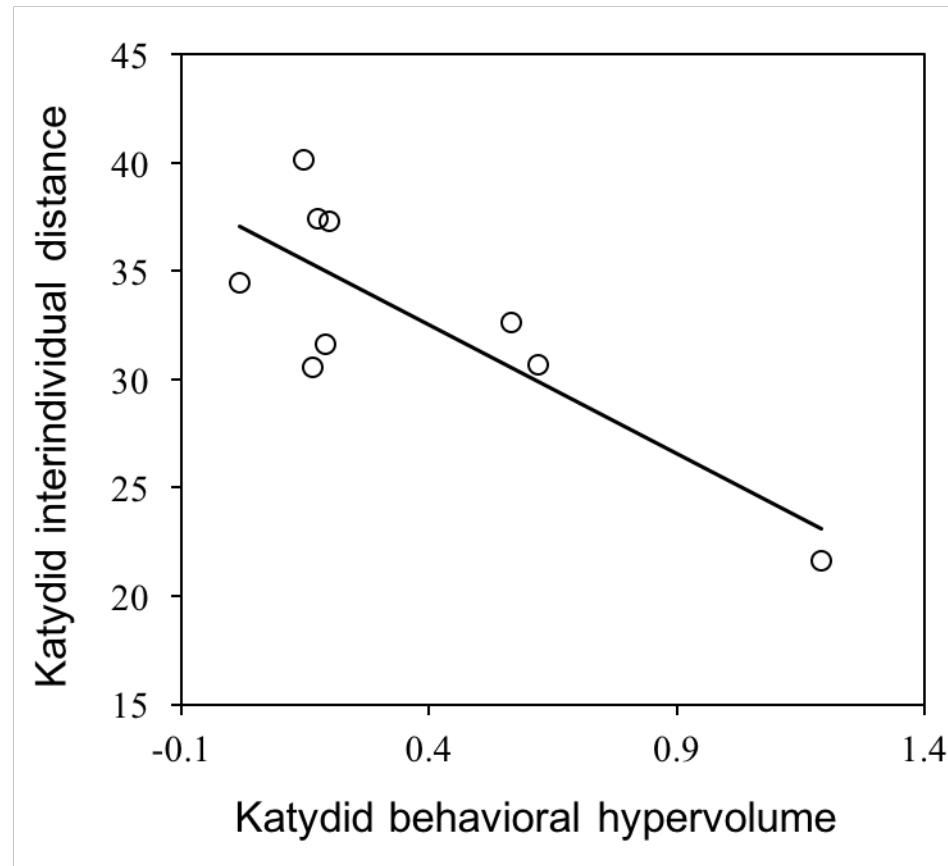
We obtained 32 froghopper behavioural hypervolumes and 32 katydid behavioural hypervolumes. Examples of both are shown in Figure 2.1. The behavioural hypervolumes of froghoppers did not differ significantly between the high and low froghopper densities (t -test: $t = 1.77$, $p = 0.09$), thus population density and behavioural hypervolume were not conflated in these experiments.

Repeatability estimates

We found that both katydids and froghoppers were significantly repeatable in their perch height, activity level, and boldness. As we mentioned before, we found that katydid groups

were consistent in their interindividual distance across hourly observations in their space use trials.

Figure 2.2. The relationship between katydid (*Scudderia* nymphs) behavioural hypervolume and katydid interindividual distance. Katydid behavioural hypervolume was negatively correlated with their interindividual distance (GLM: $R^2 = 0.660$, L-R Chi square = 9.709, $p = 0.002$). Line represents a best-fit linear regression.



Tendency to associate

Katydid groups' average interindividual distances were negatively correlated with their

behavioural hypervolumes (GLM: $R^2 = 0.660$, L-R Chi square = 9.709, $p = 0.002$; Figure 2.2), meaning that katydid groups composed of behaviourally unlike individuals tended to remain closer together.

Table 2.1. The outputs of normally distributed GLMs predicting the survival of froghoppers. The predictor variable column begins with the whole model output, followed by the effect tests of the predictor variables that comprise the whole model. Significant p values are in bold.

Predictor Variable	R2	DF	L-R Chi2	p
Whole model	0.355	25	14.45	0.0437
Density treatment		1	0.77	0.3810
Froghopper behavioural hypervolume		1	0.05	0.8200
Katydid behavioural hypervolume		1	7.28	0.0070
Froghopper hypervolume*Katydid hypervolume		1	4.58	0.0324
Density treatment*Froghopper hypervolume		1	0.80	0.3714
Density treatment*Katydid hypervolume		1	2.75	0.0971
Density treatment*Froghopper hypervolume*Katydid hypervolume		1	6.50	0.0108

Survival

Froghopper survival was best explained by models using behavioural hypervolumes, which exhibited an Akaike weight ($AICc = 0.16$, $AICc$ weight = 0.85) over nine times greater than the next best model ($AICc = 4.6$, $AICc$ weight = 0.09) and others using the simple average of any one behaviour. Froghopper survival related to the behavioural hypervolumes of both froghoppers and katydids, and was impacted by froghopper density. Our whole model predicting froghopper survival was statistically significant (Table 2.1), predicting over 35% of variation in froghopper survival. Katydid behavioural hypervolume was negatively correlated with froghopper survival (Table 2.1; Figure 2.3), and we detected a significant katydid hypervolume by froghopper hypervolume interaction term (Table 2.1) and a

significant katydid hypervolume by froghopper hypervolume by froghopper density interaction term (Table 2.1). Specifically, in high froghopper density mesocosms, more froghoppers survived when both the katydid and froghopper hypervolumes were small (Figure 2.4). Examples of large hypervolumes and small hypervolumes like those that disfavoured or favoured froghopper survival (respectively) can be found in Figure 2.1.

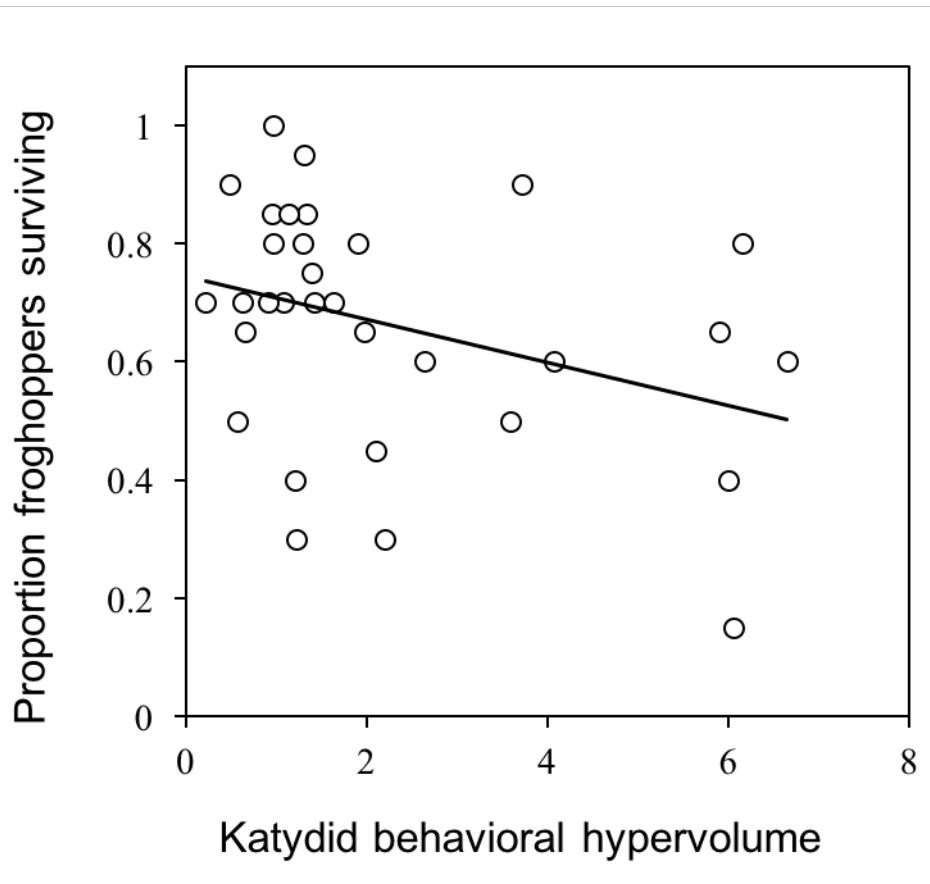


Figure 2.3. The relationship between katydid (*Scudderia* nymphs) behavioural hypervolume and the proportion of froghoppers (*Philaenus spumarius*) that survived. Katydid behavioural volume was negatively correlated with froghopper survival (GLM effect test: L-R Chi square = 7.279, p = 0.007). Line represents a best-fit linear regression.

DISCUSSION:

Much prior work has related animal personality to various aspects of individuals' ecology (Sih et al., 2012; Wolf & Weissing, 2012), such as their body condition (Johnson, Miles,

Trubl, & Hagenmaier, 2014; Wright, Keiser, & Pruitt, 2016) and social niche (Laskowski & Pruitt, 2014), by examining only one personality trait at a time (Smith & Blumstein, 2008; Sweeney et al., 2013). Here we used a multi-trait approach to examine whether the behavioural hypervolumes occupied by groups of individuals shaped both intraspecific and interspecific interactions. Consistent with our hypotheses, we found that the behavioural hypervolumes of katydid groups were negatively correlated with their average interindividual distance in staged mesocosms (Figure 2.2), conveying that behaviourally diverse groups tolerate each other more. The hypervolumes of these insects had no effect on katydid survival, because few katydids perished. This suggests that the time frame of this experiment might have been too short to track the survival of these sturdy insects. Moreover, katydid hypervolumes were negatively correlated with the survival of an invasive froghopper (*Philaenus spumarius*; Figure 2.3). Froghopper survival was greatest when both froghopper groups and katydid groups exhibited small hypervolumes (Figure 2.4), but these interactive effects appeared only under high froghopper density conditions. This suggests that both high density and large behavioural hypervolume each increase interaction intensity subtly on their own, but far more strongly together. Thus, groups with higher densities and large behavioural hypervolumes have more intense inter-specific interactions. Had we considered only single behaviours, much variation in froghopper mortality would have gone unexplained. However, these behavioural measures might be associated with age or size, so population structure may play a further role in explaining our findings. Nonetheless, they hint that behavioural hypervolumes can be helpful for predicting the outcome of both intra- and interspecific interactions.

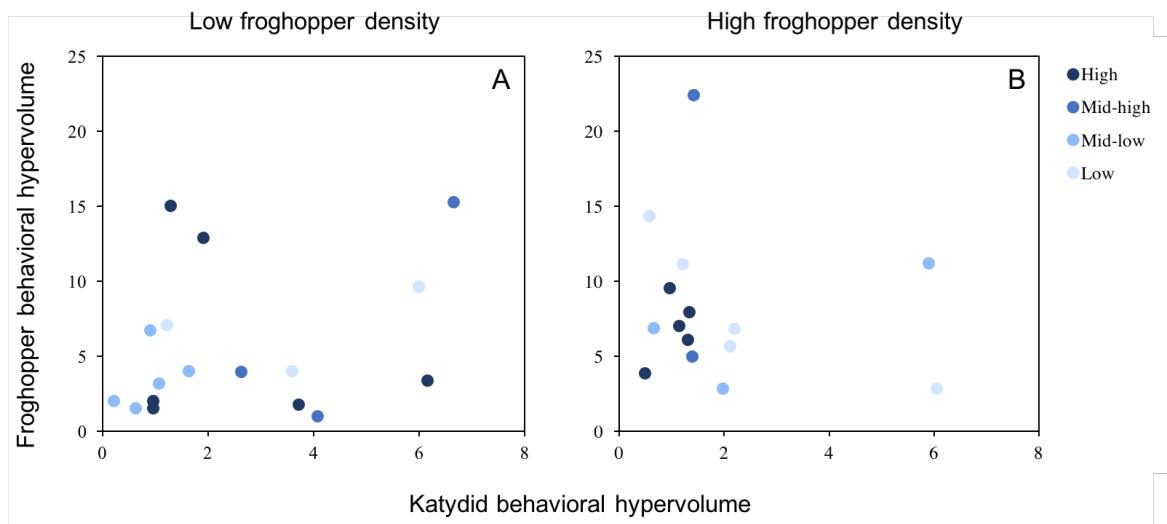


Figure 2.4. The survival of froghoppers (*Philaenus spumarius*) as predicted by the interaction between froghopper behavioural hypervolume and katydid (*Scudderia* nymphs) behavioural hypervolume at low (A) and high (B) froghopper densities. Froghoppers survived best when both species had low behavioural hypervolumes, particularly at high froghopper densities (GLM effect test: L-R Chi square = 6.498, p = 0.011; panel B). Dark blue points represent high survival (High: 100% - 80%), blue points represent mid-high survival (Mid-high: 79% - 66%), light blue points represent mid-low survival (Mid-low: 65% - 51%), and the lightest blue points represent low survival (Low: 50% - 15%).

Considerable evidence suggests that animal personality can determine how individuals interact with conspecifics (Bergmüller & Taborsky, 2010; Kurvers et al., 2009; Pinter-Wollman, Keiser, Wollman, & Pruitt, 2016). Specifically, theoretical and empirical work on social heterosis has found that behavioural diversity improves the performance of social groups (Jandt et al., 2014; Modlmeier & Foitzik, 2011; Modlmeier, Liebmann, & Foitzik, 2012; Nonacs & Kapheim, 2007, 2008; Pruitt & Riechert, 2011). Our findings add to these lines of evidence by showing that katydid groups occupying greater hypervolumes in behavioural space, i.e., those composed of more behaviourally dissimilar individuals, tolerate each other's presence more and potentially even aggregate. It is possible that behaviourally dissimilar katydids only aggregate in the presence of froghoppers. However, katydids live in

the presence of froghoppers across most of their geographic range, and thus, to consider the space use of katydids in the absence of froghoppers would be somewhat artificial and at odds with the conditions used for our survival experiments. Drawing evidence from studies linking animal personality with variation in individuals' ecological niches (Boyer, Réale, Marmet, Pisanu, & Chapuis, 2010; A. D. Wilson & McLaughlin, 2007; D. S. Wilson et al., 1993), we reason that katydids in groups with high behavioural hypervolumes may associate more closely with one another because of low competition. This is consistent with studies of social heterosis, showing that more behaviourally diverse social groups (Burns & Dyer, 2008; Dyer, Croft, Morrell, & Krause, 2009; Modlmeier & Foitzik, 2011; Modlmeier et al., 2012; Pruitt & Riechert, 2011), non-social groups (Pruitt et al., 2017), or even whole communities (Pruitt et al., 2016) compete with each other less and therefore exhibit enhanced collective success. Our study provides some evidence that behavioural hypervolumes can shape the outcome of intraspecific competition in territorial species, like katydids, and may have consequences for their population biology under natural conditions.

A growing number of studies have shown that animal personality can predict the outcome of interspecific interactions (Keiser, Slyder, Carson, & Pruitt, 2015; Lichtenstein, Pruitt, & Modlmeier, 2015; Royauté & Pruitt, 2015; Sweeney et al., 2013; Toscano & Griffen, 2014). We found that katydid behavioural hypervolume was negatively correlated with froghopper survival rates (Figure 2.3), and that froghopper survival was highest when both species had low behavioural hypervolumes (Figure 2.4). This is consistent with our hypothesis that larger behavioural hypervolumes could increase the intensity of the interaction between two competing species. We propose that this increased intensity of interactions might have accelerated the rate with which froghoppers starved to death.

Furthermore, our finding that the effects of both species' behavioural hypervolumes on froghopper survival were more pronounced at higher froghopper densities suggests that these effects are density-dependent. High densities of competing species typically increase the intensity of their interaction (Hairston, Smith, & Slobodkin, 1960). Because behavioural hypervolumes predict the outcome of a species interactions (Figure 2.3), behavioural hypervolumes should be more important when the interactions are more intense (Figure 2.4). This result does not help us to determine whether intraspecific competition is stronger than interspecific competition (or vice versa). Rather, it suggests that increased intraspecific competition intensifies the signature of interspecific competition. Taken together, these findings illustrate the potential for behavioural hypervolumes to predict the outcome of species interactions, even when single behaviours do not.

Conclusions

We found that behavioural hypervolumes can help predict the outcomes of katydid interactions with conspecifics and heterospecific invaders. Furthermore, models using behavioural hypervolumes outperformed those using univariate personality traits by a factor of nine. Multiple behavioural traits predict more variation in mortality than single behavioural traits. This adds to the growing body evidence that animal personality can predict the outcome of species interactions (DiRienzo et al., 2013; Keiser & Pruitt, 2013; Pruitt & Ferrari, 2011; Webster et al., 2009). However, the present study builds on these prior studies by 1) adopting an extrema-based multivariate approach, which has been useful in general ecology, and 2) considering how the behavioural hypervolumes of two interacting species can jointly help to predict the outcome of their interaction (Figure 2.4). This expands

upon prior studies that used behavioural hypervolumes of only a single species or that lumped multiple species into one volume as a predictive metric. After all, species interactions by definition transpire between populations, thus, we reason that the predictability of most interactions will be enhanced by considering the traits of both (or all) species involved in the interaction module. Behavioural hypervolumes and related trait-based ecology methods therefore provide us with yet another interesting set of tools for predicting system-level dynamics. We suspect that behavioural hypervolumes may shape the outcome of numerous other ecological processes, and we hope our results will serve to inspire others to evaluate these relationships.

REFERENCES:

- Akaike, H. (1987). Factor analysis and AIC. *Psychometrika*, 52(3), 317-332.
- Belgrad, B. A., & Griffen, B. D. (2016). Predator-prey interactions mediated by prey personality and predator hunting mode. *Proceedings of the Royal Society of London B: Biological Sciences*, 283(1828), 20160408. doi: 10.1098/rspb.2016.0408
- Bergmüller, R., & Taborsky, M. (2010). Animal personality due to social niche specialisation. *Trends in Ecology & Evolution*, 25(9), 504-511.
- Boyer, N., Réale, D., Marmet, J., Pisanu, B., & Chapuis, J. L. (2010). Personality, space use and tick load in an introduced population of Siberian chipmunks *Tamias sibiricus*. *Journal of Animal Ecology*, 79(3), 538-547.
- Burnham, K. P., & Anderson, D. R. (2003). *Model selection and multimodel inference: a practical information-theoretic approach*: Springer Science & Business Media.
- Burns, J. G., & Dyer, A. G. (2008). Diversity of speed-accuracy strategies benefits social insects. *Current Biology*, 18(20), R953-R954.
- Burrows, M. (2003). Biomechanics: froghopper insects leap to new heights. *Nature*, 424(6948), 509-509.
- Cantrall, I. J. (1943). *The ecology of the Orthoptera and Dermaptera of the George Reserve, Michigan*: University of Michigan Press.
- Chang, C.-c., Teo, H. Y., Norma-Rashid, Y., & Li, D. (2017). Predator personality and prey behavioural predictability jointly determine foraging performance. *Scientific Reports*, 7. doi: 10.1038/srep40734
- DiRienzo, N., Pruitt, J. N., & Hedrick, A. V. (2013). The combined behavioural tendencies of predator and prey mediate the outcome of their interaction. *Animal Behaviour*, 86(2), 317-322. doi: 10.1016/j.anbehav.2013.05.020

- Dyer, J. R., Croft, D. P., Morrell, L. J., & Krause, J. (2009). Shoal composition determines foraging success in the guppy. *Behavioral Ecology*, 20(1), 165-171.
- Gosling, S. D. (2001). From mice to men: what can we learn about personality from animal research? *Psychological Bulletin*, 127(1), 45. doi: 10.1037/0033-2909.127.1.45
- Hairston, N. G., Smith, F. E., & Slobodkin, L. B. (1960). Community structure, population control, and competition. *The American Naturalist*, 94(879), 421-425.
- Jandt, J. M., Bengston, S., Pinter-Wollman, N., Pruitt, J. N., Raine, N. E., Dornhaus, A., & Sih, A. (2014). Behavioural syndromes and social insects: personality at multiple levels. *Biological Reviews*, 89(1), 48-67.
- Johnson, J. C., Miles, L. S., Trubl, P. J., & Hagenmaier, A. (2014). Maternal effects on egg investment and offspring performance in black widow spiders. *Animal Behaviour*, 91, 67-73.
- Keiser, C. N., & Pruitt, J. N. (2013). Spider aggressiveness determines the bidirectional consequences of host-inquiline interactions. *Behavioral Ecology*, art096.
- Keiser, C. N., Slyder, J. B., Carson, W. P., & Pruitt, J. N. (2015). Individual differences in predators but not producers mediate the magnitude of a trophic cascade. *Arthropod-Plant Interactions*, 9(3), 225-232.
- Kralj-Fišer, S., & Schuett, W. (2014). Studying personality variation in invertebrates: why bother? *Animal Behaviour*, 91, 41-52.
- Kurvers, R. H., Eijkelenkamp, B., van Oers, K., van Lith, B., van Wieren, S. E., Ydenberg, R. C., & Prins, H. H. (2009). Personality differences explain leadership in barnacle geese. *Animal Behaviour*, 78(2), 447-453.
- Laskowski, K. L., & Bell, A. M. (2013). Competition avoidance drives individual differences in response to a changing food resource in sticklebacks. *Ecology Letters*, 16(6), 746-753.
- Laskowski, K. L., & Pruitt, J. N. (2014). Evidence of social niche construction: persistent and repeated social interactions generate stronger personalities in a social spider. *Proceedings of the Royal Society of London B: Biological Sciences*, 281(1783), 20133166.
- Lichtenstein, J. L., Pruitt, J. N., & Modlmeier, A. P. (2015). Intraspecific variation in collective behaviors drives interspecific contests in acorn ants. *Behavioral Ecology*, arv188.
- Lichtenstein, J. L., Wright, C. M., Luscuskie, L. P., Montgomery, G. A., Pinter-Wollman, N., & Pruitt, J. N. (2016). Participation in cooperative prey capture and the benefits gained from it are associated with individual personality. *Current Zoology*, 63(5), 561-567.
- Meyer, G. A. (1993). A Comparison of the Impacts of Leaf-And Sap-Feeding Insects on Growth and Allocation of Goldenrod. *Ecology*, 74(4), 1101-1116.
- Meyer, G. A., & Root, R. B. (1993). Effects of herbivorous insects and soil fertility on reproduction of goldenrod. *Ecology*, 74(4), 1117-1128.
- Modlmeier, A. P., & Foitzik, S. (2011). Productivity increases with variation in aggression among group members in Temnothorax ants. *Behavioral Ecology*, arr086.
- Modlmeier, A. P., Liebmann, J. E., & Foitzik, S. (2012). Diverse societies are more productive: a lesson from ants. *Proceedings of the Royal Society of London B: Biological Sciences*, rspb20112376.

- Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4(2), 133-142.
- Nonacs, P., & Kapheim, K. (2007). Social heterosis and the maintenance of genetic diversity. *Journal of Evolutionary Biology*, 20(6), 2253-2265.
- Nonacs, P., & Kapheim, K. (2008). Social heterosis and the maintenance of genetic diversity at the genome level. *Journal of Evolutionary Biology*, 21(2), 631-635.
- Pearish, S., Hostert, L., & Bell, A. M. (2013). Behavioral type–environment correlations in the field: a study of three-spined stickleback. *Behavioral Ecology and Sociobiology*, 67(5), 765-774. doi: 10.1007/s00265-013-1500-2
- Pinter-Wollman, N., Keiser, C. N., Wollman, R., & Pruitt, J. N. (2016). The Effect of Keystone Individuals on Collective Outcomes Can Be Mediated through Interactions or Behavioral Persistence. *The American Naturalist*, 188(2), 240-252.
- Pruitt, J. N., Bolnick, D. I., Sih, A., DiRienzo, N., & Pinter-Wollman, N. (2016). Behavioural hypervolumes of spider communities predict community performance and disbandment. *Proceedings of the Royal Society of London B: Biological Sciences*, 283(1844), 20161409.
- Pruitt, J. N., & Ferrari, M. C. (2011). Intraspecific trait variants determine the nature of interspecific interactions in a habitat-forming species. *Ecology*, 92(10), 1902-1908.
- Pruitt, J. N., Howell, K. A., Gladney, S. J., Yang, Y., Lichtenstein, J. L., Spicer, M. E., . . . Pinter-Wollman, N. (2017). Behavioral Hypervolumes of Predator Groups and Predator-Predator Interactions Shape Prey Survival Rates and Selection on Prey Behavior. *The American Naturalist*, 189(3), 254-266.
- Pruitt, J. N., & Riechert, S. E. (2011). How within-group behavioural variation and task efficiency enhance fitness in a social group. *Proceedings of the Royal Society of London B: Biological Sciences*, 278(1709), 1209-1215.
- Root, R. B., & Cappuccino, N. (1992). Patterns in population change and the organization of the insect community associated with goldenrod. *Ecological Monographs*, 62(3), 393-420.
- Royauté, R., & Pruitt, J. N. (2015). Varying predator personalities generates contrasting prey communities in an agroecosystem. *Ecology*, 96(11), 2902-2911.
- Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*, 19(7), 372-378.
- Sih, A., Cote, J., Evans, M., Fogarty, S., & Pruitt, J. (2012). Ecological implications of behavioural syndromes. *Ecology Letters*, 15(3), 278-289. doi: 10.1111/j.1461-0248.2011.01731.x
- Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: a meta-analysis. *Behavioral Ecology*, 19(2), 448-455.
- Sweeney, K., Cusack, B., Armagost, F., O'Brien, T., Keiser, C. N., & Pruitt, J. N. (2013). Predator and prey activity levels jointly influence the outcome of long-term foraging bouts. *Behavioral Ecology*, 24(5), 1205-1210. doi: 10.1093/beheco/art052
- Toscano, B. J., & Griffen, B. D. (2014). Trait-mediated functional responses: predator behavioural type mediates prey consumption. *Journal of Animal Ecology*, 83(6), 1469-1477.
- Weaver, C. R., & King, D. (1954). Meadow spittlebug, *Philaenus leucophthalmus* (L.).

- Webster, M., Ward, A., & Hart, P. (2009). Individual boldness affects interspecific interactions in sticklebacks. *Behavioral Ecology and Sociobiology*, 63(4), 511-520.
- Wilson, A. D., & McLaughlin, R. L. (2007). Behavioural syndromes in brook charr, *Salvelinus fontinalis*: prey-search in the field corresponds with space use in novel laboratory situations. *Animal Behaviour*, 74(4), 689-698.
- Wilson, D. S., Coleman, K., Clark, A. B., & Biederman, L. (1993). Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): An ecological study of a psychological trait. *Journal of Comparative Psychology*, 107(3), 250. doi: 10.1037/0735-7036.107.3.250
- Wolf, M., & Weissing, F. J. (2012). Animal personalities: consequences for ecology and evolution. *Trends in Ecology & Evolution*, 27(8), 452-461. doi: 10.1016/j.tree.2012.05.001
- Wright, C. M., Holbrook, C. T., & Pruitt, J. N. (2014). Animal personality aligns task specialization and task proficiency in a spider society. *Proceedings of the National Academy of Sciences*, 111(26), 9533-9537.
- Wright, C. M., Keiser, C. N., & Pruitt, J. N. (2016). Colony personality composition alters colony-level plasticity and magnitude of defensive behaviour in a social spider. *Animal Behaviour*, 115, 175-183.

CHAPTER 3. HABITAT STRUCTURE CHANGES THE RELATIONSHIPS BETWEEN PREDATOR BEHAVIOR, PREY BEHAVIOR, AND PREY SURVIVAL RATES

ABSTRACT:

The individual behavioral traits of predators and prey sometimes determine the outcome of their interactions. Here, we examine whether changes to habitat complexity could 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 behavioral volumes best predict survival rates 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 added structural complexity increases the effect of intraspecific behavioral variation on prey survival. 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 estimated.

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 predators (Chang, Teo, Norma-Rashid, & Li, 2017; DiRienzo, Pruitt, & Hedrick, 2013; Sweeney et al., 2013). This conveys that the behavioral tendencies of individuals can at times predict the outcome of predator-prey interactions (Ballew, Mittelbach, & Scribner, 2017; Finke & Snyder, 2008; Hulthén, Chapman, Nilsson, Hollander, & Brönmark, 2014; Sih, Kats, & Maurer, 2003; Smith & Blumstein, 2008). However, in other cases, intraspecific behavioral variation is unrelated to predation outcomes (Keiser, Ingle, Toscano, Scharf, & Pruitt, 2017; Keiser, Slyder, Carson, & Pruitt, 2015; Lichtenstein, Chism, Kamath, & Pruitt, 2017; Lichtenstein, Rice, & Pruitt, 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, Hostert, & Bell, 2013). We therefore aim to determine when intraspecific behavioral variation predicts the outcome of predator-prey interactions and when it does not.

Conflict between studies suggesting that personality 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 & Streams, 1984; Crowder & Cooper, 1982), and individuals' behavioral characteristics determine the kinds of habitats they use (Pearish et al., 2013; A. D. Wilson & 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 parallel 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 compare the performance of predators and prey on behavioral tests to their survival rates in staged interactions between groups of predator and prey mesocosms filled with contrasting structural features. We further compare the predictive value of single-trait group-level behavioral metrics against a composite multidimensional trait diversity metric expressed by groups of predator and prey: behavioral hypervolumes

The behavioral hypervolume concept was adapted for intraspecific behavioral variation by Pruitt, Bolnick, Sih, DiRienzo, and Pinter-Wollman (2016). They are defined as the multidimensional behavioral space occupied by an individual, group, or community. 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 hypervolumes (Lichtenstein, Wright, McEwen, Pinter-Wollman, & Pruitt, 2017; Pruitt et al., 2016; Pruitt et al., 2017). Individuals' hypervolumes would be made of up multiple iterations of multiple tests for individuals, whereas hypervolumes for groups are composed of single measurements of multiple traits for each group member. Here, we make volumes for groups. For groups of conspecifics, each individual's performance on the behavioral tests of behavioral space is plotted along the three or more axes in behavioral space, and the group's behavioral hypervolume is the space encompassed by the irregular convex polytope the group members form. Here we build polytopes in three dimensions, so calculate behavioral volumes rather than hypervolumes.

Greater behavioral dissimilarity and individuals with extreme behavioral types thus increase groups' volumes (Pruitt et al., 2017). This makes behavioral hypervolumes a metric of behavioral diversity that is sensitive to extreme behavioral tendencies. This behavioral diversity metric can determine habitat use and the outcome of species interactions. For example, large hypervolumes in competing mixed-species herbivore groups sharing a host plant are associated with decreased survival and conspecifics clustering in space (Lichtenstein, Wright, et al., 2017). And, groups of predators occupying larger hypervolumes 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 large predator hypervolumes decrease prey survival, but that 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 & Balasubramaniam, 1992; McElhinny, Gibbons, Brack, & Bauhus, 2005; V. Moran, 1980; Sugihara & May, 1990), but typically refers to the presence of refuges, obstacles, or three-dimensional substrate (Attrill, Strong, & Rowden, 2000). For example, macroalgae in ponds and vegetation layers in forests offer structural complexity (Crowder & Cooper, 1982; Diehl, 1992; McElhinny et al., 2005). This increased habitat complexity tends to reduce predation, because it provides refuges and avenues of escape (Cook & Streams, 1984; Crowder & Cooper, 1982; Diehl, 1992; Keiser et al., 2017; Uetz, 1991; Vince, Valielia, Backus, & Teal, 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, Houston, & McNamara, 2004; Smith & 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 sinsensis*) and common meadow katydids (*Orchelimum vulgare*). We chose these species because mantises are common, cannibalistic, opportunistic predators that tend to reduce herbivore biomass (L. Hurd & R. Eisenberg, 1984; Hurd & Eisenberg, 1990; Prete, Hurd, & Wells, 1999) and increase plant biomass (M. D. Moran & Hurd, 1997; M. D. Moran, Rooney, & Hurd, 1996) in the eastern United States, 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 & Stiles, 1983; Southwood, Brown, & Reader, 1979). This allowed us to test first whether dead *Solidago* stalks enhanced the effect of insect behavioral test performance on the survival of mantises and katydids (hypothesis 4). However, to test this, we first needed to confirm whether structural complexity increases insect survival (hypothesis 1) and whether the performance of insects on behavioral tests had an effect on prey survival for structural complexity to enhance (hypotheses 2 & 3).

To confirm whether structural complexity decreases predation in this system, we evaluate (1) whether increased structural complexity in the form of added dead *Solidago* stalks increases the survival rates of prey or their cannibalistic predators. Next, we needed to confirm whether (2) large predator behavioral volumes/diversity decreases cannibalism among predators and reduces prey survival, consistent with prior findings from both marine (Pruitt et al., 2017) and terrestrial (Finke & Snyder, 2008; Royauté & Pruitt, 2015) systems. We further examined whether (3) prey behavioral volume increases prey survival, because behaviorally diversity should increase the odds that at least some individuals survive predator encounters. This allowed us to (4) evaluate whether adding habitat structural complexity increased the effects of behavior on survival. To exhaustively gauge the importance of behavioral volumes, (5) we compared the predictive ability of behavioral volumes to models containing the coefficient of variation of each single trait, the range of single traits, the averages of single traits, or the average body size of individuals in 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 ($41^{\circ}34'09.6''$ N, $80^{\circ}27'51.4''$ 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 sinsensis*). 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 with regard to their sex. Katydids were on average 10.02 ± 0.12 SE mm in length ranging from 0.08-43.00 mm head to tip, and weighed on average 35 ± 7 SE mg ranging from 1-150 mg. These ranges are large because they represent over a month (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 (L. Hurd & R. Eisenberg, 1984; Hurd & Eisenberg, 1990; M. D. Moran & Hurd, 1997; M. D. Moran et al., 1996). These species' ranges overlap across the whole of the eastern United States 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 all katydids in 50ml 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 hours.

Behavioral assays:

We ran 377 mantises and 1169 katydids through three assays once in the following order: activity level, boldness, and perch height. These traits were used to construct behavioral volumes, which we compared to their survival in predator-prey interactions trials. We ran

insects through three assays in the following order: activity level, boldness, and perch height. 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 five days, totaling five trials. To ensure that insects did not grow weak over the course of these five days, mantises were fed with a katydid every day, including the day prior to testing, and 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 1cm graph paper attached to the outside. We used vertically oriented arenas because these insects occupy and climb through vertically stratified habitat. After a 30 second acclimation period, we counted how many squares the insects' heads crossed over the course of 300 seconds for mantises and 120 seconds 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, Both, Drent, van Oers, & van Noordwijk, 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 containers identical to those they were maintained in. 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 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, David, Tregenza, & Rodríguez-Muñoz, 2015; Hedrick & Kortet, 2012; Müller & Müller, 2015; Niemelä, Vainikka, Hedrick, & Kortet, 2012).

Perch height: To assess how these insects use space, we placed them in arenas and measured how high they perched within an arena. 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, and were draped at a height where the top of each plant would just touch the top of the enclosure. We placed the insects in the arenas though the sealable opening at the base, and then measured the height of their heads after a ten-minute 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, Wright, et al., 2017), 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 been estimated. Katydids 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 five individuals because this is just above the minimum number needed to calculate a volume, and katydid groups contained fifteen because this is roughly twice the number we estimated five 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 ($N_{mesocosms} = 74$, $N_{insects} = 1480$). Eight is well within the natural range of dead stems present in these fields. The presence of dead goldenrod stems from previous years is a facet of habitat structural complexity that varies naturally in old fields (McDonnell & Stiles, 1983; Southwood et al., 1979). We stocked and sealed the mesocosms between 1600 and 1800 hours, and then left them for 23 hours, allowing an hour for setup. After 23 hours 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 we collected them.

Statistical methods:

We assessed the repeatability of all three behavioral traits for both species using the rptR package (Nakagawa & 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. Finally, we tested whether each of these behavioral traits was correlated with insect mass. We constructed these linear models in JMP version 13 (SAS), and used R for all repeatability analyses.

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, Marshall, and Uetz (1996). We also checked for correlations between behavior traits with linear regressions.

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 Delauney 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 Figure 3.1. We used MATLAB for all behavioral volume calculations.

Figure 3.1.

Examples of

behavioral

volumes.

Green volumes

represent

mantises

(group size =

5) and red

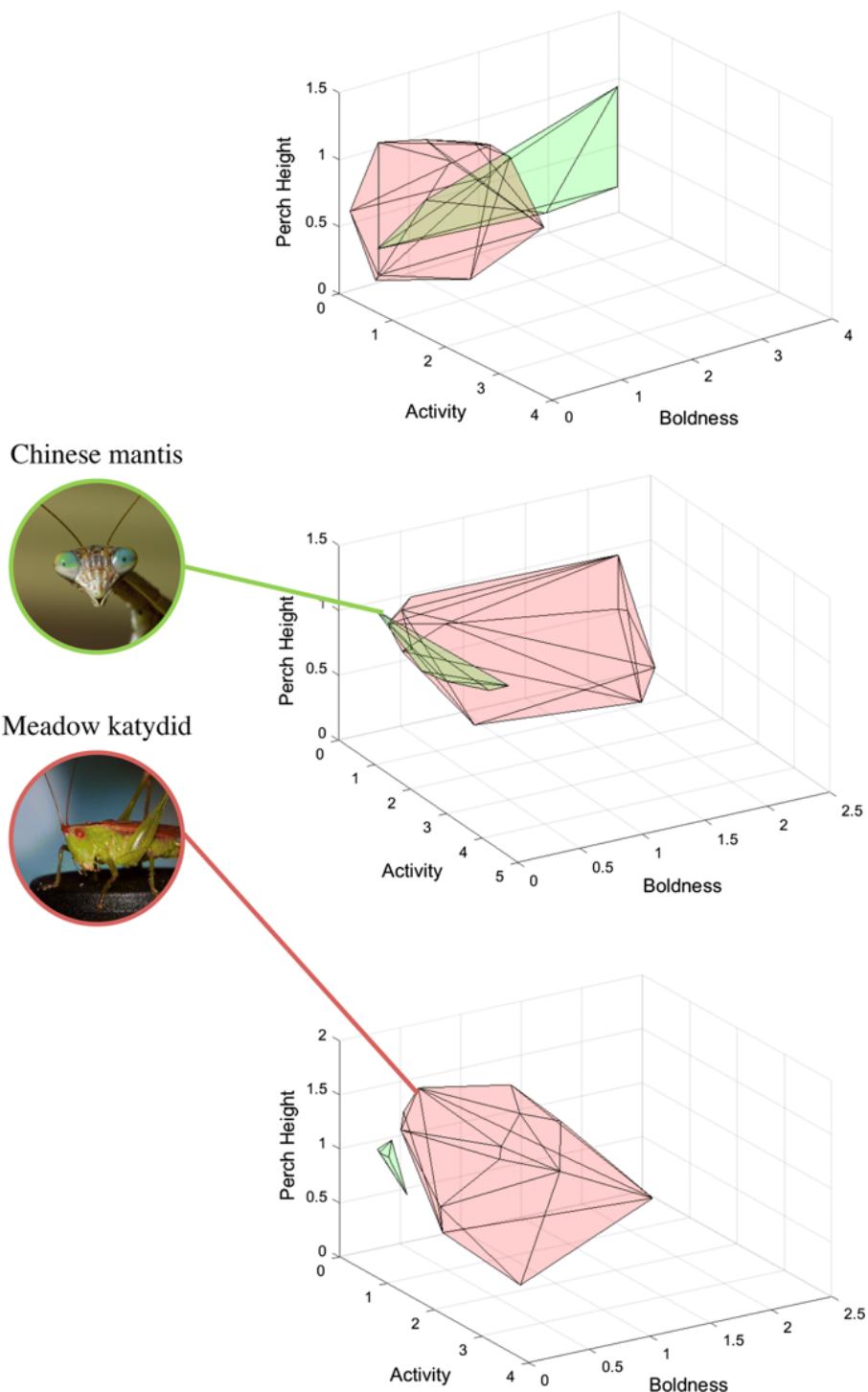
volumes

represent

katydids

(group size =

15).



Next, to assess what factors predict mantis and katydid mortality, we made twenty-four 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 (supplementary perches +/-), the mantis behavioral trait (varied by model), the katydid behavioral trait (varied by model), and associated interaction terms. The traits supplied 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 & 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 (Rosseel, 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. Next, we made two models with the same structure, but split by low complexity and high complexity mesocosms. Second, to look for effects of mantis cannibalism on katydid 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 seconds 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 seconds 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.

Mantis mass was negatively correlated with their activity level, explaining 1% of all activity level variation (Supplementary Table S2). Katydid mass positively correlated with katydid activity level and perch height, and negatively correlated 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 correlated positively with mantis boldness, katydid body condition was positively correlated with katydid perch height, and katydid body condition negatively correlated with katydid boldness (Supplementary table S2). Similarly, body condition explained 1% of mantis boldness, 1% of katydid boldness, and 2% of katydid perch height respectively (Supplementary Table S2).

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

Table 3.1. Model comparisons of models predicting katydid survival and mantis survival. We used the Akaike weight information procedure to compare models that took into account behavioral volumes, the coefficient of variation 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.

Response variable	Personality metric	R2	p	AICc	Relative AICc	Akaike Weight
Katydid survival						
	Behavioral hypervolume	0.245	0.005	-71.399	0.990	0.373
	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
	Tube Average	0.112	0.280	-59.497	0.825	0.001
	Perch Average	0.256	0.003	-72.147	1.000	0.543
	Average mass	0.109	0.300	-59.254	0.821	0.001
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	0.013
	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
	Tube Average	0.169	0.060	-58.184	-0.803	0.001
	Perch Average	0.207	0.019	-59.514	-0.821	0.001
	Average mass	0.317	0.000	-72.493	-1.000	0.984

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, explaining 34.1 and 31.7% of all variation in mantis survival respectively and with Akaike weights over 77 times greater than the third-best model (Table 3.1). All mantises that died in these mesocosms were partially or entirely eaten, and we personally observed numerous instances of cannibalism. Mantises were 8.7% more likely to survive in structurally complex mesocosms (Table 3.2), and average katydid mass positively correlated with mantis survival (Table 3.2). There were significant mantis length by katydid length, mantis length by katydid length by treatment, and mantis mass by katydid mass interaction terms (Table 3.2). 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 strongly correlated, so we disregarded these interaction terms, because we suspect them to be artifacts of multicollinearity.

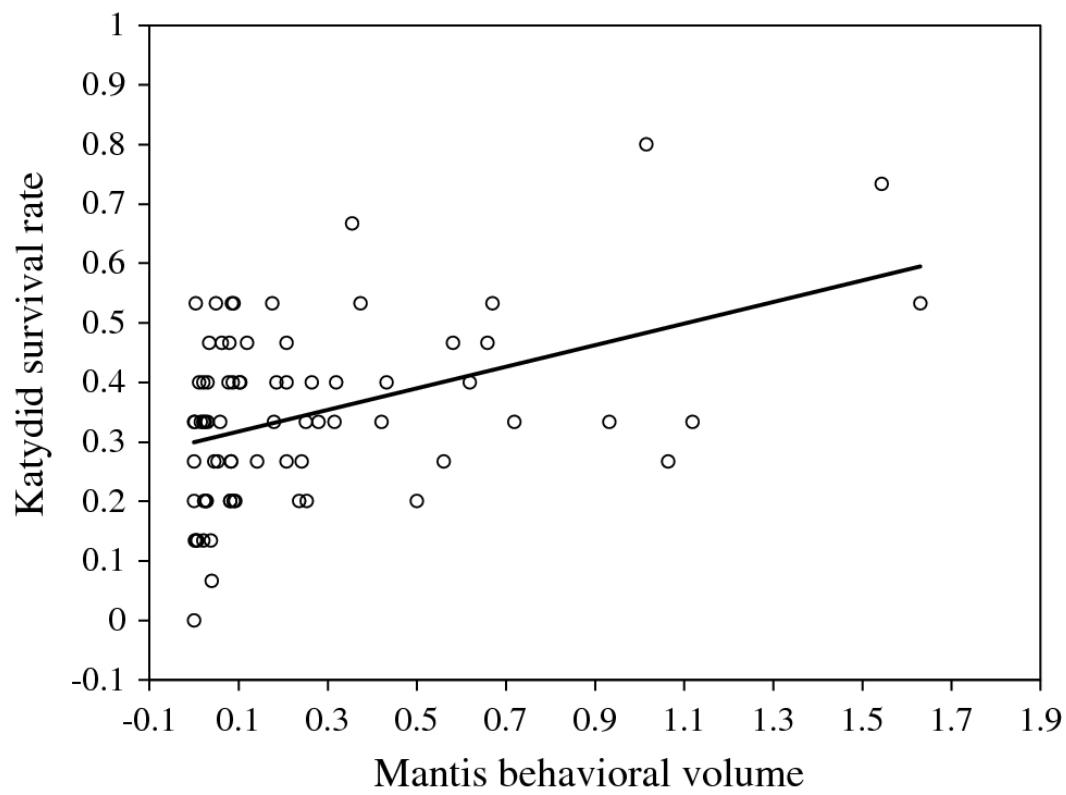


Figure 3.2. Mantis behavioral hypervolume is directly proportional to katydid survival (glm effect test: $\text{Chi}^2_1 = 12.771$, $p = 0.004$). Line represents linear regression.

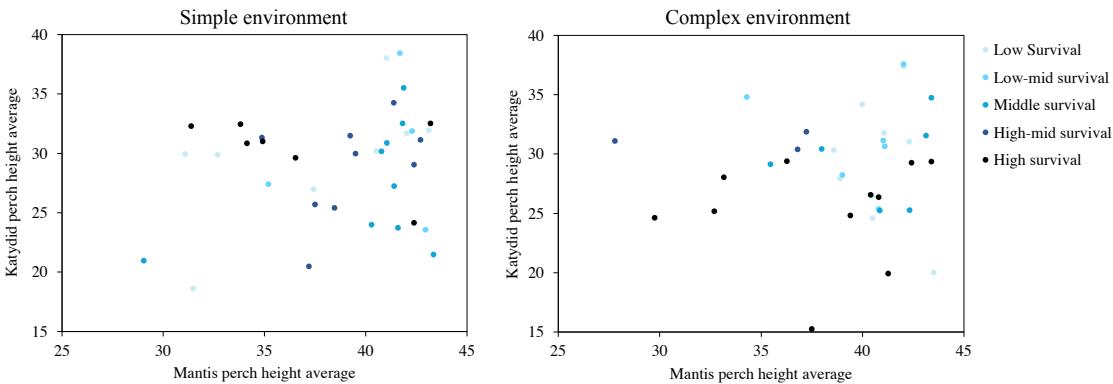


Figure 3.3. In structurally complex environments, mantises eat more katydids when both species have high average perch heights (glm effect test: $\text{Chi}^2_1 = 7.366, p = 0.007$). Low survival refers to katydid survival rates between 11%-20%, mid-low refers to 21%-30% katydid survival, middle survival 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

On average, $34.13 \pm 1.7\%$ SE of katydids in a group survived mesocosm trials. The behavioral volume model ($\text{AICc} = -71.399$, Akaike weight = 0.375) and the average perch height model ($\text{AICc} = -72.147$, Akaike weight = 0.544) were roughly equal predictors of katydid survival, with Akaike weights over six times greater than the third best model (Table 3.1). We therefore have chosen to report both the volume and average perch height models. Mantis behavioral volume positively correlated with katydid survival (Figure 3.2), seemingly more so in structurally complex environments, although this interaction term was only marginally significant (Table 3.2). Average mantis perch height was associated with decreased katydid survival (Table 3.2). 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 3.2; Figure 3.3).

Table 3.2. The outputs of the two best models explaining katydid survival and the best model explaining mantis survival. 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 ($AIC_c = -73.671$, Akaike weight = 0.639) and the mass model ($AIC_c = -72.493$, Akaike weight = 0.355) were very similar predictors of mantis survival. The behavioral volume model ($AIC_c = -71.399$, Akaike weight = 0.375) and the average perch height model ($AIC_c = -72.147$, 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.

Predictor variable	R2	$\beta \pm$ standard error	DF	Chi2	p
Katydid survival					
Whole model	0.25	-	7.00	20.53	0.01
Structural complexity		-0.01 ± 0.02	1.00	0.59	0.44
Mantis volume		0.17 ± 0.05	1.00	12.77	0.00
Katydid volume		0.01 ± 0.01	1.00	0.52	0.47
Mantis volume*structure		-0.09 ± 0.05	1.00	3.65	0.06
Katydid volume*structure		-0.01 ± 0.01	1.00	0.84	0.36
Mantis volume*katydid volume		0.02 ± 0.04	1.00	0.15	0.70
Mantis volume*katydid volume*structure		0.01 ± 0.04	1.00	0.04	0.85
Katydid survival					
Whole model	0.26	-	7.00	21.24	0.00
Structural complexity		-0.00 ± 0.02	1.00	0.03	0.87
Mantis average perch height		-0.01 ± 0.00	1.00	9.52	0.00
Katydid average perch height		-0.001 ± 0.00	1.00	3.60	0.06
Mantis perch*structure		0.00 ± 0.00	1.00	0.96	0.33
Katydid perch*structure		0.01 ± 0.00	1.00	2.90	0.09
Mantis perch*katydid perch		0.00 ± 0.00	1.00	0.07	0.79
Mantis perch*katydid perch*structure		-0.00 ± 0.00	1.00	7.37	0.01
Mantis survival					
Whole model	0.32	-	7.00	27.85	0.00
Structural complexity		-0.06 ± 0.02	1.00	6.89	0.01
Mantis average mass		-0.12 ± 0.13	1.00	0.90	0.34
Katydid average mass		5.62 ± 1.73	1.00	9.81	0.00
Mantis mass*structure		-0.01 ± 0.13	1.00	0.00	0.97
Katydid mass*structure		-0.75 ± 1.73	1.00	0.19	0.67
Mantis mass*katydid mass		-10.61 ± 4.79	1.00	4.75	0.03
Mantis mass*katydid mass*structure		6.26 ± 4.79	1.00	1.68	0.19

Mantis survival

Whole model	0.32	-	7.00	30.01	0.00
Structural complexity	-0.07 ± 0.02	1.00	10.18		0.00
Mantis average length	-0.00 ± 0.00	1.00	0.08	0.78	
Katydid average length	0.02 ± 0.01 $-0.002 \pm$	1.00	3.78	0.05	
Mantis length*structural complexity	0.00	1.00	0.72	0.40	
Katydid length*structural complexity	$0.01 \pm .01$	1.00	0.47	0.49	
Mantis length*katydid length	-0.00 ± 0.00	1.00	9.97		0.00
Mantis length*katydid length*structure	$0.00 \pm .00$	1.00	5.91		0.02

Post-hoc path analyses revealed that average perch height negatively correlates with behavioral volumes, behavioral volumes correlate with prey survival, but average perch height did not directly predict prey survival (Figure 3.4). 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 (Figure 3.4). Additionally, mantis survival was not significantly related to katydid survival (GLM: R² = 0.029, Chi²₇₂ = 2.199, p = 0.138).

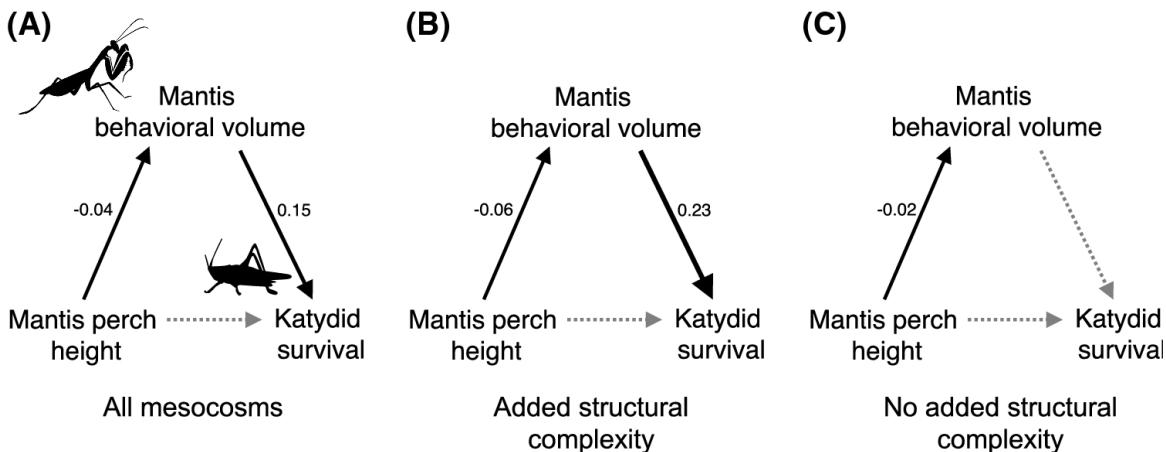


Figure 3.4. Path diagrams showing relationships between mantis average perch height, mantis behavioral volume, and katydid survival in mesocosms. Diagram (A) was built using all mesocosms, diagram (B) was built with only mesocosms with added structural complexity, and diagram C) was built with mesocosm 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.

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 lab study. Mantis survival was not associated with any behavioral metric considered here (Table 3.1). Mantises were instead less likely to cannibalize each other in structurally complex environments and when katydids were larger (Table 3.2). Katydids were more likely to survive in mesocosms with more behaviorally diverse mantis groups, which together occupied a larger volume in behavioral trait space (Figure 3.2). This was especially true when these mesocosms were structurally complex (Table 3.2). This means that the trait diversity present in the predator population can have risk-reducing effects for prey. Katydids were 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, Orrock, & Schmitz, 2007; Royauté & Pruitt, 2015; Schmitz, 2007; Toscano, Gownaris, Heerhartz, & Monaco, 2016; Toscano & 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 more so in structurally complex mesocosms. Unfortunately, our design did not account for sex, so 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 (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 & 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 & Katsuhiro, 1997; Qin & Fast, 1996), conveying that conspecifics are potentially non-preferred prey (L. Hurd & R. M. Eisenberg, 1984). Alternatively, larger prey could satiate mantises reducing their appetites for conspecifics. However, we cannot distinguish between the effects of age and size within our current 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 & Saleem, 1982; Polis, Myers, & Holt, 1989; Thompson, 1975).

Multiple predator effects (MPEs) are cases where the presence of multiple predator species have non-additive effects on prey survival (Sih, Englund, & Wooster, 1998; Soluk, 1993), although the term has been borrowed to refer to non-additive interactions between individual predators of the same species (Royauté & Pruitt, 2015). Existing evidence implies that the trait compositions present in predator populations can generate variation in MPEs (Royauté & Pruitt, 2015). For instance, more behaviorally diverse populations of predators often prove more lethal to groups of prey (Finke & Snyder, 2008; Pruitt et al., 2017; Royauté

& 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, Dlugos, Wilcox, & Wilson, 2009; Sih & 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 strong predictor of prey survival. Future studies aimed at teasing apart the relationships between space use and intraspecific 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 in arenas, and our boldness and activity level tests were designed to estimate what insects do in the space 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 react to challenges in that space. And yet, patterns of predator space use described by average perch

height appear to predict prey survival on their own. Katydidids perched on average 30 cm high, 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 katydidids' preferred perch height) consumed more katydidids. This was especially true in structurally complex mesocosms (Table 3.2): in environments with added structural complexity, mantises did not eat more than 50% of katydidids unless both species had high average perch heights (Figure 3.3). 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, Réale, Marmet, Pisanu, & Chapuis, 2010; Pearish et al., 2013; Spiegel, Leu, Sih, Godfrey, & Bull, 2015; A. D. Wilson & McLaughlin, 2007; D. S. Wilson, Coleman, Clark, & Biederman, 1993), potentially conveying that findings like our own could hold in a variety of other systems.

However, post-hoc path analysis revealed that behavioral volumes mediate the effect of average perch height on katydid survival (Figure 3.4). 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 a composite measure that includes perch height. Instead, this mediation conveys that mantis perch height determines katydid survival as a part of a composite metric of mantis space use preferences and what mantises do in that space. Behavioral volumes and hypervolumes are aimed at capturing a greater breadth of animals' behavioral repertoires, i.e. the full range of animals' behavior, compared to single traits (Pruitt et al., 2016). Predator behavioral volumes mediating the effect of predator perch height on prey survival (Figure 3.4) suggests that individual behavioral traits

may only determine the outcome of species interactions because they comprise small parts of animals' emergent behavioral repertoires. This reaffirms the importance of a multtrait approach to relating intraspecific behavioral variation to ecological outcomes (Sih, Bell, & Johnson, 2004; Sih, Cote, Evans, Fogarty, & Pruitt, 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 3.2; Figure 3.3). Furthermore, structural complexity alone had no effect on katydid survival (Table 3.2), which is inconsistent with earlier research, which found that structural complexity increases prey survival (Cook & Streams, 1984; Crowder & 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, Toscano, & Gatto, 2012; Keiser et al., 2015; Lichtenstein, Chism, et al., 2017; Pruitt & Ferrari, 2011) and there is considerable evidence that behavioral traits determine how animals use their environments (Pearish et al., 2013; A. D. Wilson & 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.

REFERENCES:

- Akaike, H. (1987). Factor analysis and AIC. *Psychometrika*, 52(3), 317-332.
- Amarasinghe, M., & Balasubramaniam, S. (1992). Structural properties of two types of mangrove stands on the northwestern coast of Sri Lanka *The Ecology of Mangrove and Related Ecosystems* (pp. 17-27): Springer.
- Attrill, M. J., Strong, J. A., & Rowden, A. A. (2000). Are macroinvertebrate communities influenced by seagrass structural complexity? *Ecography*, 23(1), 114-121.
- Ballew, N. G., Mittelbach, G. G., & Scribner, K. T. (2017). Fitness consequences of boldness in juvenile and adult largemouth bass. *The American Naturalist*, 189(4), 396-406.
- Boyer, N., Réale, D., Marmet, J., Pisanu, B., & Chapuis, J. L. (2010). Personality, space use and tick load in an introduced population of Siberian chipmunks *Tamias sibiricus*. *Journal of Animal Ecology*, 79(3), 538-547.
- Burnham, K. P., & Anderson, D. R. (2003). *Model selection and multimodel inference: a practical information-theoretic approach*: Springer Science & Business Media.
- Chang, C.-c., Teo, H. Y., Norma-Rashid, Y., & Li, D. (2017). Predator personality and prey behavioural predictability jointly determine foraging performance. *Scientific Reports*, 7. doi: 10.1038/srep40734
- Connell, J. H. (1970). A Predator-Prey System in the Marine Intertidal Region. I. *Balanus glandula* and Several Predatory Species of *Thais*. *Ecological Monographs*, 40(1), 49-78.
- Cook, W., & Streams, F. (1984). Fish predation on *Notonecta* (Hemiptera): relationship between prey risk and habitat utilization. *Oecologia*, 64(2), 177-183.
- Crowder, L. B., & Cooper, W. E. (1982). Habitat structural complexity and the interaction between bluegills and their prey. *Ecology*, 63(6), 1802-1813.
- Cushing, J. M., & Saleem, M. (1982). A predator prey model with age structure. *Journal of Mathematical Biology*, 14(2), 231-250.
- Dall, S. R., Houston, A. I., & McNamara, J. M. (2004). The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters*, 7(8), 734-739. doi: 10.1111/j.1461-0248.2004.00618.x
- Diehl, S. (1992). Fish predation and benthic community structure: the role of omnivory and habitat complexity. *Ecology*, 73(5), 1646-1661.
- Dingemanse, N. J., Both, C., Drent, P. J., van Oers, K., & van Noordwijk, A. J. (2002). Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour*, 64(6), 929-938.
- DiRienzo, N., Pruitt, J. N., & Hedrick, A. V. (2013). The combined behavioural tendencies of predator and prey mediate the outcome of their interaction. *Animal Behaviour*, 86(2), 317-322. doi: 10.1016/j.anbehav.2013.05.020
- Eldakar, O. T., Dlugos, M. J., Wilcox, R. S., & Wilson, D. S. (2009). Aggressive mating as a tragedy of the commons in the water strider *Aquarius remigis*. *Behavioral Ecology and Sociobiology*, 64(1), 25.

- Finke, D. L., & Snyder, W. E. (2008). Niche partitioning increases resource exploitation by diverse communities. *Science*, 321(5895), 1488-1490.
- Fisher, D. N., David, M., Tregenza, T., & Rodríguez-Muñoz, R. (2015). Dynamics of among-individual behavioral variation over adult lifespan in a wild insect. *Behavioral Ecology*, 26(4), 975-985.
- Griffen, B. D., Toscano, B. J., & Gatto, J. (2012). The role of individual behavior type in mediating indirect interactions. *Ecology*, 93(8), 1935-1943.
- Hedrick, A. V., & Kortet, R. (2012). Sex differences in the repeatability of boldness over metamorphosis. *Behavioral Ecology and Sociobiology*, 66(3), 407-412.
- Hironori, Y., & Katsuhiro, S. (1997). Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field. *Biocontrol*, 42(1), 153-163.
- Hulthén, K., Chapman, B. B., Nilsson, P. A., Hollander, J., & Brönmark, C. (2014). Express yourself: bold individuals induce enhanced morphological defences. *Proceedings of the Royal Society of London B: Biological Sciences*, 281(1776), 20132703.
- Hurd, L., & Eisenberg, R. (1984). Experimental density manipulations of the predator *Tenodera sinensis* (Orthoptera: Mantidae) in an old-field community. II. The influence of mantids on arthropod community structure. *The Journal of Animal Ecology*, 53(3), 955-967.
- Hurd, L., & Eisenberg, R. M. (1984). Experimental density manipulations of the predator *Tenodera sinensis* (Orthoptera: Mantidae) in an old-field community. I. Mortality, development and dispersal of juvenile mantids. *The Journal of Animal Ecology*, 53(1), 269-281.
- Hurd, L., & Eisenberg, R. M. (1990). Arthropod community responses to manipulation of a bitrophic predator guild. *Ecology*, 71(6), 2107-2114.
- Jakob, E. M., Marshall, S. D., & Uetz, G. W. (1996). Estimating fitness: a comparison of body condition indices. *Oikos*, 77(1), 61-67.
- Jones, C., & DiRienzo, N. (2018). Behavioral variation post-invasion: resemblance in some, but not all, behavioral patterns among invasive and native praying mantids. *Behavioural Processes*, 153, 92-99.
- Keiser, C. N., Ingle, S. J., Toscano, B. J., Scharf, I., & Pruitt, J. N. (2017). Habitat complexity dampens selection on prey activity level. *Ethology*. doi: 10.1111/eth.12700
- Keiser, C. N., Slyder, J. B., Carson, W. P., & Pruitt, J. N. (2015). Individual differences in predators but not producers mediate the magnitude of a trophic cascade. *Arthropod-Plant Interactions*, 9(3), 225-232.
- Kurvers, R. H., Eijkelenkamp, B., van Oers, K., van Lith, B., van Wieren, S. E., Ydenberg, R. C., & Prins, H. H. (2009). Personality differences explain leadership in barnacle geese. *Animal Behaviour*, 78(2), 447-453.
- Lichtenstein, J. L., Chism, G. T., Kamath, A., & Pruitt, J. N. (2017). Intraindividual Behavioral Variability Predicts Foraging Outcome in a Beach-dwelling Jumping Spider. *Scientific Reports*, 7(1), 18063.
- Lichtenstein, J. L., Rice, H. K., & Pruitt, J. N. (2018). Personality variation in two predator species does not impact prey species survival or plant damage in staged mesocosms. *Behavioral Ecology and Sociobiology*, 72(4), 70.

- Lichtenstein, J. L., Wright, C. M., McEwen, B., Pinter-Wollman, N., & Pruitt, J. N. (2017). The multidimensional behavioural hypervolumes of two interacting species predict their space use and survival. *Animal Behaviour*, 132, 129-136. doi: 10.1016/j.anbehav.2017.08.01
- McDonnell, M. J., & Stiles, E. W. (1983). The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia*, 56(1), 109-116.
- McElhinny, C., Gibbons, P., Brack, C., & Bauhus, J. (2005). Forest and woodland stand structural complexity: its definition and measurement. *Forest Ecology and Management*, 218(1), 1-24.
- Moran, M. D., & Hurd, L. (1997). A trophic cascade in a diverse arthropod community caused by a generalist arthropod predator. *Oecologia*, 113(1), 126-132.
- Moran, M. D., Rooney, T. P., & Hurd, L. (1996). Top-down cascade from a bitrophic predator in an old-field community. *Ecology*, 77(7), 2219-2227.
- Moran, V. (1980). Interactions between phytophagous insects and their *Opuntia* hosts. *Ecological Entomology*, 5(2), 153-164.
- Müller, T., & Müller, C. (2015). Behavioural phenotypes over the lifetime of a holometabolous insect. *Frontiers in Zoology*, 12(1), S8.
- Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4(2), 133-142.
- Niemelä, P. T., Vainikka, A., Hedrick, A. V., & Kortet, R. (2012). Integrating behaviour with life history: boldness of the field cricket, *Gryllus integer*, during ontogeny. *Functional Ecology*, 26(2), 450-456.
- Pearish, S., Hostert, L., & Bell, A. M. (2013). Behavioral type–environment correlations in the field: a study of three-spined stickleback. *Behavioral Ecology and Sociobiology*, 67(5), 765-774. doi: 10.1007/s00265-013-1500-2
- Polis, G. A., Myers, C. A., & Holt, R. D. (1989). The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual review of ecology and systematics*, 20(1), 297-330.
- Preisser, E. L., Orrock, J. L., & Schmitz, O. J. (2007). Predator hunting mode and habitat domain alter nonconsumptive effects in predator–prey interactions. *Ecology*, 88(11), 2744-2751.
- Prete, F. R., Hurd, L. E., & Wells, P. H. (1999). *The praying mantids*: JHU Press.
- Pruitt, J. N., Bolnick, D. I., Sih, A., DiRienzo, N., & Pinter-Wollman, N. (2016). Behavioural hypervolumes of spider communities predict community performance and disbandment. *Proceedings of the Royal Society of London B: Biological Sciences*, 283(1844), 20161409.
- Pruitt, J. N., & Ferrari, M. C. (2011). Intraspecific trait variants determine the nature of interspecific interactions in a habitat-forming species. *Ecology*, 92(10), 1902-1908.
- Pruitt, J. N., Howell, K. A., Gladney, S. J., Yang, Y., Lichtenstein, J. L., Spicer, M. E., ... Pinter-Wollman, N. (2017). Behavioral Hypervolumes of Predator Groups and Predator-Predator Interactions Shape Prey Survival Rates and Selection on Prey Behavior. *The American Naturalist*, 189(3), 254-266.
- Qin, J., & Fast, A. W. (1996). Size and feed dependent cannibalism with juvenile snakehead *Channa striatus*. *Aquaculture*, 144(4), 313-320.

- Rosseel, Y. (2012). Lavaan: An R package for structural equation modeling and more. Version 0.5–12 (BETA). *Journal of Statistical Software*, 48(2), 1-36.
- Royauté, R., & Pruitt, J. N. (2015). Varying predator personalities generates contrasting prey communities in an agroecosystem. *Ecology*, 96(11), 2902-2911.
- Schmitz, O. J. (2007). Predator diversity and trophic interactions. *Ecology*, 88(10), 2415-2426.
- Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*, 19(7), 372-378.
- Sih, A., Cote, J., Evans, M., Fogarty, S., & Pruitt, J. (2012). Ecological implications of behavioural syndromes. *Ecology Letters*, 15(3), 278-289. doi: 10.1111/j.1461-0248.2011.01731.x
- Sih, A., Englund, G., & Wooster, D. (1998). Emergent impacts of multiple predators on prey. *Trends in Ecology & Evolution*, 13(9), 350-355.
- Sih, A., Kats, L. B., & Maurer, E. F. (2003). Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish–salamander system. *Animal Behaviour*, 65(1), 29-44.
- Sih, A., & Watters, J. V. (2005). The mix matters: behavioural types and group dynamics in water striders. *Behaviour*, 142(9-10), 1417-1431.
- Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: a meta-analysis. *Behavioral Ecology*, 19(2), 448-455.
- Soluk, D. A. (1993). Multiple predator effects: predicting combined functional response of stream fish and invertebrate predators. *Ecology*, 74(1), 219-225.
- Southwood, T. R., Brown, V., & Reader, P. (1979). The relationships of plant and insect diversities in succession. *Biological Journal of the Linnean society*, 12(4), 327-348.
- Spiegel, O., Leu, S. T., Sih, A., Godfrey, S. S., & Bull, C. M. (2015). When the going gets tough: behavioural type-dependent space use in the sleepy lizard changes as the season dries. *Proceedings of the Royal Society of London B: Biological Sciences*, 282(1819), 20151768.
- Sugihara, G., & May, R. M. (1990). Applications of fractals in ecology. *Trends in Ecology & Evolution*, 5(3), 79-86.
- Sweeney, K., Cusack, B., Armagost, F., O'Brien, T., Keiser, C. N., & Pruitt, J. N. (2013). Predator and prey activity levels jointly influence the outcome of long-term foraging bouts. *Behavioral Ecology*, 24(5), 1205-1210. doi: 10.1093/beheco/art052
- Thompson, D. (1975). Towards a predator-prey model incorporating age structure: the effects of predator and prey size on the predation of *Daphnia magna* by *Ischnura elegans*. *The Journal of Animal Ecology*, 44(3), 907-916.
- Toscano, B. J., Gownaris, N. J., Heerhartz, S. M., & Monaco, C. J. (2016). Personality, foraging behavior and specialization: integrating behavioral and food web ecology at the individual level. *Oecologia*, 182(1), 1-15.
- Toscano, B. J., & Griffen, B. D. (2014). Trait-mediated functional responses: predator behavioural type mediates prey consumption. *Journal of Animal Ecology*, 83(6), 1469-1477.
- Uetz, G. (1991). Habitat structure and spider foraging *Habitat structure* (pp. 325-348): Springer.
- Vince, S., Valiela, I., Backus, N., & Teal, J. (1976). Predation by the salt marsh killifish *Fundulus heteroclitus* (L.) in relation to prey size and habitat structure: consequences

- for prey distribution and abundance. *Journal of Experimental Marine Biology and Ecology*, 23(3), 255-266.
- Wilson, A. D., & McLaughlin, R. L. (2007). Behavioural syndromes in brook charr, *Salvelinus fontinalis*: prey-search in the field corresponds with space use in novel laboratory situations. *Animal Behaviour*, 74(4), 689-698.
- Wilson, D. S., Coleman, K., Clark, A. B., & Biederman, L. (1993). Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): An ecological study of a psychological trait. *Journal of Comparative Psychology*, 107(3), 250. doi: 10.1037/0735-7036.107.3.250

CHAPTER 4. TOP-DOWN EFFECTS OF INTRASPECIFIC PREDATOR BEHAVIORAL VARIATION

ABSTRACT:

Intraspecific variation in predator behavioral traits is widespread and has major implications for species interactions. However, the effects of this scale of behavioral diversity across trophic levels have been seldom considered in community ecology. By considering within-population diversity in predator behavior, we could increase our ability to predict top-down effects on ecosystems. We thus manipulated predator behavioral diversity in experimental patches of old fields and quantified the resulting impacts on subsequent trophic levels: herbivores and plant biomass. Specifically, we created old field plots containing mantis (*Tenodera sinensis*) groups with contrasting densities and degrees of behavioral diversity (variation in activity level). Prior to releasing mantises, we further estimated their aggressiveness (i.e., ability to capture a hard-to-subdue prey species, *Philaenus spumarius*). Behaviorally diverse mantis groups of predators increased plant biomass by 8.0%, particularly when they contained less aggressive individuals, increasing plant biomass by 14.1%. When mantises are highly aggressive, high predator densities increased prey biomass by 17.1%. Both cascading effects are likely due to increased interference between mantises. Our results are among the first to demonstrate that behavioral diversity can have sizable density-dependent top-down effects on open species-rich communities, controlling both herbivore prey communities and plant biomass.

INTRODUCTION:

Ecologists have long aimed to predict the top-down effects of predators on ecosystems (Paine, 1969). These efforts typically fail to consider intraspecific variation in predator functional traits, focusing instead on predator density or between-species variation in functional traits (e.g. hunting mode; but see Des Roches, Shurin, Schluter, & Harmon, 2013; Harmon et al., 2009; Katano, 2011; Miller, Ament, & Schmitz, 2014; Post, Palkovacs, Schielke, & Dodson, 2008). Theory predicts that predator intraspecific trait variation supports the coexistence of their prey species, also resulting in top-down control on ecosystems (Schreiber, Bürger, and Bolnick (2011)). However, this prediction has been rarely tested experimentally in field conditions (Post et al., 2008; Toscano, Gownaris, Heerhartz, & Monaco, 2016).

Consistent intraspecific behavioral variation, better known as animal personality (Gosling, 2001), varies dramatically and ubiquitously within and across populations (A. Bell, 2005; Bengston & Dornhaus, 2015) and can predict salient ecological outcomes (Keiser, Ingle, Toscano, Scharf, & Pruitt, 2017; Wolf & Weissing, 2012). For instance, individuals' activity level (tendency of animals to move around their habitat) can predict their dispersal tendencies (Cote, Clobert, Brodin, Fogarty, & Sih, 2010; Duckworth, Belloni, & Anderson, 2015; Michelangeli, Smith, Wong, & Chapple, 2017; Wellington, 1964), space use patterns (Boyer, Réale, Marmet, Pisanu, & Chapuis, 2010; Pearish, Hostert, & Bell, 2013; Spiegel, Leu, Sih, Godfrey, & Bull, 2015; van Overveld & Matthysen, 2009; Wilson & McLaughlin, 2007), and diet (Harrison et al., 2017; Nakayama, Rapp, & Arlinghaus, 2017; Nannini, Parkos III, & Wahl, 2012; Nannini & Wahl, 2016; Oudman et al., 2016). Personality traits, like activity level, are thus increasingly recognized as individual-level functional traits that

not only drive population dynamics but potentially shape the functioning of ecosystems (Toscano et al., 2016).

If intra-population variation in personality is functional trait variation (Toscano et al., 2016), then variation in behavioral diversity present in one trophic level could cascade up and down food webs (Start, Weis, & Gilbert, 2019; Toscano, Lichtenstein, & Costa-Pereira, 2020). These effects appear to be driven, for instance, by locomotor crossover, wherein active predators are more likely to capture inactive prey (Huey & Pianka, 1981). Thus, having both active and inactive prey reduces competition between predators and exposes prey with different locomotor patterns to predation risk. Therefore, intra-population variation in predator activity level can increase their effects on the survival of prey in laboratory settings (Pruitt et al., 2017), potentially cascading to effect primary producers (Keiser, Slyder, Carson, & Pruitt, 2015; Sentis et al., 2020; Start & Gilbert, 2017).

However, the vast majority of previous studies probing the top-down effects of predator personality were executed in non-natural and species-poor enclosed settings, like petri dishes, small mesocosms, or cattle tanks (Chang, Teo, Norma-Rashid, & Li, 2017; DiRienzo, Pruitt, & Hedrick, 2013; Griffen, Toscano, & Gatto, 2012; Lichtenstein et al., 2019; Start & Gilbert, 2017). These studies provide vital insight, but may vastly under- or overestimate the impact of predator behavior, with one study finding a 66% increase in the effect (ω^2) of polyculture on seaweed growth in field vs mesocosm conditions (Skelly, 2002; Stachowicz, Best, Bracken, & Graham, 2008). Here, we rigorously investigated the degree to which diversity in predator personality regulates the top-down impacts of predator in unenclosed and species-rich natural habitats.

We evaluated the top-down effects of Chinese mantis (*Tenodera sinensis*) behavioral diversity on meadow communities, because these invasive predators can decrease insect biomass and increase plant biomass in meadows (L. Hurd & R. Eisenberg, 1984; Moran & Hurd, 1997; Moran, Rooney, & Hurd, 1996). Mesocosm studies (Pruitt et al., 2017) and the locomotor crossover hypothesis (Sweeney et al., 2013) predict that behavioral diversity in mantises would increase how many and which types of prey they kill, reducing prey biomass, potentially changing prey communities and increasing the biomass of plants. Theory on the effects of intraspecific trait variation (Schreiber et al., 2011) predicts that predator behavioral diversity dilutes their effects on any one prey species, thereby increasing coexistence between prey species and thereby prey diversity. Alternatively, behaviorally divergent predators may antagonize or even eat each other (Eldakar, Dlugos, Wilcox, & Wilson, 2009; Sih & Watters, 2005; Vallon et al., 2016); highly aggressive group members, in particular, can increase antagonistic interactions between group members in other species (Eldakar et al., 2009; Sih & Watters, 2005). We therefore predict that many aggressive individuals will decrease the effects of behavioral diversity of mantises on ecosystem structure, because our theoretical underpinnings of these effects rely on behaviorally different predators competing and interfering with each other less than behaviorally similar predators. Gauging the effects of mantis behavioral diversity on meadow ecosystem structure could determine whether intraspecific variation in predator behavior can regulate trophic cascades, rather than the well-established interspecific behavioral variation alone triggering cascades (Preisser, Orrock, & Schmitz, 2007; Schmitz & Suttle, 2001).

We thus evaluated the following hypotheses: (1) Predator groups with high within-group variation in activity level will (i) *decrease* prey biomass, (ii) *increase* prey diversity,

and (iii) *increase* plant biomass relative to behaviorally homogenous groups. To track how exactly predator behavior affects these community outcomes, we measured the effects of mantis behavior on prey functional groups like predators, herbivores, or fungivores. (2) Highly aggressive predator groups will antagonize each other, and thereby decrease the effects of Hypothesis 1. Specifically, we tested whether the coefficient of variation of activity level (behavioral diversity) interacted with group average aggressiveness to affect ecosystems. As predator-prey interactions are often regulated by density-dependent processes (Arditi & Ginzburg, 1989; Holling, 1965), we also tested how mantis density interacts with behavioral diversity to determine community structure. Evaluating these hypotheses *in situ* serves two purposes. First, it helps to predict the top-down effects of between-population variation (A. Bell, 2005; Costa-Pereira, Rudolf, Souza, & Araújo, 2018; Michelangeli, Chapple, Goulet, Bertram, & Wong, 2018; van Dongen, Maldonado, Sabat, & Vásquez, 2010) in predator traits on the ecosystems they inhabit. Second, it evaluates the efficacy of targeted behavioral manipulations in achieving desired community outcomes, like optimizing biocontrol agents (Finke & Snyder, 2008) and ecosystem management practices (Jallow, Cunningham, & Zalucki, 2004).

MATERIALS & METHODS:

Study species and site:

We studied Chinese mantises (*Tenodera sinensis*), because they are widespread, invasive, marketed as biocontrol agents, and have strong effects on the biomass of many insect and plant species (Hurd & Eisenberg, 1990; Moran et al., 1996). We collected mantises and

constructed experimental plots at the Donald S. Wood field laboratory of the Pymatuning Laboratory of Ecology, located in northwest Pennsylvania ($41^{\circ}34'09.6''N$, $80^{\circ}27'51.4''W$). The property contains a mixture of deciduous forest and old fields. These fields are largely composed of *Solidago canadensis* and to a lesser extent *Poaceae* spp., with *Toxicodendron radicans* growing beneath the level of the *S. canadensis*. These fields were also interspersed with *Cornus racemosa*, *Rubus* spp., *Rosa* spp., and other *Solidago* spp. Among these plant species, we focused on Canada goldenrod (*S. canadensis*), the most common herb, and grey dogwood (*C. racemosa*), the most common woody plant. From these fields, we collected roughly 450 mantises via sweep net from June 26th to July 9th 2018, between their 4th and 6th instars. Until their 8th instar, mantises are flightless. We measured mantises' head to tip length using digital calipers (Fisher Traceable) and mass using portable scales (Fisher Scientific Education). Mantises had an average head to tip length of $31.23\text{ mm} \pm 6.42\text{ SD}$, ranging from 19-56 mm, and an average mass of $100\text{ mg} \pm 61\text{ SD}$, ranging from 15-400 mg. Upon collection, we housed each mantis in 600 ml plastic containers containing two sticks for perching and 2 cm of dampened topsoil to maintain humidity. To help standardize hunger level and motivation to forage, each mantis was fed a large size-matched katydid nymph (*Orchelimum vulgare*) upon collection. The next day we began behavioral testing.

Behavioral tests:

The day after capture, we quantified variation in mantises' activity level and then, two hours later, their aggressiveness towards prey. To decrease the interference of multiple tests and extended lab stay in our experiment, mantises deployed to plots ($n = 405$) were assessed only once each. These tests were used to create mantis groups with either high or low activity

level diversity. We ran a separate pool of mantises ($n = 19$) through four iterations of activity and aggressiveness tests to evaluate how repeatable these behaviors are across time. This second cohort of mantises was given a katydid upon capture and their activity level and aggressiveness were evaluated the next day. We then fed them another katydid and repeated this sequence thrice more (four tests in total across eight days).

Individual aggressiveness predicted the activity level of individual mantises (Linear regression: $R^2 = 0.02$, $t = 17.8$, $p = 0.005$), but the effect size of this relationship was negligible, suggesting that these are indeed largely separate traits. However, average aggressiveness did not predict the coefficient of variation of activity level, which are the two principal group-level behavioral metrics of our study, suggesting that these variables are likely independent (ANOVA: $R^2 < 0.01$, $t = 4.78$, $p = 0.501$).

Activity level: Activity level refers to animals' propensity to move around their environment, which determines their hunting mode (Huey & Pianka, 1981; Savino & Stein, 1989; Schmitz, 2008), space use patterns (Wilson & McLaughlin, 2007), and vulnerability to predation (Keiser et al., 2017; Smith & Blumstein, 2008; Start, 2018a). Activity level was estimated by open field test. We gently placed mantises ($n = 447$) in the bottom of 28 cm wide, 16 cm deep, and 36 cm tall plastic arenas with 1 cm graph paper taped to the outside of the top, back, left and right sides. After we gently placed mantises in the bottom of these containers, we gave them a 30 s acclimation period and counted how many squares the mantises crossed with their heads over the next 300 s, using the grid on whichever surface they were climbing. We cleaned arenas with 90% isopropyl alcohol between trials. This focal population of

Chinese mantises behaves consistently on a very similar activity level test conducted using differently sized containers (Lichtenstein et al., 2019).

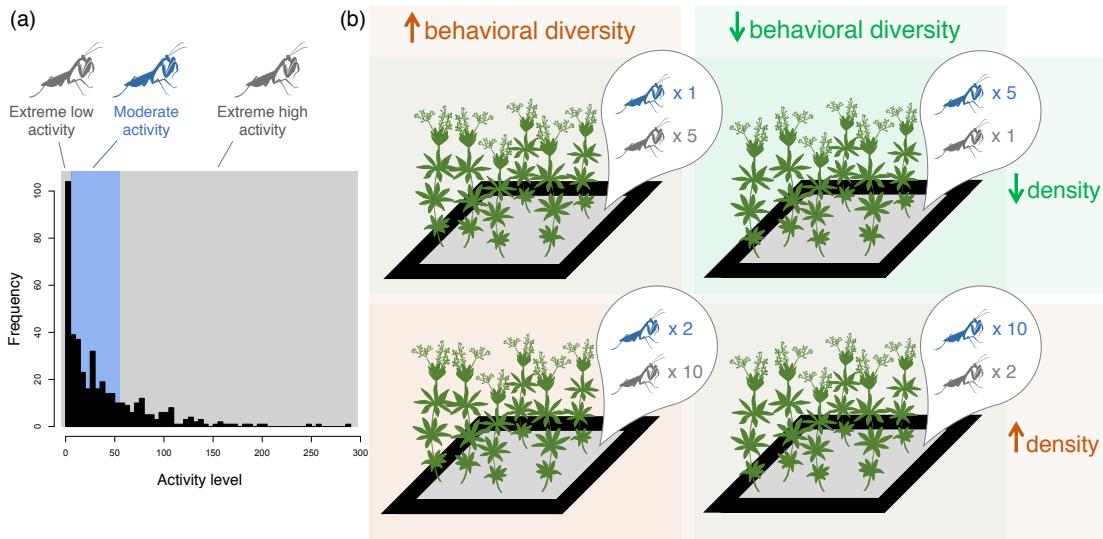


Figure 4.1. Schematic of plot setup. We categorized mantises as moderate activity or extreme activity mantises (a) based on their distance from the average activity level, with moderate mantises being between the 26th and 75th percentiles and extreme mantises being between the 1st and 25th and 76th and 100th percentiles. We assigned (b) one extreme mantis with five moderate mantises to low diversity plots and five extreme mantises with one moderate mantis to high diversity plots. We assigned double these numbers to high density plots. Mantises of these set numbers were chosen from extreme and moderate categories randomly.

The next day, we categorized mantises into extreme or moderate activity level pools (Figure 4.1a). Mantises within the 26th and 75th percentiles in activity level were deemed moderately active, and those between the 1st and 25th percentiles and 76th and 100th percentiles were both deemed relatively extreme mantises. Set numbers of mantises from the extreme and moderate pools were assigned to plot groups randomly (Figure 4.1b). Low density, low behavioral diversity treatment plots received five moderately active mantises and one extreme mantis. High density, low diversity plots received ten moderately active mantises and two extreme mantises. Low density, high diversity treatment plots received one

moderate activity mantis and five extreme mantises. High density, high diversity plots received two moderate activity mantises and ten extreme mantises. These diversity manipulations increased plots' activity level coefficient of variation by 321.7% (Linear model: $F_{1,46} = 90.650$, $R^2 = 0.66$, $p < 0.001$) without altering average activity (Linear model: $F_{1,46} = 2.371$, $R^2 = 0.05$, $p = 0.131$). Density manipulations altered neither activity level CV (Linear model: $F_{1,46} = 0.909$, $R^2 = 0.02$, $p = 0.345$) nor average activity (Linear model: $F_{1,46} = 0.43$, $R^2 < 0.01$, $p = 0.515$). All treatments received some extreme and moderate mantises so that behavioral diversity was effectively manipulated without sharply compressing the range of phenotypes present among treatment groups. These mantis groups do not include 22 individuals that died between testing and deployment.

Aggressiveness: We estimated mantis aggressiveness by their ability to capture prey during staged encounters with froghoppers (*Philaenus spumarius*). Meadow froghoppers are relatively sedentary (Lichtenstein, Wright, McEwen, Pinter-Wollman, & Pruitt, 2017), and yet they can jump faster relative to their size than fleas (Burrows, 2003). We predicted that these traits would render them difficult to subdue for mantises (Jones & DiRienzo, 2018; Prete, Hurd, & Wells, 1999). Two hours after activity tests concluded (1500-1700 hours), we added one froghopper to each mantis' home container. Twenty-four hours later we reopened the containers and recorded whether the mantis had successfully subdued the insect or not. We often found discarded pieces of eaten insects, but mantises are sometimes capable of eating insects entirely. Attacking prey stimuli is a common metric of aggressiveness (Lichtenstein et al., 2016; Pruitt, Grinsted, & Settepani, 2013). To estimate the aggressiveness of mantis groups, we averaged the froghopper survival of each plot, to get a

group-level metric of mantis aggressiveness. We allowed average mantis activity level to vary randomly across plots.

Plot construction:

After mantis groups were assembled, we placed them into one of 60 open air plots: twelve of each density and behavioral diversity combination (Figure 4.1b) and twelve plots with no mantises (controls). Plots were spaced 2 m apart. It took twelve days to assemble these 60 plots. High density (3 mantis/m^2) and low density (1.5 mantises/m^2) treatments match local densities that arise from egg cases of different sizes (L. Hurd & R. Eisenberg, 1984). The plots' design was based on those deployed by Moran et al. (1996), only smaller. A prior study showed that less than 10% of mantises added to similar plots attempted to leave (L. Hurd & R. Eisenberg, 1984), suggesting that juvenile mantises disperse relatively little. Our plots were constructed by mowing 4 m^2 squares into an old field in early April 2018, before leaves began to emerge. At this time, mantis ootheca were very easy to locate, so we removed them (~100 in total) and transported them to another old field over 100 m from the experimental plots. We then lined the perimeter of plots with 30 cm of black plastic sheeting held down with landscaping staples to prevent plant growth along plot borders.

To gauge pre-mantis community composition, we estimated each plot's insect family diversity and Canada goldenrod biomass in June 2018. We estimated insect diversity nondestructively by sweep net, with eight swipes (two per side) roughly 75 cm above the ground per plot. This assessed insects from the lower to upper canopy of the plants. Insects were identified to family in the sweep nets and returned to the plots. During these collections, we lined plots with 120 cm tall moveable polystyrene barriers to hamper jumping insects'

escape. No mantises were found during these collections, confirming that our ootheca removals were successful. We estimated average goldenrod biomass by placing meter sticks at five randomly generated coordinates within each plot and measuring the height of each Canada goldenrod that touched the sticks. This sampling method did not locate enough grey dogwood to estimate pre-mantis dogwood biomass. We acknowledge that these sampling methods likely recovered different insect taxa at different rates. Therefore, comparison between insect communities before versus after mantis addition must be made with that caveat in mind.

To estimate aboveground biomass based on stem height, we created allometric equations for Canada goldenrod and grey dogwood after Crutsinger et al. (2006). We measured the height of 48 Canada goldenrod and 36 grey dogwood stems, dried them in drying ovens at 35°C for 24 hours and weighed them immediately. We used AIC_c weight model selection to determine the best model for each species (Akaike, 1987; Burnham & Anderson, 2003). Both models had R² values above 0.85.

After these initial measurements, we clipped all plants between the plots and 20 cm into the plots, to prevent mantises from exiting by leaping from tall plants. We lined the center of the black plastic with a 10 cm wide coat of Tanglefoot to capture any immigrants or emigrants. On several occasions, we observed mantises walk up to the Tanglefoot, touch it, and then retreat. We patrolled the plots twice daily to remove overgrown plants and reapply Tanglefoot.

Next, we applied mantis treatments to plots. Each day, from June 26th to July 9th 2018, until 1200 hours we collected as many mantises as possible from the property. Upon completion of activity level tests and aggressiveness estimates, we assigned mantises into the

density and diversity treatments described above (Figure 4.1). Plots were established in groups one of each treatment, with the ordering of treatments randomly determined within each group of plots. This procedure allowed a relatively homogenous yet randomly distributed set of treatments across space. We added mantises to the plots between 1500 and 1700 hours over the course of twelve days and maintained the plots for 40 days.

Plot deconstruction and measurements:

We maintained the plots for 40 days to ensure that mantises were in the plots long enough before they reached sexual maturity and dispersed away in mid-August. We collected all data blind to treatment group. We sampled insects using a Craftsman (41BS2BVG799) 27cc leaf blower with the included vacuum kit, after Stewart and Wright (1995). To catch insects, we set organza wedding gift bags in the vacuum nozzle kept in place with wire rings. After assembling the 120 cm tall polystyrene barriers, we ran the vacuum over the plants for 120 s switching sides every 30 s. This technique also sampled insects from the lower to upper canopy of the plants. Bags were sealed and removed from the vacuum while the vacuum ran to prevent insect escape. Bags were then immediately placed in 90% ethanol. We collected at least 50 insect families, although we were unable to identify all Thysanopterans, because most specimens were very small and damaged. Upon transport back to the University of California Santa Barbara, insects were identified to family, counted, and their body lengths were measured. Dipterans and parasitoid wasps were excluded from the analysis, because high dispersal ability permits these taxa to move between plots with ease. We calculated the Simpson's diversity of arthropod families for each plot using arthropod abundances. We used allometric equations to estimate the biomass of insects from each family using the family-

specific allometric equations presented in Ganihar (1997). These estimates corroborated the less taxa-specific equation proposed by Rogers, Hinds, and Buschbom (1976). When calculating total biomass, we removed two large orthopterans, because they were more than twice the combined mass of all other arthropods sampled from their plots and their inclusion resulted in two clear outliers. For the purpose of understanding how our treatments affect prey functional categories, these arthropods were sorted into five functional categories: predators, herbivores, fungivores, non-eaters (insects that only eat as larvae), and ants. Ants have a feeding strategy so unlike any of our other families that we put them in a unique category of their own. Families were assigned to these groups based on available information of their diets. We then calculated the total biomass of each group for each plot.

Within 48h of each plot's deconstruction, we measured the height of every Canada goldenrod ($n = 14,182$) and grey dogwood ($n = 736$) stem of all sizes. We used the allometric equations described above to estimate the aboveground biomass of each stem. We calculated average stem biomass of each plot rather than total biomass, because total biomass is heavily influenced by stem density, which the mantises were unlikely to change in 40 days. They could, however, plausibly influence the growth of stems already sprouted when they arrived. All plot deconstruction transpired over twelve days.

Statistical analyses:

We estimated the repeatability of mantis activity level and aggressiveness across four trials using generalized linear mixed models (GLMM) fit with 1000 bootstrap iterations in the rptR package (Stoffel, Nakagawa, & Schielzeth, 2017) in R 3.4.1. The models had "trial number" as a fixed effect, "mantis ID" as a random effect, and either "activity level" or

“aggressiveness” for its response variable. The activity level models were fit with Poisson distributions, and the mantis aggressiveness model was fit with a binomial distribution. Because body length could potentially influence activity level and aggressiveness via stride length, we fit a linear model with body length as the predictor variable and activity level as the response variable and a logistic regression with body length as the predictor variable and aggressiveness as the response variable. While these tests were underway, we measured facets of pre-mantis community structure.

Specifically, we checked whether plant biomass and insect diversity differed across treatments before mantis addition using linear models. Each model had “behavioral diversity”, “predator density”, “average aggressiveness” and all interaction terms as predictor variables, and either “arthropod family Simpson’s diversity” or “average goldenrod biomass” as response variables. Pre-mantis Simpson’s diversity and goldenrod biomass conformed to normal distributions as judged by quantile-quantile (q-q) plots. The pre-mantis Simpson’s diversity did not conform to a normal distribution by Shapiro-Wilk test ($W = 0.923$, $p = 0.0010$), but we did not perform any corrections because its W value was still relatively high. We removed non-significant interaction terms from final models.

Because we included mantis aggressiveness in models predicting community structure, the plots without mantises could not be included in these analyses. Therefore, we ran a series of general linear models (t-tests) with “mantis presence” as the predictor variable and either “arthropod biomass”, “arthropod Simpson’s diversity”, “average goldenrod biomass”, and the natural log of “average grey dogwood biomass” as response variables.

We then assessed the effects of mantis density, behavioral diversity, and group aggressiveness on community outcomes using linear models. These models also had

“diversity treatment”, “density treatment”, “average aggressiveness”, and all interaction terms as predictor variables, and either total “arthropod biomass”, “arthropod family Simpson’s diversity”, “average goldenrod biomass”, or the natural log of “average grey dogwood biomass” as response variables. Arthropod biomass, arthropod family Simpson’s diversity, and average goldenrod biomass appeared normal by q-q plot. Goldenrod biomass did not conform to a normal distribution by Shapiro-Wilk test ($W = 0.960$, $p = 0.045$), and once again we did not perform any corrections because its W value was still relatively high. However, average grey dogwood biomass also did not conform to a normal distribution by Shapiro-Wilk test ($W = 0.686$, $p < 0.001$). This W value was relatively low, so we log-transformed these data after which it did conform to a normal distribution.

Finally, we assessed the effects of mantis density, behavioral diversity, and group aggressiveness on the structure of prey communities by analyzing the relative biomass of our five arthropod functional groups: herbivores, predators, fungivores, non-eaters, and ants. We used the package vegan in R to fit a Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson, 2014) based on the Bray-Curtis dissimilarities of the multivariate data (i.e., relative biomass of prey functional groups). We used the relative biomass of these categories to control for large differences in biomass between plots. This model had “diversity treatment”, “density treatment”, “average aggressiveness”, and all interaction terms as predictor variables. Additionally, we visualized the relationship between mantis behavioral variation and prey communities with non-metric multi-dimensional scaling (nMDS).

RESULTS:

Mantises were consistent across time in their activity level ($R = 0.40$, 95% CI lower = 0.14, 95% CI upper = 0.62). This means that between-individual variation accounted for 40% of variation in mantis activity level, similar to the overall repeatability average for all animals, 37% (A. M. Bell, Hankison, & Laskowski, 2009). Mantises killed their froghoppers only $40.09 \pm 3.17\%$ SE of the time and exhibited consistent differences in their aggressiveness over two trials ($R = 0.64$, 95% CI lower = 0.011, 95% CI upper = 0.99) but not four trials ($R = 0.05$, 95% CI lower = 0, 95% CI upper = 0.307). Mantis aggressiveness therefore appears consistent across time, but extended captivity seems to dull these differences, potentially due to satiation. Mantis body-length correlated with mantis activity level, but this relationship was weak (Linear regression: $F_{1,416} = 12.160$, $R^2 = 0.03$, $p = 0.001$). Mantis body length also predicted mantis aggressiveness (Logistic regression: McFadden's $R^2 = 0.07$, $p < 0.001$), although this relationship was not strong either. Thus, activity level and aggression are not strongly driven by stride length.

Before we added mantises to the plots, experimental treatments (predator density and behavioral diversity) and mantis aggressiveness were not significantly related to prey diversity (Linear regression: $F_{3,44} = 1.735$, $R^2 = 0.05$, $p = 0.174$) or Canada goldenrod biomass (Linear regression: $F_{3,44} = 1.679$, $R^2 = 0.103$, $p = 0.185$). At the end of the experiment, the presence of this key predator had no significant effect on insect biomass (T-test: $R^2 < 0.01$, $F_{1,58} = 0.05$, $p = 0.818$), arthropod family Simpson's diversity (T-test: $R^2 = 0.06$, $F_{1,58} = 3.541$, $p = 0.065$), Canada goldenrod biomass (T-test: $R^2 = 0.01$, $F_{1,58} = 0.267$, $p = 0.607$) or grey dogwood biomass (T-test: $R^2 < 0.01$, $F_{1,57} < 0.014$, $p = 0.906$).

Table 4.1. Linear models predicting insect biomass diversity and goldenrod biomass. β estimates for density and behavioral diversity refer to the estimated difference between low density or diversity and high. Non-significant interaction terms were removed from models unless they constituted a higher order interaction term.

Response variable	Predictor variables	F	R2	β std error	T	p
Insect biomass		1.492	0.122			0.222
	Mantis behavioral diversity (low)			0.918 \pm 6.765	0.136	0.893
	Mantis density (low)			22.579 \pm 14.542	1.553	0.123
	Mantis aggressiveness			34.012 \pm 22.207	1.532	0.133
	Aggressiveness*density			-69.805 \pm 31.620	-2.208	0.033
Prey taxonomic diversity		0.855	0.055			0.472
	Mantis behavioral diversity (low)			-0.010 \pm 0.024	-0.420	0.676
	Mantis density (low)			0.030 \pm 0.024	1.214	0.231
	Mantis aggressiveness			-0.049 \pm 0.057	-0.855	0.397
Canada goldenrod biomass		2.888	0.212			0.033
	Mantis behavioral diversity (low)			-1.435 \pm 0.481	-2.985	0.005
	Mantis density (low)			0.338 \pm 0.223	1.516	0.137
	Mantis aggressiveness			-0.807 \pm 0.784	-1.029	0.309
	Aggressiveness*diversity			2.471 \pm 1.051	2.352	0.023
Grey dogwood biomass		0.255	0.017			0.858
	Mantis behavioral diversity (low)			0.042 \pm 0.408	0.102	0.919
	Mantis density (low)			-0.344 \pm 0.408	-0.844	0.403
	Mantis aggressiveness			0.151 \pm 0.945	0.16	0.874

Predator trait-driven community changes:

Mantis density, behavioral diversity (intra-group activity level variability), and aggressiveness substantially altered the biomass of communities (Table 4.1). In groups composed of aggressive mantises, high mantis density plots had significantly more (17.1%) arthropod biomass than low mantis density plots, but when groups were composed of docile mantises, mantis density appeared unrelated to arthropod biomass (Table 4.1; Figure 4.2).

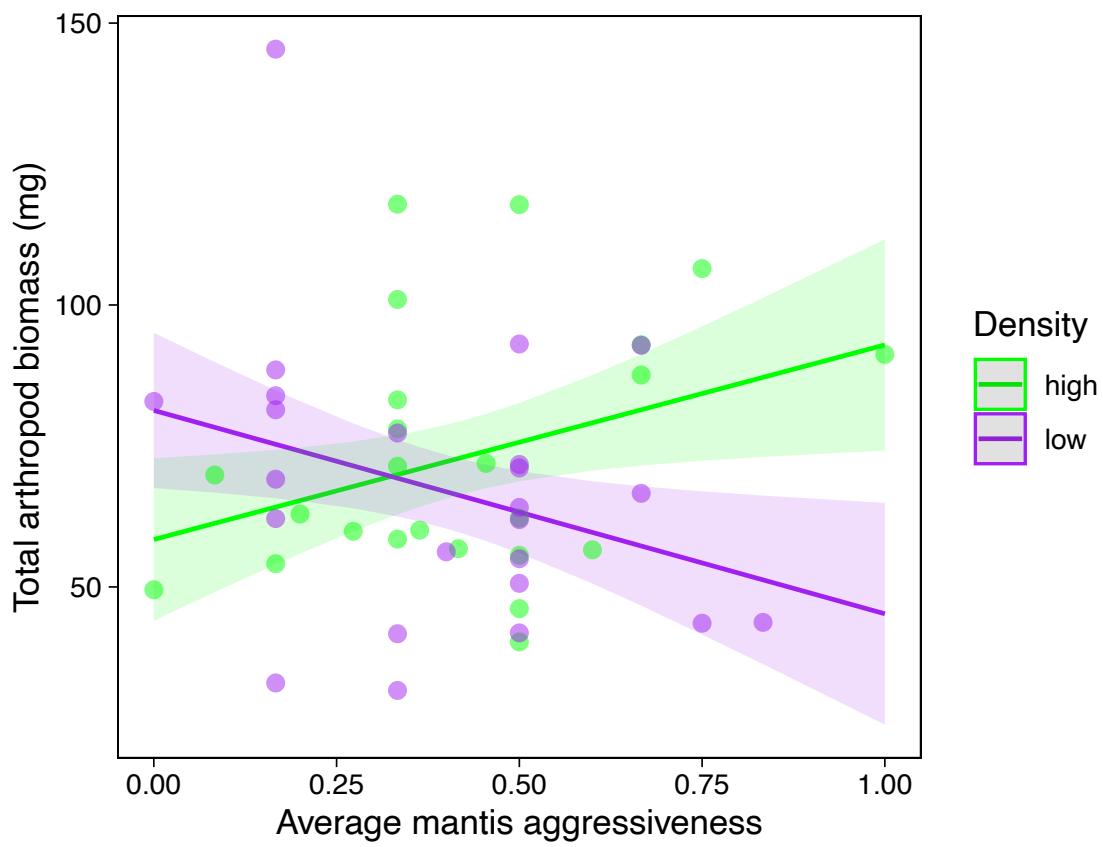


Figure 4.2. Arthropod biomass at low and high mantis density across a spectrum of mantis aggressiveness. Green lines and points refer to high mantis density plots, and purple points refer to low mantis density plots. Shaded areas around best fit regression lines are 84% confidence intervals, and 84% confidence intervals approximate significant differences at a 95% confidence level. Arthropod biomass therefore significantly differs between high and low density plots when the 84% confidence intervals do not overlap.

Behavioral diversity alone had a marginally significant effect of the composition of arthropod functional groups (PERMANOVA: $F_1 = 2.956$, $p = 0.069$). This marginally significant effect appears to be driven by behaviorally diverse mantises resulting in communities with more ants and non-eating insects, whereas behaviorally homogenous mantises resulted in communities containing more predators, herbivores, and fungus eaters (Figure 4.3).

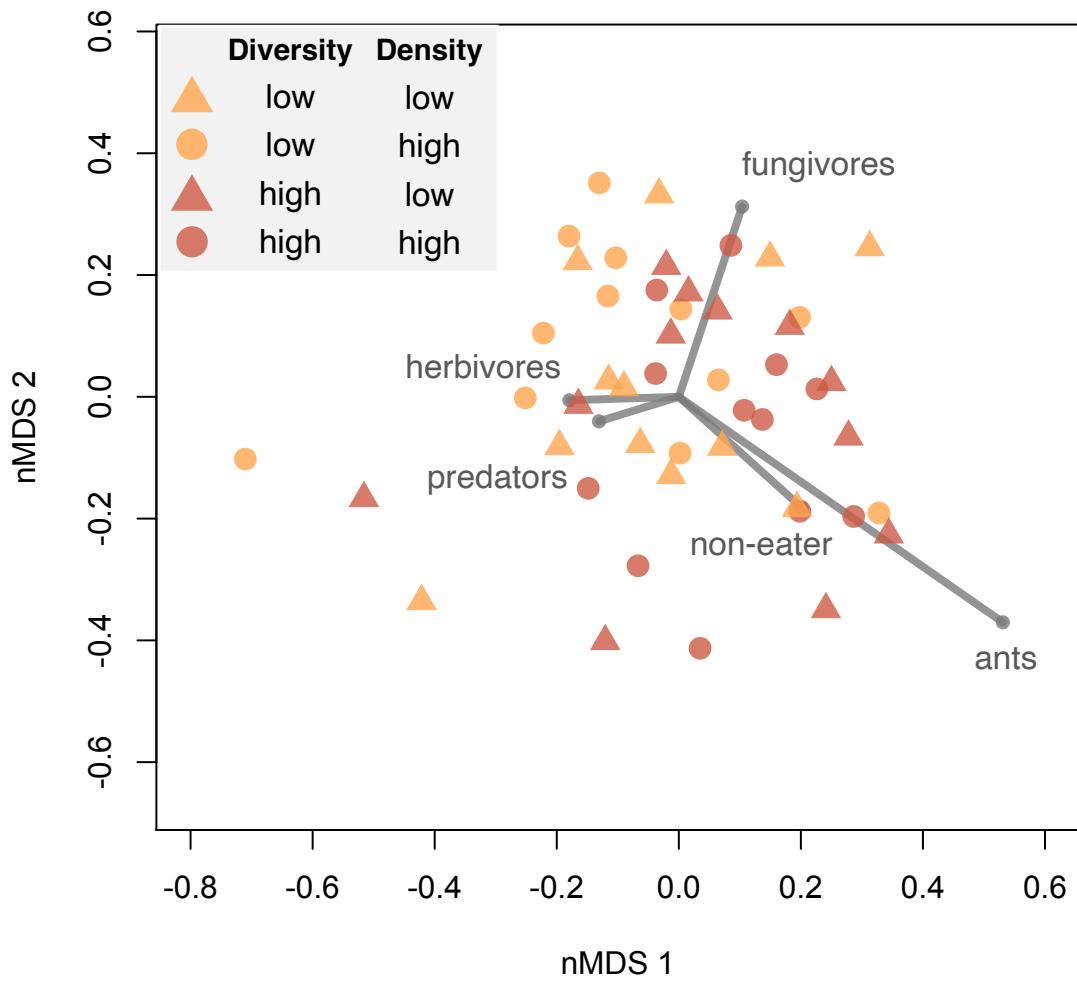


Figure 4.3. Arthropod functional category composition across high and low mantis behavioral diversity plots. Non-linear multidimensional scaling (NMDS) plot was constructed with five insect functional categories using Bray-Curtis dissimilarities. Grey lines represent how prey functional categories fall along NMDS axes.

Mantis behavioral diversity had cascading effects on plant biomass. Behaviorally diverse groups of mantises had significantly higher Canada goldenrod biomass by 8.0% independently of aggressiveness and 15.8% more among less aggressive mantis groups

(Table 4.1; Figure 4.4). Mantis density, aggressiveness, and behavioral diversity had no significant effect on arthropod diversity or grey dogwood biomass (Table 4.1).

Goldenrod and dogwood average biomass were positively correlated, but there were no other significant correlations between arthropod biomass, arthropod diversity, and plant biomass.

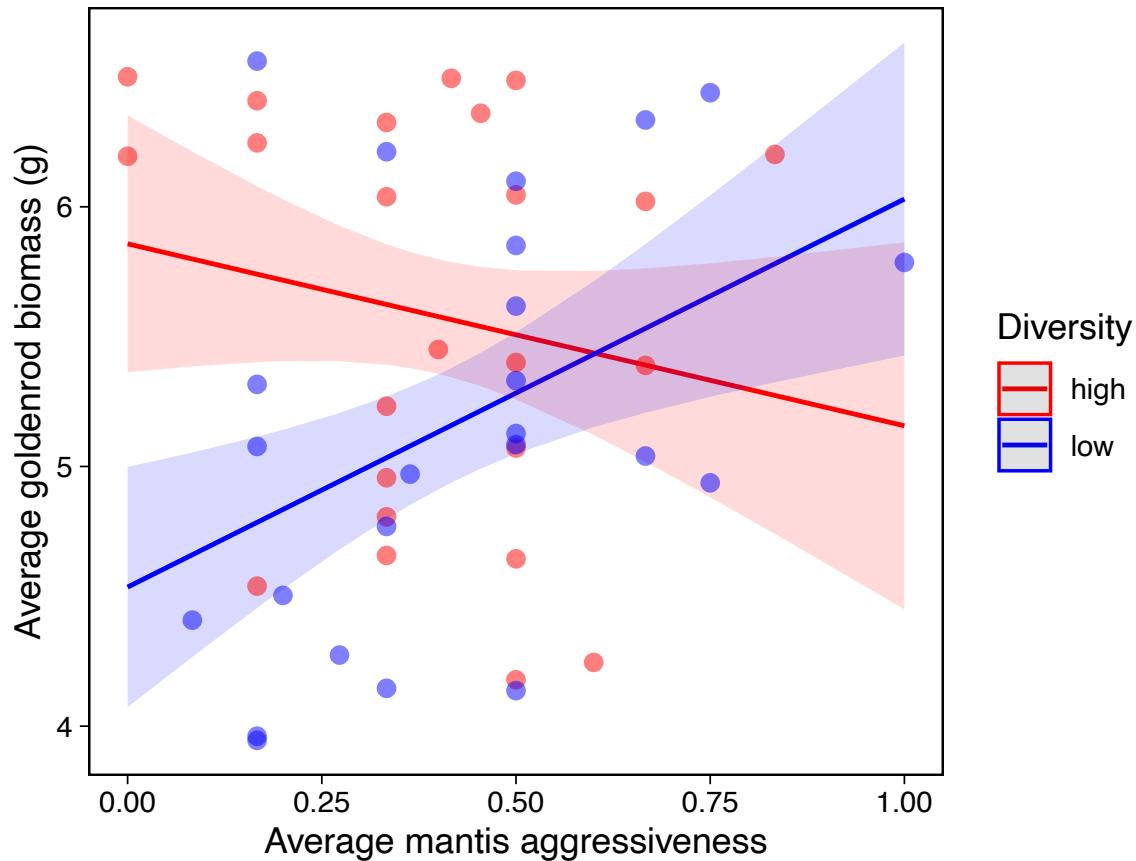


Figure 4.4. Average Canada goldenrod (*Solidago canadensis*) biomass at high and low levels of mantis behavioral and a spectrum of mantis aggressiveness. Blue lines and points refer to high mantis behavioral diversity plots, and red points refer to low mantis behavioral diversity plots. Shaded areas around best fit regression lines are 84% confidence intervals, and 84% confidence intervals approximate significant differences at a 95% confidence level. Goldenrod biomass therefore significantly differs between high and low diversity plots when the 84% confidence intervals do not overlap.

DISCUSSION:

We experimentally evaluated the top-down effects of predator between-individual behavioral diversity, average aggressiveness, and density on natural plant and insect communities. Surprisingly, mantis presence alone had no detectable effect on community outcomes (Moran & Hurd, 1997; Moran et al., 1996). This is consistent with long-standing theory that predator density will not be directly proportional to prey mortality in multiple-predator systems (Abrams, 1993; Sih, Englund, & Wooster, 1998) and empirical work finding that predators do not exert strong top-down effects in goldenrod-dominated systems (Schmitz, 2004). Had we looked only at predator presence, we would have overlooked that it was intra-population behavioral diversity, in conjunction with predator aggressiveness and density, which determined arthropod and plant biomass. The top-down effects of intra-population behavioral diversity have never been evaluated in free-living field conditions, and this variation is normally invisible to ecologists (Sih, Cote, Evans, Fogarty, & Pruitt, 2012; Wolf & Weissing, 2012). Our findings reveal that predators' intraspecific personality diversity can precipitate trophic cascades through ecosystems, lending novel support for the utility of accounting for individual variation in behavior when predicting ecosystem-level outcomes.

Behavior-dependent density dependence:

In our study, even the effects of predator density on prey biomass, a canonical topic in community ecology (Arditi & Ginzburg, 1989; Holling, 1965), depended on between-group variation in mantis aggressiveness. Going from less aggressive to more aggressive groups, mantis density went from having no effect to a positive effect on prey biomass (Figure 4.2).

This suggests that predator aggressiveness may modulate the effects of predator density on prey biomass by inducing cannibalism or interference between mantises, thereby driving off or killing fewer prey. Mantises are highly cannibalistic (L. Hurd & R. M. Eisenberg, 1984; Prete et al., 1999), and aggressiveness can promote cannibalism, conspecific aggression, and interference competition (Eldakar et al., 2009; Johnson & Sih, 2005; Sih & Watters, 2005; Vallon et al., 2016). Furthermore, predator cannibalism and intra-guild predation can increase prey survival (Finke & Denno, 2003; Wahlström, Persson, Diehl, & Byström, 2000). Because these plots were not enclosed, we cannot be sure whether this missing biomass was eaten or frightened away. Regardless, the outcome is the same; the insects are gone. These results convey that intraspecific trait variation can alter effects of predator density on prey abundance, perhaps by amplifying cannibalism and/or intraspecific interference.

Behavior-based trophic cascades:

A recent meta-analysis found that intraspecific trait variation has particularly strong effects on trophic cascades (Des Roches et al., 2018). Consistent with this, we found that higher predator behavioral diversity (i.e. activity level) increased plant biomass (Figure 4.4). Aggressive mantises weaken this effect, suggesting that aggressive predators increase antagonism, weakening the effects of behavioral diversity. Based on the locomotor crossover hypothesis (Huey & Pianka, 1981), we would expect active mantises to eat or frighten away inactive prey, whereas inactive mantises should tend to consume or induce fear effects in active prey. With active and inactive mantises, it stands to reason that their combined effects should be more pervasive across the community, potentially explaining why behaviorally diverse plots had more goldenrod biomass. This highlights the importance of considering (i)

multiple behavioral traits (e.g., activity level and aggressiveness) and (ii) both between- and within-population trait variability when evaluating the vertical (i.e., bottom-up and top-down) effects of individual behavioral diversity on ecosystems (Costa-Pereira, Araújo, Souza, & Ingram, 2019; Ingram, Costa-Pereira, & Araújo, 2018).

The effects of mantis behavior on goldenrod biomass may be driven by behaviorally diverse mantises resulting in marginally more non-eating insects (e.g., adult lampyrids and some lepidopterans) and ants relative to herbivores, predators, and fungivores (Figure 4.3). This prey community shift away from herbivores may have decreased the effects of herbivory on goldenrods, explaining increases in goldenrod biomass. Because we cannot tell whether insects were chased away or eaten, we cannot be sure whether this a mortality- or trait-based trophic cascade, wherein predators alter plant biomass by changing herbivore feeding behavior (Schmitz, Krivan, & Ovadia, 2004). Trait-based trophic cascades and intraspecific variation in predator personality are taxonomically widespread from wolves to wolf spiders (A. M. Bell et al., 2009; Beschta & Ripple, 2009; MacDonald, 1983; Schmitz, Beckerman, & O'Brien, 1997; Schmitz et al., 2004), and in laboratory mesocosms, predator personality can regulate trait-based trophic cascades (Belgrad & Griffen, 2016; Keiser et al., 2015). Our results show that predator personality can also regulate the strength of trophic cascades in nature, further highlighting the value of considering intraspecific trait variation in trait-based trophic cascades.

Conclusions:

Because activity level relates closely to how and what predators hunt (Harrison et al., 2017; Sweeney et al., 2013), diversity in this predator functional trait is predicted to affect

ecosystem structure (Schreiber et al., 2011). Prior mesocosm studies have partially supported these claims by showing how predator personality traits might determine ecosystem structure and function (Griffen et al., 2012; Start, 2018b; Start & Gilbert, 2017; Toscano & Griffen, 2014). Our results confirm this assertion and build upon it by showing that predator behavioral diversity can shape the biomass of multiple trophic levels in diverse and free-living communities. Accounting for intraspecific behavioral variation here increased the predictability of top-down effects. This implies that targeted manipulations to predator behavioral diversity could be used to achieve desired community outcomes, like eliminating crop pests or augmenting carbon sequestration, for instance. Thus, weaving intraspecific behavioral variation into community, food web, and restoration ecology may help us understand the problems that plague ecosystems worldwide and possibly serve as tools to fix them.

REFERENCES:

- Abrams, P. A. (1993). Why predation rate should not be proportional to predator density. *Ecology*, 74(3), 726-733.
- Akaike, H. (1987). Factor analysis and AIC. *Psychometrika*, 52(3), 317-332.
- Anderson, M. J. (2014). Permutational multivariate analysis of variance (PERMANOVA). *Wiley StatsRef: Statistics Reference Online*, 1-15.
- Arditi, R., & Ginzburg, L. R. (1989). Coupling in predator-prey dynamics: ratio-dependence. *Journal of Theoretical Biology*, 139(3), 311-326.
- Belgrad, B. A., & Griffen, B. D. (2016). Predator-prey interactions mediated by prey personality and predator hunting mode. *Proceedings of the Royal Society of London B: Biological Sciences*, 283(1828), 20160408. doi: 10.1098/rspb.2016.0408
- Bell, A. (2005). Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). *Journal of Evolutionary Biology*, 18(2), 464-473.
- Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, 77(4), 771-783. doi: 10.1016/j.anbehav.2008.12.022

- Bengston, S., & Dornhaus, A. (2015). Latitudinal variation in behaviors linked to risk tolerance is driven by nest-site competition and spatial distribution in the ant *Temnothorax rugatulus*. *Behavioral Ecology and Sociobiology*, 69(8), 1265-1274.
- Beschta, R. L., & Ripple, W. J. (2009). Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation*, 142(11), 2401-2414.
- Boyer, N., Réale, D., Marmet, J., Pisanu, B., & Chapuis, J. L. (2010). Personality, space use and tick load in an introduced population of Siberian chipmunks *Tamias sibiricus*. *Journal of Animal Ecology*, 79(3), 538-547.
- Burnham, K. P., & Anderson, D. R. (2003). *Model selection and multimodel inference: a practical information-theoretic approach*: Springer Science & Business Media.
- Burrows, M. (2003). Biomechanics: froghopper insects leap to new heights. *Nature*, 424(6948), 509-509.
- Chang, C.-c., Teo, H. Y., Norma-Rashid, Y., & Li, D. (2017). Predator personality and prey behavioural predictability jointly determine foraging performance. *Scientific Reports*, 7. doi: 10.1038/srep40734
- Costa-Pereira, R., Araújo, M. S., Souza, F. L., & Ingram, T. (2019). Competition and resource breadth shape niche variation and overlap in multiple trophic dimensions. *Proceedings of the Royal Society B*, 286(1902), 20190369.
- Costa-Pereira, R., Rudolf, V. H., Souza, F. L., & Araújo, M. S. (2018). Drivers of individual niche variation in coexisting species. *Journal of Animal Ecology*, 87(5), 1452-1464.
- Cote, J., Clobert, J., Brodin, T., Fogarty, S., & Sih, A. (2010). Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 4065-4076.
- Crutsinger, G. M., Collins, M. D., Fordyce, J. A., Gompert, Z., Nice, C. C., & Sanders, N. J. (2006). Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science*, 313(5789), 966-968. doi: 10.1126/science.1128326
- Des Roches, S., Post, D. M., Turley, N. E., Bailey, J. K., Hendry, A. P., Kinnison, M. T., . . . Palkovacs, E. P. (2018). The ecological importance of intraspecific variation. *Nature ecology & evolution*, 2(1), 57.
- Des Roches, S., Shurin, J. B., Schlüter, D., & Harmon, L. J. (2013). Ecological and evolutionary effects of stickleback on community structure. *PLoS One*, 8(4), e59644.
- DiRienzo, N., Pruitt, J. N., & Hedrick, A. V. (2013). The combined behavioural tendencies of predator and prey mediate the outcome of their interaction. *Animal Behaviour*, 86(2), 317-322. doi: 10.1016/j.anbehav.2013.05.020
- Duckworth, R. A., Belloni, V., & Anderson, S. R. (2015). Cycles of species replacement emerge from locally induced maternal effects on offspring behavior in a passerine bird. *Science*, 347(6224), 875-877.
- Eldakar, O. T., Dlugos, M. J., Wilcox, R. S., & Wilson, D. S. (2009). Aggressive mating as a tragedy of the commons in the water strider *Aquarius remigis*. *Behavioral Ecology and Sociobiology*, 64(1), 25.
- Finke, D. L., & Denno, R. F. (2003). Intra-guild predation relaxes natural enemy impacts on herbivore populations. *Ecological Entomology*, 28(1), 67-73.
- Finke, D. L., & Snyder, W. E. (2008). Niche partitioning increases resource exploitation by diverse communities. *Science*, 321(5895), 1488-1490.

- Ganihar, S. (1997). Biomass estimates of terrestrial arthropods based on body length. *Journal of Biosciences*, 22(2), 219-224.
- Gosling, S. D. (2001). From mice to men: what can we learn about personality from animal research? *Psychological Bulletin*, 127(1), 45. doi: 10.1037/0033-2909.127.1.45
- Griffen, B. D., Toscano, B. J., & Gatto, J. (2012). The role of individual behavior type in mediating indirect interactions. *Ecology*, 93(8), 1935-1943.
- Harmon, L. J., Matthews, B., Des Roches, S., Chase, J. M., Shurin, J. B., & Schlüter, D. (2009). Evolutionary diversification in stickleback affects ecosystem functioning. *Nature*, 458(7242), 1167.
- Harrison, P., Gutowsky, L., Martins, E., Ward, T., Patterson, D., Cooke, S., & Power, M. (2017). Individual isotopic specializations predict subsequent inter-individual variation in movement in a freshwater fish. *Ecology*, 98(3), 608-615.
- Holling, C. S. (1965). The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Entomological Society of Canada*, 97(S45), 5-60.
- Huey, R. B., & Pianka, E. R. (1981). Ecological consequences of foraging mode. *Ecology*, 62(4), 991-999. doi: 10.2307/1936998
- Hurd, L., & Eisenberg, R. (1984). Experimental density manipulations of the predator *Tenodera sinensis* (Orthoptera: Mantidae) in an old-field community. II. The influence of mantids on arthropod community structure. *The Journal of Animal Ecology*, 53(3), 955-967.
- Hurd, L., & Eisenberg, R. M. (1984). Experimental density manipulations of the predator *Tenodera sinensis* (Orthoptera: Mantidae) in an old-field community. I. Mortality, development and dispersal of juvenile mantids. *The Journal of Animal Ecology*, 53(1), 269-281.
- Hurd, L., & Eisenberg, R. M. (1990). Arthropod community responses to manipulation of a bitrophic predator guild. *Ecology*, 71(6), 2107-2114.
- Ingram, T., Costa-Pereira, R., & Araújo, M. S. (2018). The dimensionality of individual niche variation. *Ecology*, 99(3), 536-549.
- Jallow, M. F., Cunningham, J. P., & Zalucki, M. P. (2004). Intra-specific variation for host plant use in *Helicoverpa armigera* (Hübner)(Lepidoptera: Noctuidae): implications for management. *Crop Protection*, 23(10), 955-964.
- Johnson, J. C., & Sih, A. (2005). Precopulatory sexual cannibalism in fishing spiders (*Dolomedes triton*): a role for behavioral syndromes. *Behavioral Ecology and Sociobiology*, 58(4), 390-396.
- Jones, C., & DiRienzo, N. (2018). Behavioral variation post-invasion: resemblance in some, but not all, behavioral patterns among invasive and native praying mantids. *Behavioural Processes*, 153, 92-99.
- Katano, O. (2011). Effects of individual differences in foraging of pale chub on algal biomass through trophic cascades. *Environmental Biology of Fishes*, 92(1), 101.
- Keiser, C. N., Ingleby, S. J., Toscano, B. J., Scharf, I., & Pruitt, J. N. (2017). Habitat complexity dampens selection on prey activity level. *Ethology*. doi: 10.1111/eth.12700
- Keiser, C. N., Slyder, J. B., Carson, W. P., & Pruitt, J. N. (2015). Individual differences in predators but not producers mediate the magnitude of a trophic cascade. *Arthropod-Plant Interactions*, 9(3), 225-232.

- Lichtenstein, J. L., Daniel, K. A., Wong, J. B., Wright, C. M., Doering, G. N., Costa-Pereira, R., & Pruitt, J. N. (2019). Habitat structure changes the relationships between predator behavior, prey behavior, and prey survival rates. *Oecologia*, 1-12.
- Lichtenstein, J. L., DiRienzo, N., Knutson, K., Kuo, C., Zhao, K. C., Brittingham, H. A., . . . David, Z. (2016). Prolonged food restriction decreases body condition and reduces repeatability in personality traits in web-building spiders. *Behavioral Ecology and Sociobiology*, 70(11), 1793-1803.
- Lichtenstein, J. L., Wright, C. M., McEwen, B., Pinter-Wollman, N., & Pruitt, J. N. (2017). The multidimensional behavioural hypervolumes of two interacting species predict their space use and survival. *Animal Behaviour*, 132, 129-136. doi: 10.1016/j.anbehav.2017.08.01
- MacDonald, K. (1983). Stability of individual differences in behavior in a litter of wolf cubs (*Canis lupus*). *Journal of Comparative Psychology*, 97(2), 99.
- Michelangeli, M., Chapple, D. G., Goulet, C. T., Bertram, M. G., & Wong, B. (2018). Behavioral syndromes vary among geographically distinct populations in a reptile. *Behavioral Ecology*.
- Michelangeli, M., Smith, C. R., Wong, B. B., & Chapple, D. G. (2017). Aggression mediates dispersal tendency in an invasive lizard. *Animal Behaviour*, 133, 29-34.
- Miller, J. R., Ament, J. M., & Schmitz, O. J. (2014). Fear on the move: predator hunting mode predicts variation in prey mortality and plasticity in prey spatial response. *Journal of Animal Ecology*, 83(1), 214-222. doi: 10.1111/1365-2656.12111
- Moran, M. D., & Hurd, L. (1997). A trophic cascade in a diverse arthropod community caused by a generalist arthropod predator. *Oecologia*, 113(1), 126-132.
- Moran, M. D., Rooney, T. P., & Hurd, L. (1996). Top-down cascade from a bitrophic predator in an old-field community. *Ecology*, 77(7), 2219-2227.
- Nakayama, S., Rapp, T., & Arlinghaus, R. (2017). Fast-slow life history is correlated with individual differences in movements and prey selection in an aquatic predator in the wild. *Journal of Animal Ecology*, 86(2), 192-201.
- Nannini, M. A., Parkos III, J., & Wahl, D. H. (2012). Do Behavioral Syndromes Affect Foraging Strategy and Risk-Taking in a Juvenile Fish Predator? *Transactions of the American Fisheries Society*, 141(1), 26-33. doi: 10.1080/00028487.2011.639268
- Nannini, M. A., & Wahl, D. H. (2016). Does prey community composition affect the way different behavioral types interact with their environment? *Oecologia*, 182(2), 453-462.
- Oudman, T., Bijleveld, A. I., Kavelaars, M. M., Dekkinga, A., Cluderay, J., Piersma, T., & van Gils, J. A. (2016). Diet preferences as the cause of individual differences rather than the consequence. *Journal of Animal Ecology*, 85(5), 1378-1388.
- Paine, R. T. (1969). The Pisaster-Tegula interaction: prey patches, predator food preference, and intertidal community structure. *Ecology*, 50(6), 950-961.
- Pearish, S., Hostert, L., & Bell, A. M. (2013). Behavioral type–environment correlations in the field: a study of three-spined stickleback. *Behavioral Ecology and Sociobiology*, 67(5), 765-774. doi: 10.1007/s00265-013-1500-2
- Post, D. M., Palkovacs, E. P., Schielke, E. G., & Dodson, S. I. (2008). Intraspecific variation in a predator affects community structure and cascading trophic interactions. *Ecology*, 89(7), 2019-2032. doi: 10.1890/07-1216.1

- Preisser, E. L., Orrock, J. L., & Schmitz, O. J. (2007). Predator hunting mode and habitat domain alter nonconsumptive effects in predator–prey interactions. *Ecology*, 88(11), 2744-2751.
- Prete, F. R., Hurd, L. E., & Wells, P. H. (1999). *The praying mantids*: JHU Press.
- Pruitt, J. N., Grinsted, L., & Settepani, V. (2013). Linking levels of personality: personalities of the ‘average’ and ‘most extreme’ group members predict colony-level personality. *Animal Behaviour*, 86(2), 391-399.
- Pruitt, J. N., Howell, K. A., Gladney, S. J., Yang, Y., Lichtenstein, J. L., Spicer, M. E., . . . Pinter-Wollman, N. (2017). Behavioral Hypervolumes of Predator Groups and Predator-Predator Interactions Shape Prey Survival Rates and Selection on Prey Behavior. *The American Naturalist*, 189(3), 254-266.
- Rogers, L. E., Hinds, W., & Buschbom, R. L. (1976). A general weight vs. length relationship for insects. *Annals of the Entomological Society of America*, 69(2), 387-389.
- Savino, J. F., & Stein, R. A. (1989). Behavior of fish predators and their prey: habitat choice between open water and dense vegetation. *Environmental Biology of Fishes*, 24(4), 287-293.
- Schmitz, O. J. (2004). Perturbation and abrupt shift in trophic control of biodiversity and productivity. *Ecology letters*, 7(5), 403-409.
- Schmitz, O. J. (2008). Effects of predator hunting mode on grassland ecosystem function. *Science*, 319(5865), 952-954.
- Schmitz, O. J., Beckerman, A. P., & O'Brien, K. M. (1997). Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology*, 78(5), 1388-1399.
- Schmitz, O. J., Krivan, V., & Ovadia, O. (2004). Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters*, 7(2), 153-163.
- Schmitz, O. J., & Suttle, K. B. (2001). Effects of top predator species on direct and indirect interactions in a food web. *Ecology*, 82(7), 2072-2081.
- Schreiber, S. J., Bürger, R., & Bolnick, D. I. (2011). The community effects of phenotypic and genetic variation within a predator population. *Ecology*, 92(8), 1582-1593.
- Sentis, A., Bertram, R., Dardenne, N., Simon, J.-C., Magro, A., Pujol, B., . . . Hemptinne, J.-L. (2020). Intraspecific difference among herbivore lineages and their host-plant specialization drive the strength of trophic cascades. *bioRxiv*, 722140.
- Sih, A., Cote, J., Evans, M., Fogarty, S., & Pruitt, J. (2012). Ecological implications of behavioural syndromes. *Ecology Letters*, 15(3), 278-289. doi: 10.1111/j.1461-0248.2011.01731.x
- Sih, A., Englund, G., & Wooster, D. (1998). Emergent impacts of multiple predators on prey. *Trends in Ecology & Evolution*, 13(9), 350-355.
- Sih, A., & Watters, J. V. (2005). The mix matters: behavioural types and group dynamics in water striders. *Behaviour*, 142(9-10), 1417-1431.
- Skelly, D. K. (2002). Experimental venue and estimation of interaction strength. *Ecology*, 83(8), 2097-2101.
- Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: a meta-analysis. *Behavioral Ecology*, 19(2), 448-455.
- Spiegel, O., Leu, S. T., Sih, A., Godfrey, S. S., & Bull, C. M. (2015). When the going gets tough: behavioural type-dependent space use in the sleepy lizard changes as the

- season dries. *Proceedings of the Royal Society of London B: Biological Sciences*, 282(1819), 20151768.
- Stachowicz, J. J., Best, R. J., Bracken, M. E., & Graham, M. H. (2008). Complementarity in marine biodiversity manipulations: reconciling divergent evidence from field and mesocosm experiments. *Proceedings of the national Academy of Sciences*, 105(48), 18842-18847.
- Start, D. (2018a). Animal behaviour and algal camouflage jointly structure predation and selection. *Journal of Evolutionary Biology*, 31(5), 773-778.
- Start, D. (2018b). Ontogeny and consistent individual differences mediate trophic interactions. *The American Naturalist*, 192(3), 301-310.
- Start, D., & Gilbert, B. (2017). Predator personality structures prey communities and trophic cascades. *Ecology Letters*, 20(3), 366-374.
- Start, D., Weis, A. E., & Gilbert, B. (2019). Indirect Interactions Shape Selection in a Multispecies Food Web. *The American Naturalist*, 193(3), 000-000.
- Stewart, A. J., & Wright, A. F. (1995). A new inexpensive suction apparatus for sampling arthropods in grassland. *Ecological Entomology*, 20(1), 98-102.
- Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 8(11), 1639-1644. doi: 10.1111/2041-210X.12797
- Sweeney, K., Cusack, B., Armagost, F., O'Brien, T., Keiser, C. N., & Pruitt, J. N. (2013). Predator and prey activity levels jointly influence the outcome of long-term foraging bouts. *Behavioral Ecology*, 24(5), 1205-1210. doi: 10.1093/beheco/art052
- Toscano, B. J., Gownaris, N. J., Heerhartz, S. M., & Monaco, C. J. (2016). Personality, foraging behavior and specialization: integrating behavioral and food web ecology at the individual level. *Oecologia*, 182(1), 55-69.
- Toscano, B. J., & Griffen, B. D. (2014). Trait-mediated functional responses: predator behavioural type mediates prey consumption. *Journal of Animal Ecology*, 83(6), 1469-1477.
- Toscano, B. J., Lichtenstein, J. L. L., & Costa-Pereira, R. (2020). Intraspecific Behavioral Variation Mediates Insect Prey Survival via Direct and Indirect Effects. *Diversity*, 12(4), 152. doi: <https://doi.org/10.3390/d12040152>
- Vallon, M., Grom, C., Kalb, N., Sprenger, D., Anthes, N., Lindström, K., & Heubel, K. U. (2016). You eat what you are: personality-dependent filial cannibalism in a fish with paternal care. *Ecology and Evolution*, 6(5), 1340-1352.
- van Dongen, W. F., Maldonado, K., Sabat, P., & Vásquez, R. A. (2010). Geographic variation in the repeatability of a personality trait. *Behavioral Ecology*, arq145.
- van Overveld, T., & Matthysen, E. (2009). Personality predicts spatial responses to food manipulations in free-ranging great tits (*Parus major*). *Biology Letters*, 6(2), 187-190.
- Wahlström, E., Persson, L., Diehl, S., & Byström, P. (2000). Size-dependent foraging efficiency, cannibalism and zooplankton community structure. *Oecologia*, 123(1), 138-148.
- Wellington, W. (1964). Qualitative changes in populations in unstable environments. *The Canadian Entomologist*, 96(1-2), 436-451.

- Wilson, A. D., & McLaughlin, R. L. (2007). Behavioural syndromes in brook charr, *Salvelinus fontinalis*: prey-search in the field corresponds with space use in novel laboratory situations. *Animal Behaviour*, 74(4), 689-698.
- Wolf, M., & Weissing, F. J. (2012). Animal personalities: consequences for ecology and evolution. *Trends in Ecology & Evolution*, 27(8), 452-461. doi: 10.1016/j.tree.2012.05.001

CHAPTER 5: AFTER ALL THAT WHAT IS THE ECOLOGY OF PERSONALITY?

Thousands of studies have linked individuals' personality traits to virtually every aspect of their lives (Dingemanse & Réale, 2005; Wolf & Weissing, 2012), from learning ability (Groothuis & Carere, 2005) to microhabitat preference (Pearish, Hostert, & Bell, 2013; Wilson & McLaughlin, 2007). This endless indirect evidence suggests that animal personality traits are indeed functional traits that may affect species interactions and thereby the structure of ecological communities (Toscano, Gownaris, Heerhartz, & Monaco, 2016). Consistent with this notion, the behavioral traits of individuals determine how they interact with other species (Chang, Teo, Norma-Rashid, & Li, 2017; Pretorius, Lichtenstein, Eliason, Stier, & Pruitt, 2019; Start, 2018; Start & Gilbert, 2017). These studies, however, considered interactions between individuals not populations, and tended to do so in homogenous environments with only a few interacting species. This left the ecology of personality largely unexplored, because many core ecological topics, like population demography and community assembly, have population-level outcomes. I therefore addressed three questions to gain insights into the role of between-population variation in personality diversity in ecology. These insights form the background of future research into the eco-evo dynamics of personality, and these dynamics can be harnessed to benefit humanity.

THE ROLE OF BETWEEN-POPULATION VARIATION IN PERSONALITY IN SPECIES

INTERACTIONS:

The first unanswered question I tackled was how the effects of animal personality on interactions between species depend on interactions between members of the same species. Individual niche theory predicts that intraspecific competition will favor the evolution of between-individual trait variation, and interspecific competition will select against it, so the balance between intra- and interspecific competition will determine the extent of intraspecific variation (Van Valen, 1965). This prediction relies on complementarity. Complementarity arises when individuals with differing traits compete, antagonize, or interfere with each other less, increasing their effects on other species (Sih, Englund, & Wooster, 1998). I found that members of behaviorally diverse groups repelled each other less (Figure 2.2), while also reducing the survival of other species (Figure 2.3). This suggests that behaviorally diverse groups compete less with members of their own species but more with members of other species, consistent with the complementarity effects predicted by individual niche theory. Applying individual niche theory to a functional trait (predator behavior is often studied as a functional trait; Preisser, Orrock, & Schmitz, 2007; Schmitz, 2008) increased our ability to predict the outcome of these interactions. Consequently, intraspecific interactions, namely complementarity/antagonism, seem like a key mechanism in how personality shapes ecological processes.

Continuing to probe the mechanisms behind the ecology of personality, I asked how the effect of personality on species interactions depended on cannibalism amongst predators and the physical environments in which they hunt. Structural complexity (three-dimensional

climbing structure) increased the effects of predator behavior on prey survival (Figure 3.3; Table 3.2), but predator cannibalism was unrelated to personality or prey survival. The relationship (or lack thereof) between mantis personality and cannibalism will turn out to be of great interest for the mechanisms behind the unusual effect of behavioral diversity on species interactions detected here. In contrast with previous evidence (Lichtenstein, Wright, McEwen, Pinter-Wollman, & Pruitt, 2017; Pruitt et al., 2017), higher predator behavioral diversity resulted in greater prey survival (Figure 3.2). This may be because mantises on average preferred to perch at the same height as katydids, and mantis groups closer to this average killed more katydids, whereas those that deviated from this average killed fewer katydids and tended to have higher levels of behavioral diversity. Behavioral diversity had ecological consequences because diverse groups are more likely to contain ecologically salient individual phenotypes. This kind of effect of trait diversity is called a sampling effect (Duffy, 2002).

Why then did complementarity matter in Chapter 2 while a sampling effect acts in Chapter 3? The most likely explanation is that in Chapter 3 mantis behavior had no effect on cannibalism. Instead, cannibalism was overwhelmingly decided by size and secondarily by habitat structure, suggesting that the behavioral traits we measured and intraspecific interaction were unrelated. Perhaps sampling effects are more likely to occur when intraspecific interactions are unrelated to the traits of interest. Work distinguishing whether sampling or complementarity effects explain the effects of trait diversity on ecosystem function (Huston, 1997; Tilman, 1997) found that both could work in parallel, and now new work must move to explain why different mechanisms work in different cases (Fargione & Tilman, 2005). Our results suggest that how personality relates to intraspecific interactions

determines which mechanism underlies diversity effects, giving clues to where and how personality affects ecology.

However, these experiments, like all similar studies (Griffen, Toscano, & Gatto, 2012; Lichtenstein, Chism, Kamath, & Pruitt, 2017; Nannini, Parkos III, & Wahl, 2012; Start & Gilbert, 2017), were run in simple species-poor environments. In a complex ecosystem where the presence, absence, and average trait levels of hundreds of species could affect how species interact and shape communities, the effects of individual behavioral variation seems in danger of being lost in the noise (Lichtenstein, Rice, & Pruitt, 2018). Despite this, I found that between-population variation in between-individual variation in predator behavior has modest effects on the community composition of their prey (Figure 4.3) and more substantially effects the biomass of plants (Figure 4.4). Interestingly, personality diversity only increased goldenrod biomass by 16% in mantis groups that were not aggressive on average, but had no effect in aggressive groups. It seems that functional trait averages and diversity can interact to affect ecological change. Further, the fact that aggressiveness was the average trait that decreased the effect of diversity suggests that antagonism between predators decreased the effects of behavior on ecological outcomes. Once again, the effect of personality on interspecific interactions appeared to hinge on intraspecific interactions. Even in open complex ecosystems, animal personality can shape the structure of ecosystems, perhaps because of how conspecifics interact with each other.

These chapters combine to form three novel clues into how and why between-population variation in between-individual variation in behavior affected the outcome of interactions between species and ultimately the structure of wild ecosystems. (1) On the most general level, I found that how animal personality affects interactions between species

depends on how variation in behavior affects interactions within species.

Complementary/antagonistic interactions appeared to drive the effects of behavioral diversity in Chapters 2 and 4, but not in Chapter 3. In chapter 3, intraspecific interactions were overwhelmingly driven by size, and one behavioral phenotype yielded the greatest rates of prey capture. (2) More specifically, sampling effects thus seem likely to drive species interactions, when other traits affect interactions within species, and one phenotype yields the best results. A single behavioral phenotype is unlikely to result in the highest lethality when predators hunt many prey species, as was the case in Chapter 4. In Chapter 4, behavioral variability had little to no direct effect on prey survival, but it did affect community composition and plant biomass. (3) This suggests that when a predator species hunts many prey species, its behavior will have negligible effects on each prey species, but if it effects many modestly, it can cumulatively affect outcomes that are the product of many interactions, like plant biomass (Des Roches et al., 2018). These possibilities are testable predictions for how personality acts in community dynamics, which will help form the basis for the next research steps into the eco-evo dynamics of personality.

POSSIBILITIES OF PERSONALITY ECO-EVO DYNAMICS:

Knowing how personality variation shapes species interactions in nature requires studying what drives personality variation. Extensive work already indicates that animal personality is a product of natural selection (Smith & Blumstein, 2008; van Oers & Mueller, 2010). The most common explanation for how natural selection maintains behavioral variation is cross-contextual trade-offs imposed by how they interact with members of their own species and

other species (Dingemanse, Both, Drent, & Tinbergen, 2004; Dingemanse & Réale, 2005; Smith & Blumstein, 2008). One of the few examples of this is that aggressive spiders are better at catching prey, but reduce their fitness by devouring potential mates (Johnson & Sih, 2005). Van Valen (1965) gives a more theoretical picture of how intra- and interspecific competition may impose a cross contextual tradeoff that determine the extent of variation within individuals and between individuals. There are a wide variety of potential cross contextual trade-offs, but each of them are imposed by how animals interact with members of their own species and other species, be they predator (Smith & Blumstein, 2008) or prey species (Dingemanse et al., 2004). Thus, species interactions are both the cause and consequence of animal personality.

Because personality and species interactions are each other's cause and consequence, they must form ecological-evolutionary dynamics of some sort. The behavioral traits of animals of many species in one generation affects community structure, which would then affect the behavioral traits present in these populations in the next generation. Animal personality eco-evo dynamics would work a little differently than classic eco-evo feedbacks. The eco-evo dynamics of animal personality would center not on average trait values but trait variance. My experiments give a picture of how trait variance, specifically personality diversity, can affect ecosystems via species interactions that transpire across trophic levels. The individual niche explanation gives a picture of how competition can affect trait variance (Roughgarden, 1972; Van Valen, 1965). However, predator-prey interactions must also be considered in the eco-evo dynamics of animal personality, because the ecological importance of competition is debatable compared to interactions across trophic levels (Connell, 1980), and predators impose strong selection pressure on prey personality (Bell & Sih, 2007;

Pretorius et al., 2019). The problem is that the evidence for how species interactions within trophic levels affects behavioral diversity is thin, but the evidence for how interactions across trophic levels affects behavioral variation is thinner still.

I have borrowed evidence from studies of how interactions across trophic levels affect trait diversity to generate predictions for how this might work. Studies on ecological release suggest that diverse assemblies of predator species constrict the evolution of trait diversity by narrowing the niches they can occupy (Azuma, 1992; Des Roches, Harmon, & Rosenblum, 2016). Similarly, diversity in the species animals can prey upon appears to support trait diversity by increasing the widths of those animals' niches (Araújo & Costa-Pereira, 2013; Darimont, Paquet, & Reimchen, 2009; Layman, Quattrochi, Peyer, & Allgeier, 2007). These lines of evidence are consistent with the diversity cascades proposed by Hunter and Price (1992) and Dyer and Letourneau (2003) in which different forms of diversity beget more diversity at higher trophic levels and then often decrease diversity at lower levels. It is also possible for predator diversity to lead to antagonistic effects, increasing diversity at lower levels (Schmitz, Krivan, & Ovadia, 2004). Based on the available evidence, eco-evo dynamics that travel up and down trophic levels seem like a likely framework on which to test how animal personality operates in ecosystems, plus or minus some behavioral plasticity. These dynamics would function more like eco-evo cascades than eco-evo feedbacks. What I have done with my experiments is begin mapping the ecological half of eco-evo dynamics, opening the door to interesting possibilities like the following.

FUTURE DIRECTIONS AND POTENTIAL USES:

Probing the eco-evo dynamics of animal personality opens the door to new questions and practical uses. A thorough mapping of how complex eco-evo interplay between animal personality and species interactions and how they shape ecosystems is a far flung goal of the study of the ecology of personality. Accomplishing it requires addressing many more questions, because despite hundreds of studies probing animal personality (Bell, Hankison, & Laskowski, 2009), the unanswered basic questions are innumerable. Building on my studies into the ecological impacts of one species personality, how does the personality of several or hundreds of species interact to affect ecological outcomes? The same question applies to the evolutionary side of the eco-evo dynamics; how does the personality diversity of several or hundreds of species interact to affect the total personality variation present in an ecosystem? Much work has investigated how much species diversity or trophic levels can exist in any one place (Hairston, Smith, & Slobodkin, 1960; Kamiya, O'Dwyer, Nakagawa, & Poulin, 2014; Tews et al., 2004). However, we have no idea how much personality diversity can exist in an ecosystem. Then, how does the total personality variation present in an ecosystem affect its structure and function? These questions build on my work into how the personality of single species can affect ecological processes at the population level, and they must be answered to harness animal personality to applied uses.

Personality eco-evo feedbacks form the core of applications. Already many predatory insect species are bred in captivity to be deployed for agricultural pest control (Symondson, Sunderland, & Greenstone, 2002). However, these predator species, like predatory insects from the *Orius* genus, have trouble controlling diverse prey species and often succumb to larger predators (Rosenheim, 2005). By controlling the behavioral traits present in predators, we can control how they affect ecosystems and potentially how they are affected by

ecosystems. Their rearing environment could be tweaked to select for predatory insects with desired levels of behavioral diversity and predator avoidance behavior to maximize their ability to control crop pests. For instance, quickly reproducing predator species, like *Orius* species could be raised with diverse prey and higher trophic level predator species to select for behaviorally diverse insects with the traits they need to avoid predators. Mapping animal personality eco-evo dynamics would be the basis of using artificial selection to sculpt the niches of predators to shape ecosystems for human needs. Although these dynamics are not yet well understood enough to perform this kind of ecosystem engineering, my research has brought this much closer.

These possibilities are still distant and hazy. However, my research already allows some ecological predictions based on personality data and describes limited ecosystem manipulation. We can predict that predator patches or sub-populations with more behavioral diversity than surrounding areas will result in higher localized plant biomass. Then, by manipulating the behavioral diversity of predators, I shaped the structure of wild ecosystems. This is the first time anybody has ever used animal personality to engineer the structure of ecosystems. After hundreds of hours of behavioral tests on tiny insects, I can say that measuring the behavioral traits of hundreds of captive animals is an incredibly time intensive and inefficient way to alter ecosystems. In comparison, using artificial selection to breed bespoke behavioral arrays is highly alluring. My experiment was a clumsy first attempt, but developed further it could be used to do more than control crop pests, e.g. increasing carbon sequestration and limiting species invasions. The ecology of animal personality could thus help explain how ecosystems work and then be used to protect them.

CONCLUDING THOUGHTS:

Thousands of studies on animal personality make clear that this variation is incredibly widespread (Bell et al., 2009; Gosling, 2001), appearing everywhere from daphnia (Heuschele, Ekvall, Bianco, Hylander, & Hansson, 2017) to dolphins (Highfill & Kuczaj, 2007). Personality is an extremely variable functional trait axis that is normally invisible to ecologists. Unraveling the ecological consequences of this functional trait benefited greatly from the application of individual niche theory. Before I did this, there were only clues about how behavioral traits could affect individual-scale ecological outcomes. Each time I scaled up from individual to population level effects, I drew up upon individual niche theory to generate hypotheses. The most important ideas I borrowed were the ability of trait variance to affect ecological outcomes and the importance of intraspecific interactions in determining interspecific interactions. My experiments confirmed many of these hypotheses, giving empirical backing to a battered old theory (Soule & Stewart, 1970; Van Valen & Grant, 1970). The product of this synthesis of functional ecology and individual niche theory is a very basic picture of how animal personality might affect ecological processes at the population level, but because of the ubiquity of personality variation, so will be its ecological consequences.

This basic picture forms the background for innumerable unanswered questions. For example, how does the behavioral diversity of multiple predator species interact to affect prey? Does behavioral diversity increase or decrease itself across trophic levels? How do trophic interactions contribute to the stability or loss of trait diversity? How does behavioral variation both within and between individuals interact to affect ecological processes? The

lengthy process of addressing these questions can accomplish two goals. First, it will give a clearer picture of how a ubiquitous largely invisible axis of functional trait variation affects ecological processes. My open plot experiment suggests that personality could explain a lot of variation in ecological outcomes. If the personality diversity of one species could increase plant biomass by 8% in 40 days, what could the personality of 100 species do in a year? Second, using animal personality to affect ecosystem change could potentially be used to boost ecosystem services and agricultural output. These possibilities are quite distant, but I did alter insect communities and increase plant biomass just by throwing some behaviorally diverse mantises at a meadow. I have begun to realize this potential, building a foundation to research that can benefit humanity and spawn endless new lines of investigation.

REFERENCES

- Araújo, M. S., & Costa-Pereira, R. (2013). Latitudinal gradients in intraspecific ecological diversity. *Biology Letters*, 9(6), 20130778.
- Azuma, M. (1992). Ecological release in feeding behaviour: the case of bluegills in Japan. *Hydrobiologia*, 243(1), 269-276.
- Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, 77(4), 771-783. doi: 10.1016/j.anbehav.2008.12.022
- Bell, A. M., & Sih, A. (2007). Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecology Letters*, 10(9), 828-834.
- Chang, C.-c., Teo, H. Y., Norma-Rashid, Y., & Li, D. (2017). Predator personality and prey behavioural predictability jointly determine foraging performance. *Scientific Reports*, 7. doi: 10.1038/srep40734
- Connell, J. H. (1980). Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos*, 31-138.
- Darimont, C. T., Paquet, P. C., & Reimchen, T. E. (2009). Landscape heterogeneity and marine subsidy generate extensive intrapopulation niche diversity in a large terrestrial vertebrate. *Journal of Animal Ecology*, 78(1), 126-133.
- Des Roches, S., Harmon, L. J., & Rosenblum, E. B. (2016). Colonization of a novel depauperate habitat leads to trophic niche shifts in three desert lizard species. *Oikos*, 125(3), 343-353.

- Des Roches, S., Post, D. M., Turley, N. E., Bailey, J. K., Hendry, A. P., Kinnison, M. T., . . . Palkovacs, E. P. (2018). The ecological importance of intraspecific variation. *Nature ecology & evolution*, 2(1), 57.
- Dingemanse, N. J., Both, C., Drent, P. J., & Tinbergen, J. M. (2004). Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 271(1541), 847-852.
- Dingemanse, N. J., & Réale, D. (2005). Natural selection and animal personality. *Behaviour*, 142(9-10), 1159-1184.
- Duffy, J. E. (2002). Biodiversity and ecosystem function: the consumer connection. *Oikos*, 99(2), 201-219.
- Dyer, L. A., & Letourneau, D. (2003). Top-down and bottom-up diversity cascades in detrital vs. living food webs. *Ecology Letters*, 6(1), 60-68.
- Fargione, J. E., & Tilman, D. (2005). Diversity decreases invasion via both sampling and complementarity effects. *Ecology Letters*, 8(6), 604-611.
- Gosling, S. D. (2001). From mice to men: what can we learn about personality from animal research? *Psychological Bulletin*, 127(1), 45. doi: 10.1037//0033-2909.127.1.45
- Griffen, B. D., Toscano, B. J., & Gatto, J. (2012). The role of individual behavior type in mediating indirect interactions. *Ecology*, 93(8), 1935-1943.
- Groothuis, T. G., & Carere, C. (2005). Avian personalities: characterization and epigenesis. *Neuroscience & Biobehavioral Reviews*, 29(1), 137-150.
- Hairston, N. G., Smith, F. E., & Slobodkin, L. B. (1960). Community structure, population control, and competition. *The American Naturalist*, 94(879), 421-425.
- Heuschele, J., Ekval, M. T., Bianco, G., Hylander, S., & Hansson, L. A. (2017). Context-dependent individual behavioral consistency in Daphnia. *Ecosphere*, 8(2), e01679.
- Highfill, L. E., & Kuczaj, S. (2007). Do bottlenose dolphins (*Tursiops truncatus*) have distinct and stable personalities? *Aquatic mammals*, 33(3), 380.
- Hunter, M. D., & Price, P. W. (1992). Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology*, 73(3), 724-732.
- Huston, M. A. (1997). Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia*, 110(4), 449-460.
- Johnson, J. C., & Sih, A. (2005). Precopulatory sexual cannibalism in fishing spiders (*Dolomedes triton*): a role for behavioral syndromes. *Behavioral Ecology and Sociobiology*, 58(4), 390-396.
- Kamiya, T., O'Dwyer, K., Nakagawa, S., & Poulin, R. (2014). What determines species richness of parasitic organisms? A meta-analysis across animal, plant and fungal hosts. *Biological Reviews*, 89(1), 123-134.
- Layman, C. A., Quattrochi, J. P., Peyer, C. M., & Allgeier, J. E. (2007). Niche width collapse in a resilient top predator following ecosystem fragmentation. *Ecology letters*, 10(10), 937-944.
- Lichtenstein, J. L., Chism, G. T., Kamath, A., & Pruitt, J. N. (2017). Intraindividual Behavioral Variability Predicts Foraging Outcome in a Beach-dwelling Jumping Spider. *Scientific Reports*, 7(1), 18063.
- Lichtenstein, J. L., Rice, H. K., & Pruitt, J. N. (2018). Personality variation in two predator species does not impact prey species survival or plant damage in staged mesocosms. *Behavioral Ecology and Sociobiology*, 72(4), 70.

- Lichtenstein, J. L., Wright, C. M., McEwen, B., Pinter-Wollman, N., & Pruitt, J. N. (2017). The multidimensional behavioural hypervolumes of two interacting species predict their space use and survival. *Animal Behaviour*, 132, 129-136. doi: 10.1016/j.anbehav.2017.08.01
- Nannini, M. A., Parkos III, J., & Wahl, D. H. (2012). Do Behavioral Syndromes Affect Foraging Strategy and Risk-Taking in a Juvenile Fish Predator? *Transactions of the American Fisheries Society*, 141(1), 26-33. doi: 10.1080/00028487.2011.639268
- Pearish, S., Hostert, L., & Bell, A. M. (2013). Behavioral type–environment correlations in the field: a study of three-spined stickleback. *Behavioral Ecology and Sociobiology*, 67(5), 765-774. doi: 10.1007/s00265-013-1500-2
- Preisser, E. L., Orrock, J. L., & Schmitz, O. J. (2007). Predator hunting mode and habitat domain alter nonconsumptive effects in predator–prey interactions. *Ecology*, 88(11), 2744-2751.
- Pretorius, J. D., Lichtenstein, J. L. L., Eliason, E. J., Stier, A. C., & Pruitt, J. N. (2019). Predator-induced selection on urchin activity level depends on urchin body size. *Ethology*, 125(10), 716-723. doi: 10.1111/eth.12924
- Pruitt, J. N., Howell, K. A., Gladney, S. J., Yang, Y., Lichtenstein, J. L., Spicer, M. E., ... Pinter-Wollman, N. (2017). Behavioral Hypervolumes of Predator Groups and Predator-Predator Interactions Shape Prey Survival Rates and Selection on Prey Behavior. *The American Naturalist*, 189(3), 254-266.
- Rosenheim, J. A. (2005). Intraguild predation of Orius tristicolor by Geocoris spp. and the paradox of irruptive spider mite dynamics in California cotton. *Biological Control*, 32(1), 172-179.
- Roughgarden, J. (1972). Evolution of niche width. *The American Naturalist*, 106(952), 683-718.
- Schmitz, O. J. (2008). Effects of predator hunting mode on grassland ecosystem function. *Science*, 319(5865), 952-954.
- Schmitz, O. J., Krivan, V., & Ovadia, O. (2004). Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters*, 7(2), 153-163.
- Sih, A., Englund, G., & Wooster, D. (1998). Emergent impacts of multiple predators on prey. *Trends in Ecology & Evolution*, 13(9), 350-355.
- Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: a meta-analysis. *Behavioral Ecology*, 19(2), 448-455.
- Soule, M., & Stewart, B. R. (1970). The "niche-variation" hypothesis: a test and alternatives. *The American Naturalist*, 104(935), 85-97.
- Start, D. (2018). Animal behaviour and algal camouflage jointly structure predation and selection. *Journal of Evolutionary Biology*, 31(5), 773-778.
- Start, D., & Gilbert, B. (2017). Predator personality structures prey communities and trophic cascades. *Ecology Letters*, 20(3), 366-374.
- Symondson, W., Sunderland, K., & Greenstone, M. (2002). Can generalist predators be effective biocontrol agents? *Annual review of entomology*, 47(1), 561-594.
- Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M., & Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of biogeography*, 31(1), 79-92.
- Tilman, D. (1997). Distinguishing between the Effects of Species Diversity and Species Composition. *Oikos*, 80(1), 185-185. doi: 10.2307/3546532

- Toscano, B. J., Gownaris, N. J., Heerhartz, S. M., & Monaco, C. J. (2016). Personality, foraging behavior and specialization: integrating behavioral and food web ecology at the individual level. *Oecologia*, 182(1), 55-69.
- van Oers, K., & Mueller, J. C. (2010). Evolutionary genomics of animal personality. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 3991-4000.
- Van Valen, L. (1965). Morphological variation and width of ecological niche. *The American Naturalist*, 99(908), 377-390.
- Van Valen, L., & Grant, P. R. (1970). Variation and niche width reexamined. *The American Naturalist*, 104(940), 589-590.
- Wilson, A. D., & McLaughlin, R. L. (2007). Behavioural syndromes in brook charr, *Salvelinus fontinalis*: prey-search in the field corresponds with space use in novel laboratory situations. *Animal Behaviour*, 74(4), 689-698.
- Wolf, M., & Weissing, F. J. (2012). Animal personalities: consequences for ecology and evolution. *Trends in Ecology & Evolution*, 27(8), 452-461. doi: 10.1016/j.tree.2012.05.001