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Heterogeneity in body size and habitat complexity influence community structure

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ABSTRACT

Food web studies commonly ignore individual variation within a population and variation in the environment and assume these factors have insignificant effects on community dynamics relative to interspecific interactions. However, variation in body sizes within a population (size structure) and the physical structure of habitats (habitat complexity) can both affect interspecific interactions independently, with possible interactive effects. Using experimental mesocosms, we examined effects of predator size structure and habitat complexity on predation by two common predators in fishless ponds: larval aquatic beetles (*Cybister fimbriolatus)* and larval dragonflies (*Anax junius)*. Cannibalism, intraguild predation, and predation on shared prey were measured at two levels of habitat complexity crossed with six size-structured pairs of predators. We found that highly complex habitats sustain a higher prey density because prey can take refuge from predators. Additionally, size structure had direct (size better predicted predation rate than did species identity) and indirect (IGP and cannibalism lowered predation rates) effects on consumptive interactions, which changed the composition and density of the predator guild. The identified size- and habitat-mediated mechanisms can change the frequencies of intraguild vs. interguild predation (a balance important in determining top–down control of predators), and therefore we argue that these sources of heterogeneity should be included in community ecology studies where possible.

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Introduction

A perennial challenge in ecology is to develop models that are detailed enough to describe complex systems but general enough to apply to multiple systems. For tractability, many simple models of species interactions treat all conspecific individuals identically and ignore environmental variation. Models typically consider the average individual of a population and average environmental conditions, but natural populations and ecosystems have heterogeneity that is critical for understanding complex community dynamics (Bolnick et al. 2011; Gibert and Brassil 2014). It becomes important to know which sources of heterogeneity matter and how they interact to influence community structure (Bolnick et al. 2011). Two sources of heterogeneity known to influence predator–prey interactions are variation in individual body size within a population (size structure) (Crumrine 2005; Petchey et al. 2008) and variation in vegetation density (a component of habitat complexity) (Finke and Denno 2006; Reichstein et al. 2013). This picture is further complicated when effects of

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intraguild predation (IGP) and cannibalism are considered, because these interactions affect the density and composition of the predator community (Polis et al. 1989; Wagner and Wise 1996). Understanding how these sources of variation affect species interactions could help explain coexistence of functionally similar organisms and guide development of models with greater explanatory power.

Size structure within a population plays an important role in driving the consumptive interactions that shape community structure (Rudolf 2012; Violle et al. 2012; Krenek and Rudolf 2014). Food web studies commonly ignore size structure and consider each species as a uniform entity, even though explicitly accounting for size structure in food webs can yield qualitatively different outcomes (Miller and Rudolf 2011; Rudolf and Lafferty 2011). Traditional representations of a single uniform species therefore often inadequately explain community dynamics (Rudolf 2012), because different stages/sizes of individuals of the same species are considered as functionally equivalent, when in reality they play different roles. Consideration of size structure could help clarify the persistence of seemingly unstable models of coexistence, including IGP, which occurs when predators competing for a resource prey on each other (Polis et al. 1989; Hin et al. 2011). Theoretical models predict that IGP should be rare and that when it does occur, asymmetric IGP (where the intermediate predator does not eat the top predator) should be more common. However, IGP is ubiquitous in nature and symmetric IGP is far more common than models predict (Polis et al. 1989; Holt and Polis 1997; Arim and Marquet 2004; Crumrine et al. 2008). Models including size structure could explain these deviations from theoretical predictions because larger predators typically consume smaller predators and increasing body-size difference between predatory species can increase IGP rates (Wissinger 1992; Armsby and Tisch 2006; Okuyama 2007; Rudolf and Armstrong 2008; Krenek and Rudolf 2014). Additionally, if both predator populations show ample size structure, interactions can become more symmetrical because size structure in both populations increases the likelihood that the largest stages of an intermediate predator could consume the smallest stages of a top predator (Werner and Gilliam 1984). In this case, top vs. intermediate predator distinctions become meaningless because an organism's interactions change through its ontogeny.

In addition to influencing IGP, size structure can increase cannibalism in populations because larger individuals can eat smaller conspecifics (Fox 1975a). Cannibalism is ubiquitous, especially among invertebrates, but its role in influencing community structure remains understudied (but see Rudolf 2007a, 2007b, 2008). Cannibalism influences a population's density and demography and therefore significantly shapes the population's functional role in the community (Claessen et al. 2000; Wise 2006). Furthermore, cannibalism can promote the persistence of many species in a community by reducing predator populations and redirecting predators' food consumption away from other organisms (Fox 1975b; Rudolf 2008; Crumrine 2010; Ohlberger et al. 2012). We need to understand how these size-structured interactions in the predator guild impact the density of predators and fundamentally shape the rest of the community via top down effects and trophic cascades. A complete community picture must consider IGP and cannibalism since their absolute and relative frequencies significantly dictate the composition and functional role of predators (Snyder and Wise 2001; Persson et al. 2003; Claessen et al. 2004; Rudolf 2007a, 2007b).

Although the literature addressing the role of size-structured effects on predator–prey interactions is growing, few studies have examined the interaction of habitat complexity and size structure (Delclos and Rudolf 2011; Toscano and Griffen 2013; Anderson and Semlitsch 2016). Physical habitat complexity (e.g. vegetation density) is an additional parameter that can influence the strength of predator–prey interactions in two distinct ways. First, habitat complexity interacts with hunting strategies of predators (Schmitz 2009; Yee 2010). Hunting strategies of aquatic organisms range from sit-and-wait predation to active pursuit (Schmitz 2009), and predator responses to habitat complexity differ throughout this continuum. Greater habitat complexity provides refuge/ambush sites that can increase predation rates of sit-and-wait predators (Finke and Denno 2006; Janssen et al. 2007; Yee 2010; Delclos and Rudolf 2011). In contrast, predation rates of active predators decrease with greater habitat complexity because predators' movements are hindered by obstacles

(Toscano and Griffen 2013). Second, habitat complexity interacts with population size structure because small-bodied individuals can more easily take refuge from predators in complex habitats (Eklov and Persson 1995; Finke and Denno 2006; Reichstein et al. 2013) while large-bodied individuals are exposed and cannot easily locate small prey (Toscano and Griffen 2013). Because habitat can influence predator–prey interactions in two distinct ways (by interacting with hunting behavior and/or size of individuals), we expect predation outcomes to be affected by identities of predators and relative sizes of predators. Considering these two competing effect pathways, the net effects of habitat complexity on cannibalism, IGP, and interguild predation (i.e. basic predation) are difficult to predict. Likely, these three modes of predation are not equally affected by habitat complexity. Therefore, realistic models must consider how each is affected because the relative frequencies of cannibalism, IGP, and predation have important implications for the coexistence of functionally similar species and the degree of top–down control in ecosystems (Finke and Denno 2002; Persson et al. 2003; Rudolf 2007a). Our research addresses this gap through the following questions: (1) How do size structure and habitat complexity independently and interactively influence relative frequencies of IGP, cannibalism, and predation? (2) Do predators' tendencies toward cannibalism or IGP differ, and could these differences clarify seemingly unstable models of coexistence?

Materials and methods

Study species and experimental Mesocosms

Larvae of *Cybister fimbriolatus* (Coleoptera) and *Anax junius* (Odonata) are widespread in North America and were chosen as intraguild predators for this system for several reasons. First, late instars of both species significantly influence community structure in fishless aquatic ecosystems (Van Buskirk 1988; McPeek 1998; Rudolf and Rasmussen 2013b). Second, both species increase in body size (length and mass) up to 15-fold through throughout their development, making them ideal for studying size-structured interactions (Crumrine 2005; Rudolf and Armstrong 2008; Rudolf and Rasmussen 2013a). Throughout a season, populations can consist of a single cohort that is uniform in size or consist of many overlapping cohorts, making the population highly size structured. Because diets of early instars differ from those of late instars, the ecological role of these populations changes significantly throughout the season (Rudolf and Rasmussen 2013b). Finally, while *C. fimbriolatus* and *A. junius* fill seemingly similar ecological roles as top predators, they differ substantially in their hunting strategy (*C. fimbriolatus* is an active predator while *A. junius* is a sit-and-wait predator) and therefore are expected to respond differently to habitat complexity (Crumrine et al. 2008). In our study system, *C. fimbriolatus* is generally considered the top predator and *A. junius* is considered the intermediate predator (PWC, personal observation).

We focused on interactions among small (F-1 instar, length ∼3.0 cm, headwidth ∼0.2 cm) and large (F instar, length ∼5.1 cm, headwidth ∼0.5 cm) *C. fimbriolatus* and small (F-3 instar, length ∼2.2 cm, headwidth ∼0.4 cm) and large (F-1 instar, length ∼3.5 cm, headwidth ∼0.7 cm) *A. junius*. *Cybister fimbriolatus* has three juvenile instars while *A. junius* has 9–13 juvenile instars. Each predator was photographed and its instar determined from head width measured using NIH ImageJ (Wissinger 1992; Schindelin et al. 2015). F-1 instars of larval dragonfly *Pachydiplax longipennis* were used as shared prey (length ∼2.0 cm, headwidth ∼0.3 cm). *Pachydiplax longipennis* were chosen as prey because they are abundant, generally smaller in body size than *A. junius* and *C. fimbriolatus,* and commonly co-occur with them in fishless ponds of eastern North America. Predation trials show that *P. longipennis* does not consume *A. junius* or *C. fimbriolatus*, even when size differences are small (Crumrine 2010).

Trials were conducted in plastic mesocosms (50 cm L x 38 cm W x 18 cm D, 34 L volume) covered with fiberglass window screen mesh, and maintained at ambient temperature and light at Blandy Experimental Farm, Boyce, VA, USA. Aquatic mesocosms are an appropriate system to test this hypothesis because they are large enough to cultivate biologically realistic communities, but controlled enough to manipulate experimentally and measure effects (Werner and Anholt 1996; Relyea and Yurewicz 2002; Preston et al. 2012). Mesocosms were filled to a depth of 10 cm with pond water filtered through windowscreen mesh. This prevented the introduction of any unwanted macro-invertebrates but permitted the passage of zooplankton to sustain *P. longipennis*. Nylon ropes (10 cm L x 1 cm Ø) glued to the bottom of the mesocosms represented low (50 stems m^{-2}) and high (280 stems m^{-2}) habitat complexities. These densities reflect common pondweed abundances at shallow depths (Sheldon and Boylen 1977).

Experiment 1: effects of size structure and habitat complexity on cannibalism, IGP, and predation

To assess the independent and interactive effects of habitat complexity and size structure on predator–prey interactions, we used a 2 (low- and high-habitat complexity) × 6 (size-structured predator treatments) factorial design, resulting in 12 treatments. Predator treatments included the six possible pairs of the two size classes of each predator: small and large *C. fimbriolatus*, small and large *A. junius*. Pairs of mixed-size conspecifics were included in the design, but pairs of equal-sized conspecifics were not included. Seven replicate trials were conducted over three temporal blocks, initiated 19 June 2013 (three replicates), 28 June 2013 (two replicates), and 5 July 2013 (two replicates), resulting in $n = 84$. There was no significant temporal block effect, so this was not considered in any statistical analyses (GLM, $Z = -0.207$, $P = 0.84$).

Each three-day trial was initialized with ten prey and one individual of each appropriate predator species-size class. These prey and predator densities are within the range reported in field surveys for larval odonates and dytiscids (Yee 2010). Surviving prey and predators were counted at 9:00 am and 4:00 pm each day. Counting twice each day gave more precise estimates on time to predation, but counting more than twice per day was not logistically possible since each effort took 3–4 h. Predators that molted out of the appropriate instar were replaced following each count, but predators that were eaten were not replaced. Prey were never replaced. Prey and predator survival data from these trials were used in the following two analyses.

First, to determine if prey survival was affected by treatments, we fit generalized linear models using the glm function in the stats package of R (R Core Team 2014). Prey survival was predicted by habitat complexity and predator treatment as interacting fixed effects, with binomial error structure. Post-hoc planned comparisons were performed with the glht function in the R package multcomp (Hothorn et al. 2008).

We used a second pair of generalized linear models to test how size of the competing predator affected a predator's hunting success. The species of predator that consumed each prey could be determined because *C. fimbriolatus* and *A. junius* utilize different feeding modes, and the condition of prey remains reveals the identity of the predator. *Cybister fimbriolatus* leaves an empty but complete exoskeleton (Gorb and Beutel 2000), while *A. junius* leaves a torn exoskeleton or nothing at all (Pritchard 1965). Because of this difference, we were able to easily identify which predator had consumed each prey in heterospecific predator treatments. With these data, we tested whether prey consumption by a predator was affected by the size of its competing heterospecific predator. In our models (one for *A. junius* and one for *C. fimbriolatus*), the number of prey eaten by the predator was explained by the interaction of that predator's size and its competing predator's size. Post-hoc multiple comparisons were done with the glht function and targeted treatments comparing predation by a given predator-size (i.e. large *C. fimbriolatus*) competing with small heterospecifics (i.e. small *A. junius*) versus large heterospecifics (i.e. large *A. junius*). Interpredator interactions were summarized by frequency of predation events, since low predator densities (two per replicate) did not allow for rigorous statistics.

Experiment 2: choice for conspecific (cannibalism) vs. heterospecific (IGP) prey

A choice test was conducted in low-habitat complexity mesocosms to determine the likelihood of cannibalism versus IGP for large *A. junius* and large *C. fimbriolatus*. One large *C. fimbriolatus* or large *A. junius* was offered one small *C. fimbriolatus* and one small *A. junius* as prey. Mouth parts of the prey were removed to ensure all predation was by the larger predator. Previous studies with larval odonates have reported little if any change in activity level by larvae after this type of manipulation (Crumrine and Crowley 2003). Each mesocosm was monitored every 2 h until the predator had consumed one prey. Time to predation was recorded. Nine replicates were performed in two temporal blocks initiated 15 July 2013 (six replicates) and 23 July 2013 (three replicates). Binomial tests compared the preferences of large *C. fimbriolatus* and large *A. junius* for conspecific or heterospecific prey.

Results

Experiment 1: effects of size structure and habitat complexity on cannibalism, IGP, and predation

Interguild predation

The interaction term between predator treatments and habitat complexity was not significant (GLM, $Z = -1.32$, $P = 0.09$). Since the inclusion of the interaction did not affect model fit, the interaction term was dropped from the model and fixed effects were analyzed independently.

Prey consumption was 20% higher in low-habitat complexity treatments than high-habitat complexity treatments. Pooled across predator treatments, average number of prey eaten (out of 10 initial prey) was 6.98 (SE = 0.31) in low-habitat complexity treatments and 5.76 (SE = 0.33) in high-habitat complexity treatments (GLM, $Z = 3.73$, $P = 0.0002$). The trend for lower prey consumption at high-habitat complexity was true for four of the six habitat complexity treatments (Figure 1(a)). The large *C. fimbriolatus* + large *A. junius* and large *A. junius* + small *A. junius* treatments did not follow this pattern, eating an equal number of prey at low- and high-habitat complexities. Considered individually, for both *C. fimbriolatus* and *A. junius*, large size classes showed a more pronounced reduction in predation in high-habitat complexity than did the small size class, which ate a similarly low number of prey in both low and high habitats (Figure 1(b)).

Prey consumption varied significantly among predator treatments (GLM, $Z = 3.41$, $P < 0.001$). The small *C. fimbriolatus* + small *A. junius* combination was significantly different from all treatments except large *C. fimbriolatus* + small *C. fimbriolatus*, which did not differ from any treatments. Average number of prey eaten was 4.36 (SE = 0.61) for the small *C. fimbriolatus* + small *A. junius* treatment, 45% lower than other treatments. Prey consumption was higher for large predators (4.41 ± 0.31, mean ± SE) than small predators (1.89 ± 0.17, mean ± SE) (GLM, $Z = 3.49$, $P \ll 0.001$).

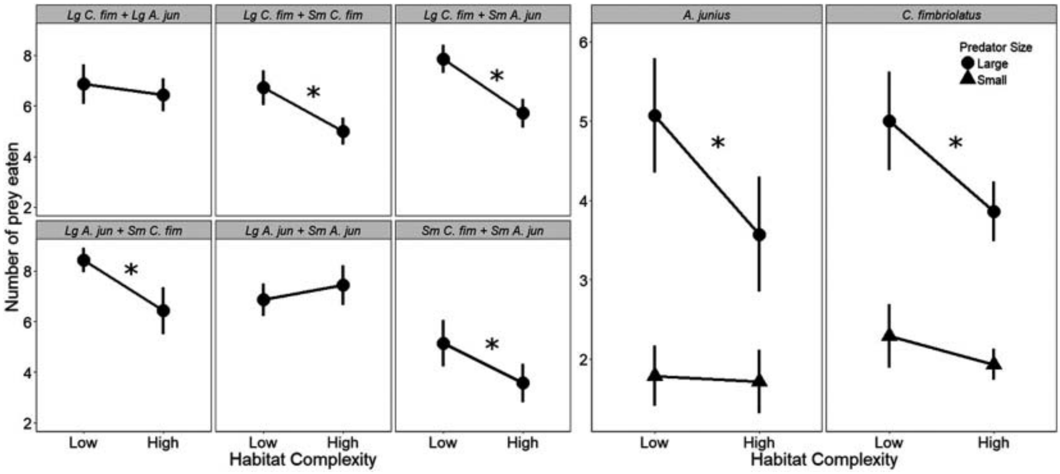

Figure 1. (**a**) A comparison of number of prey eaten by six size-structured pairs of *Anax junius* and *Cybister fimbriolatus* at low- vs. high-habitat complexity ($n = 7$, points show means ± SE). In each three-day mesocosm trial, ten *Pachydiplax longipennis* were offered as prey without replacement. (**b**) A comparison of prey eaten by large (circles) and small (triangles) size classes of *A. junius* and *C. fimbriolatus* at low- vs. high-habitat complexity ($n = 8$, points show means ± SE). Cannibalism treatments are not included because we were unable to determine whether the large or small predator had eaten the prey. $^* P < 0.05$.

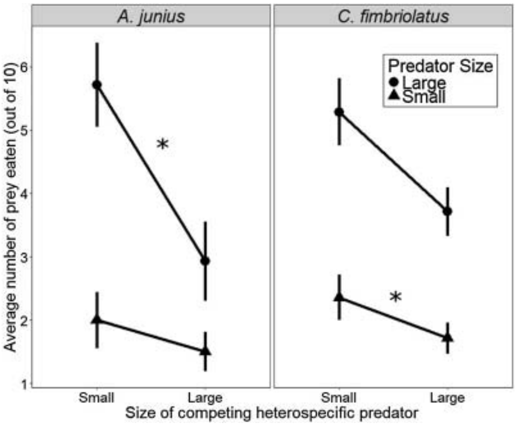

Figure 2. A comparison of prey eaten by large (circles) and small (triangles) size classes of *Anax junius* and *Cybister fimbriolatus* when the heterospecific competing predator was small vs. when the competing predator was large (n = 8, points show means ± SE). * $P < 0.05$.

There was no difference in prey consumption by *C. fimbriolatus* (3.27 ± 0.27, mean ± SE) and *A. junius* (3.04 ± 0.34, mean ± SE) (GLM, $Z = 0.52$, $P = 0.59$). Combined, these results indicate that predator size was more important than species identity for predicting prey consumption. Additionally, predation was greater in replicates where IGP or cannibalism were uncommon, because in these cases both predators were alive and predating during the entire experiment.

Two of the four predator classes (small *C. fimbriolatus* and large *A. junius*) ate fewer prey when their competing predator was large vs. when it was small (Figure 2 and Table 1). Small *C. fimbriolatus* consumed significantly more prey in the presence of small *A. junius* (2.35 ± 0.36, mean ± SE) than in the presence of large *A. junius* (1.71 ± 0.24, mean ± SE) (GLM, $Z = -2.48$, $P = 0.02$). Large *A. junius* consumed significantly more prey in the presence of small *C. fimbriolatus* (5.71 ± 0.67, mean ± SE) than in the presence of large *C. fimbriolatus* (2.93 ± 0.62, mean ± SE) (GLM, $Z = 3.51$, $P < 0.001$). This pattern was not observed for small *A. junius* or large *C. fimbriolatus.* Small *A. junius* ate an equal number of prey with small (2.00 ± 0.44, mean ± SE) and large (1.50 ± 0.31, mean ± SE) *C. fimbriolatus* (GLM, $Z = -0.92$, $P = 0.53$). Large *C. fimbriolatus* ate an equal number of prey in the presence of small *A. junius* (5.29 ± 0.53, mean ± SE) and large *A. junius* (3.71 ± 0.38, mean ± SE) (GLM, $Z = 1.61$, $P = 0.17$).

Intraguild predation and cannibalism

Habitat complexity did not influence any intraguild interactions, and therefore the following analyses pool habitat treatments. The top predator in this system was large *C. fimbriolatus*. Large *C. fimbriolatus* was never consumed by another predator and ate its competing predator in 59% (25/42) of the replicates in which it was present. By comparison, small *C. fimbriolatus* ate its competing predator in 21% of replicates, large *A. junius* in 17%, and small *A. junius* only in 2%. The most common

Table 1. Summary of statistics on prey consumption by each predator when paired with each of two size classes of competing heterospecific predator. For each combination of predators, n = 8.

Focal predator	Competing predator Sm *C. fim*	 Lg *C. fim*	
Sm *A. jun*	2.00 ± 0.44, $\bar{x} \pm$ SE	1.50 ± 0.31, $\bar{x} \pm$ SE	GLM, $Z = -0.92$, $P = 0.53$
Lg *A. jun*	5.71 ± 0.67, $\bar{x} \pm$ SE	2.93 ± 0.62, $\bar{x} \pm$ SE	GLM, $Z = 3.51$, $P < 0.001$
	Competing predator Sm *A. jun*	 Lg *A. jun*	
Sm *C. fim*	2.35 ± 0.36, $\bar{x} \pm$ SE	1.71 ± 0.24, $\bar{x} \pm$ SE	GLM, $Z = -2.48$, $P = 0.02$
Lg *C. fim*	5.29 ± 0.53, $\bar{x} \pm$ SE	3.71 ± 0.38, $\bar{x} \pm$ SE	GLM, $Z = 1.61$, $P = 0.17$

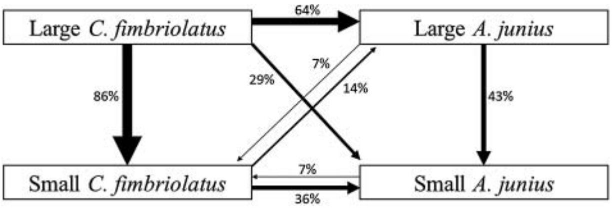

Figure 3. Frequency of intraguild predation and cannibalism for each predator pair (habitat treatments pooled, *n* = 14). Each percentage reflects the proportion of replicates that resulted in a predation event – thickness of bars corresponds to the strength of the interaction.

interpredator interaction was *C. fimbriolatus* cannibalism – large *C. fimbriolatus* ate small *C. fimbriolatus* in 86% (12/14) of replicates in which the two predators were together. For *A. junius*, 43% of trials resulted in cannibalism. For both large predators, cannibalism was more common than IGP. All intraguild and cannibalism interactions are summarized in Figure 3.

Experiment 2: choice for conspecific (cannibalism) vs. heterospecific (IGP) prey

When given a choice of prey types, large *C. fimbriolatus* consumed small *C. fimbriolatus* (i.e. cannibalism) rather than small *A. junius* significantly more often than expected by chance (Binomial test, $P = 0.039$). Likewise, large *A. junius* consumed small *C. fimbriolatus* (i.e. IGP) rather than small *A. junius* significantly more frequently than expected by chance (Binomial test, $P = 0.039$). For both large predators, small *C. fimbriolatus* was consumed first in eight of nine replicates.

Discussion

This research aimed to assess how size structure and habitat complexity interact to influence interspecific interactions and community structure. For parsimony, studies of food web interactions traditionally assume that variation among individuals within a population and variation in the environment have an insignificant effect on community dynamics relative to interspecific interactions (Miller and Rudolf 2011). However, we show that variation in predator size and habitat complexity can qualitatively change species interactions and potentially influence top down effects of the predator guild. We found that in highly complex habitats where small-bodied prey could take refuge, predation on shared prey was much lower, potentially enabling a shift from interguild predation (i.e. basic predation) to IGP. Additionally, size structure among predators affected community interactions both directly (body size was a better predictor of predation than species identity) and indirectly (some predators ate less when their competing predator was large than when it was small). Finally, differential cannibalism between top and intermediate predators may provide a mechanism for sustained coexistence of functionally similar intraguild predators.

Our experiment corroborated past results that high-habitat complexity promotes prey survival by providing refuge and lowering encounter rates with predators (Crowder and Cooper 1982; Delclos and Rudolf 2011; Toscano and Griffen 2013). To avoid larger bodied predators, *P. longipennis* could simply perch on the vertical stems of artificial vegetation and hide by moving to the side opposite the predator. This predator avoidance mechanism led to higher sustained prey abundance in high-habitat complexity mesocosms relative to low complexity mesocosms. Since predators cannot easily encounter and consume small-bodied, well-hidden prey in complex habitats, interguild predation may shift toward IGP (Gismervik and Andersen 1997). Further experiments with higher predator density sustained through multiple generations could properly explore this prediction.

Prey survival differed significantly between predator treatments, with more prey surviving in treatments where predators were small-bodied or where IGP and cannibalism were common. Prey survival was highest in the predator treatment including two small predators, likely because small predators have proportionately lower energetic demands (Devries et al. 1998; Jennings et al. 2001). Alternatively, small predators and prey were more similar in size and thus prey may have posed a greater potential risk to injury during the predation sequence for small rather than large predators. Other patterns in prey survival between predator treatments were better explained by size-mediated interactions between the two predators. For example, in predator treatments where IGP or cannibalism was common, more prey survived, likely because IGP or cannibalism eliminated one predator, leaving only one predator to feed on the prey. Prey survival was lowest in predator treatments where IGP and cannibalism were less common because two active predators remained throughout the trial. Size structure enabled consumptive interactions that redirected predators' diets from prey to predators (Sih et al. 1998; Finke and Denno 2002). In these cases, a shift from interguild predation to IGP could change the composition and density of the predator guild, leading to important top–down effects on the rest of the community (Moran et al. 1996; Holt and Polis 1997).

Our results further indicate that size structure can negate the designations of top and intermediate predators commonly used in IGP models. While *C. fimbriolatus* is generally considered a top predator, we observed predation on small *C. fimbriolatus* by *A. junius*. In alignment with previous research on communities containing size-structured populations, we found that body size better predicted predator–prey interactions than did species identity (Petchey et al. 2008; Arim et al. 2010). This suggests that an organism's ecological role can change through its development, and therefore species identity may not be the best way to classify organisms in food web studies. As a consequence, symmetric IGP is likely more common than currently reported, and designations of top vs. intermediate predators oversimplify dynamic predator–predator interactions. Additionally, we observed an indirect effect of body size on predation. Two of the four predator classes (small *C. fimbriolatus* and large *A. junius*) ate fewer prey when their competing predator was large vs. when it was small. Combined, the direct and indirect effects of size structure could change the relative frequencies of intraguild vs. interguild consumptive interactions, which is critical in determining the predator guild's top down effects on the rest of the community.

The choice test experiment showed that *C. fimbriolatus* acts more commonly as a cannibal, and *A. junius* acts more commonly as an intraguild predator. We speculate this is a consequence of *C. fimbriolatus* being an active predator while *A. junius* is a sit-and-wait predator. Continuous movement of active predators through their environments likely increases opportunities to feed, but may also increase their vulnerability to predation, especially at early instars (Crumrine et al. 2008). Active behavior increases encounter rates with predators (both conspecifics and heterospecifics), possibly reducing recruitment from early instars to more mature instars that are better predators. Final instar *C. fimbriolatus* is a strong predator on all size classes of *A. junius*, but our results indicate that *C. fimbriolatus* experiences high mortality by predation before reaching the final instar. On the other hand, the more sedentary behavior of *A. junius* makes it more likely to evade predators through early development and reach late instars where it is a more effective predator (Preisser et al. 2007; Davenport et al. 2014). Given these predictions, we expect to see a higher proportion of *A. junius* surviving early instars and advancing to later stages where they have a competitive advantage. This would give *A. junius* a numerical advantage, which could counterbalance the per-capita competitive advantage of *C. fimbriolatus*, and potentially lead to sustained coexistence of these two predators. We realize that given the short duration of our experiments, we are unable to fully explain coexistence of these predators. Rather, we aimed to explore potential mechanisms for coexistence in a short term experiment. Longer term experiments are necessary to test these mechanisms.

To conclude, we have identified several mechanisms by which habitat complexity and size structure could change interspecific interactions, particularly by changing the relative frequency of interguild vs. intraguild interactions. These identified mechanisms could change the composition and density of the predator guild, leading to trophic cascades via strong top down predator effects. Further, we have identified one mechanism (stronger cannibalism in top predator than intermediate predator) that could help explain coexistence of intraguild predators. Since we have shown that size structure and habitat complexity could be instrumental in top–down trophic cascades and coexistence of functionally similar species, we suggest that these sources of heterogeneity should be more commonly considered in community ecology research.

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Shannon K. Carter was an undergraduate student in biology at Baylor University when the research was conducted. Currently, Shannon is a PhD candidate in the Rudolf Lab at Rice University, studying how climate change-driven shifts in phenology impact aquatic communities.

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