

ABSTRACT

Effects of Habitat Complexity on Intraguild Predation and Cannibalism in an Assemblage of Size-structured Predators

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Intraguild predation (IGP) and cannibalism substantially affect community dynamics but often are poorly documented in food web studies. Feeding choices of generalist predators often relate more to size of prey than to species identity, leading to IGP and cannibalism. Size-structure of predator populations and physical habitat complexity further complicate predator-prey interactions. Densely-vegetated habitats provide refuge for prey and diminish predator hunting success. This experimental research examined effects of habitat complexity and population size-structure by intraguild larval aquatic beetles (*Cybister fimbriolatus*) and larval dragonflies (*Anax junius*), common predators in fishless ponds. In mesocosms, predation for all pairwise combinations of large and small top predator, *C. fimbriolatus*, and large and small intermediate predator, *A. junius*, was measured. Predation in replicate trials of these six predator/size combinations was measured at high and low habitat complexity. High habitat complexity decreased predator success. In some cases, the size of competing predators influenced a predator's success. In a choice test, predator preferences to consume either conspecifics (cannibalism) or heterospecifics (IGP) were also tested. *C. fimbriolatus* consistently consumed a conspecific before a heterospecific, while *A. junius* consumed a heterospecific before a conspecific. Preferential cannibalism by the top predator *C. fimbriolatus*, coupled with low cannibalism by an intermediate predator, *A. junius*, could help explain sustained coexistence of these predators.

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EFFECTS OF HABITAT COMPLEXITY ON INTRAGUILD
PREDATION AND CANNIBALISM IN AN ASSEMBLAGE OF
SIZE-STRUCTURED PREDATORS

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CHAPTER ONE

Introduction

Literature Review

Intraguild predation (IGP) and cannibalism are common interactions that influence energy flow through a system, but researchers under appreciate the impact of these interactions on community structure, especially coexistence of competing intraguild predators (Fox 1975a, Polis *et al.* 1989). Habitat complexity varies among aquatic systems and may influence the strength of these interactions. Predator-prey interactions in aquatic communities are further complicated by varied body sizes within populations. Unfortunately, food web diagrams oversimplify this complexity by ignoring size variation within a population and considering each species as a uniform entity (Miller and Rudolf 2011).

IGP occurs when two predators competing for the same resource prey on one another (Polis *et al.* 1989) (Figure 1). This interaction is either symmetric or asymmetric. In symmetric IGP, each predator preys on the other (though not necessarily in equal amounts). In asymmetric IGP, one predator species, designated the top predator, always preys on the other predator species, designated the intermediate predator (Polis *et al.* 1989). Theory predicts that sustained IGP should be rare. However, asymmetric IGP is especially common in aquatic, marine, and terrestrial communities (Polis *et al.* 1989, Holt and Polis 1997, Crumrine *et al.* 2008, Arim and Marquet 2004). Theoretical models suggest that predators engaged in IGP should only coexist when: (1) the intermediate

predator exploits shared prey better than the top predator, (2) the top predator acquires energetic benefits from eating the intermediate predator, and (3) the shared prey occurs at intermediate quantities resulting in competition between predators (Holt & Polis 1997). Despite these limitations, IGP is common in many communities (Arim and Marquet 2004). To explain the ubiquity of IGP despite theoretical restrictions, we must consider other contributing variables such as habitat complexity and size-structure within the predator population.

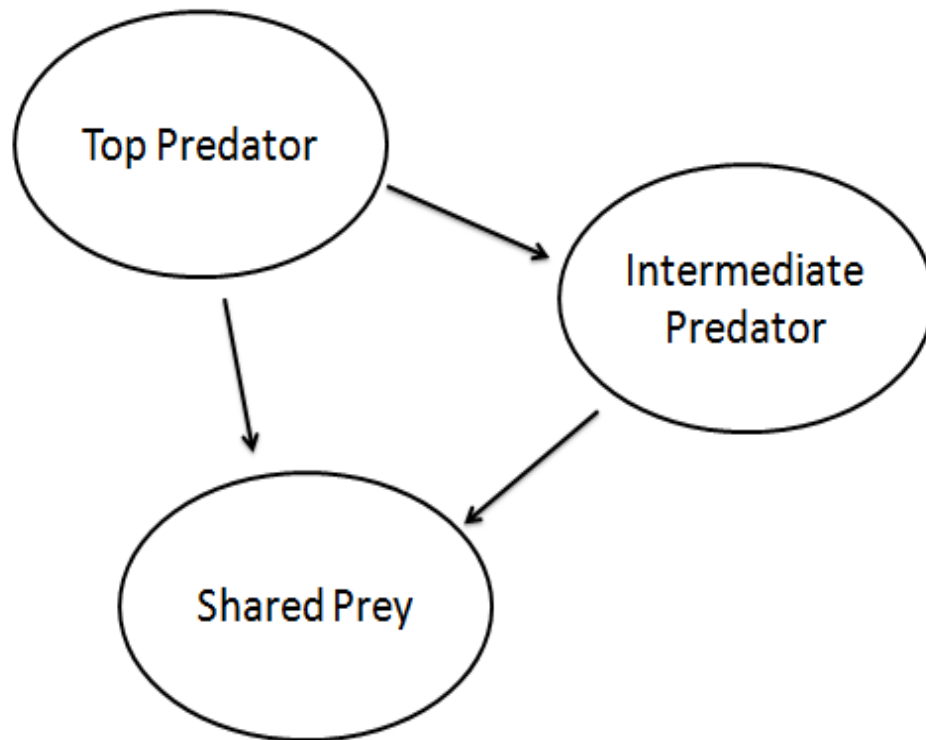


Figure 1. Intraguild predation occurs when two predators competing for the same resource also prey on one another.

During most IGP interactions, larger top predators consume smaller intermediate predators (Crumrine *et al.* 2008). Wissinger (1992) examined size-structured IGP among larval odonates and found that greater body-size differences between predatory species promoted IGP despite seasonal progression reducing competitive overlap. Another study showed that size-structured predator-prey interactions relate more to the size range of predators than to their mean size (Rudolf 2012). Empirical evidence supporting the hypothesis that greater differences in body size between predators lead to increased IGP is also available for marine (Armsby & Tisch 2006) and terrestrial (Okuyama 2007) systems.

In addition to influencing IGP, a wide range of sizes within a predator population can promote cannibalism. Cannibalism complicates community interactions and promotes ubiquitous coexistence of top predators with intermediate predators more than simple mathematical models predict (Rudolf 2007). Cannibalism occurs frequently among aquatic invertebrates, especially in populations with a broad size range (Fox 1975a). Size-selective generalist predators, including larval odonates, are the most likely cannibals in aquatic systems, as they feed on anything smaller than themselves, regardless of prey identity (Yee 2010). Cannibalistic behavior can reduce predator populations and thereby facilitate survival of other species (Fox 1975b). Cannibalism by top predators promotes coexistence with intermediate predators. This is true even when the top predator exploits shared resources more successfully because cannibalism redirects a portion of the top predator's energy needs away from the intermediate predator (Rudolf 2007).

Predator responses to habitat complexity may differ for active versus sit-and-wait predator behaviors. These responses may influence the dynamics of community interactions. Hunting strategies of aquatic organisms span a continuum from sit-and-wait to active predation (Crumrine *et al.* 2008). Sit-and-wait predators take refuge and ambush nearby prey. Habitat complexity may provide refuge and increase predation rates of sit-and-wait predators (Delclos and Rudolf 2011). Active predators continuously move through their environments seeking prey. Active predators likely have more opportunities to feed, but also may be more vulnerable to predation themselves (Crumrine *et al.* 2008). Reichstein *et al.* (2013) and Persson and Eklov (1995) showed that predation rates of active predators decrease with greater habitat complexity because their prey can more easily take refuge. But Delclos and Rudolf (2011) observed no effect of habitat complexity on predation rates. If cannibalism and IGP are affected by feeding strategies, which are variously effective at different habitat complexities, then habitat complexity should be considered when studying complex predator-prey interactions.

Few empirical studies have addressed the influence of habitat complexity on species coexistence in IGP systems. Habitat complexity influences predator-prey interactions by providing refuge and ambush spots. Research should couple size-structure with habitat complexity because both variables influence the foraging success of predators. Habitat complexity may partially modify effects of size-structured interactions in communities and alter IGP (Reichstein *et al.* 2013). Several studies (Yee 2010, Persson and Eklov 1995, Finke and Denno 2006, Swisher *et al.* 1998) have revealed that habitat complexity enhances refuge availability for prey and thus may diminish predation in an IGP system. Reichstein *et al.* (2013) suggests that when intermediate predators

took refuge in vegetation, top predators starved and died. However, robust empirical data addressing the effects of habitat complexity on IGP and cannibalism is rather limited (Reichstein *et al.* 2013).

Larvae of the predaceous diving beetle, *Cybister fimbriolatus*, family Dytiscidae, (hereafter *C. fimbriolatus*) and the common green darner dragonfly, *Anax junius*, family Aesnidae, (hereafter *A. junius*) are important predators that determine community structure in fishless aquatic ecosystems. *C. fimbriolatus* is a highly voracious active predator (Norwood 2012). *A. junius* is also a voracious predator, but feeds primarily by the sit-and-wait strategy (Oquendo 2011, Grandinetti 2012). *C. fimbriolatus* has three larval instars and *A. junius* has thirteen larval instars. Considerable size variation among these instars makes both organisms ideal for size-structure research (Borror and White 1970). Larvae of the odonate *Pachydiplax longipennis*, family Libellulidae, (hereafter (*P. longipennis*)) is a natural prey item for these predators.

Experimental Design

This research investigates variables relevant to coexistence of intraguild predators. These variables include size variation among predators, habitat complexity, and species-specific tendencies towards cannibalism. The top predator in this system was *C. fimbriolatus*, the intermediate predator was *A. junius*, and the shared prey was *P. longipennis*.

Research Questions

1. Does habitat complexity impact predation rate of these predators on shared prey *P. longipennis*?
2. Do *C. fimbriolatus* and *A. junius* have different tendencies toward cannibalism?
3. How does size variation between and among top and intermediate predators influence predation rate?
 - a. Does size variation among intermediate predators affect predation rate of a top predator?
 - b. Does size variation among top predators affect predation rate of an intermediate predator?

Hypotheses

1. Habitat complexity has no effect on the survival of *P. longipennis*.
2. There is no difference in cannibalism between *C. fimbriolatus* and *A. junius*.
3. Predation rate is not influenced by size variation in the predator guild.
 - a. Predation by the top predator is not influenced by the size of the intermediate predator
 - b. Predation by the intermediate predator is not influenced by the size of the top predator

CHAPTER TWO

Materials and Methods

Study Organisms

Top predator, intermediate predator, and prey included larvae of the dytiscid water beetle *C. fimbriolatus*, the green darner dragonfly *A. junius*, and the blue dasher dragonfly *P. longipennis* respectively. All specimens were collected from fishless ponds near Blandy Experimental Farm in Boyce, Virginia and from wetlands at the Whitetail Golf Resort near Mercersburg, Pennsylvania. Only 2nd (length 3.0 cm) and 3rd (length 5.1 cm) instars of larval *C. fimbriolatus* and 10th (length 2.2 cm) and 12th (length 3.5 cm) instars of larval *A. junius* were used in the experiments. *P. longipennis* used as prey were final larval instars although a small number (<5%) were penultimate instars.

Experimental Design and Analysis

Experiment 1

Predation rates were recorded for all pairwise combinations of two size classes of top predator (*C. fimbriolatus*) and two size classes of intermediate predator (*A. junius*), offered *P. longipennis* as prey (Figure 2). Combinations were tested at low and high habitat complexities (Table 1). Two densities of 10-cm lengths of nylon rope (1 cm diameter) anchored to the bottom of plastic mesocosms represented low (50 stems m⁻²)

and high (280 stems m⁻²) habitat complexities. These densities were similar to common abundances of pondweed at shallow depths (Sheldon 1977). Each trial was replicated seven times across three temporal blocks.

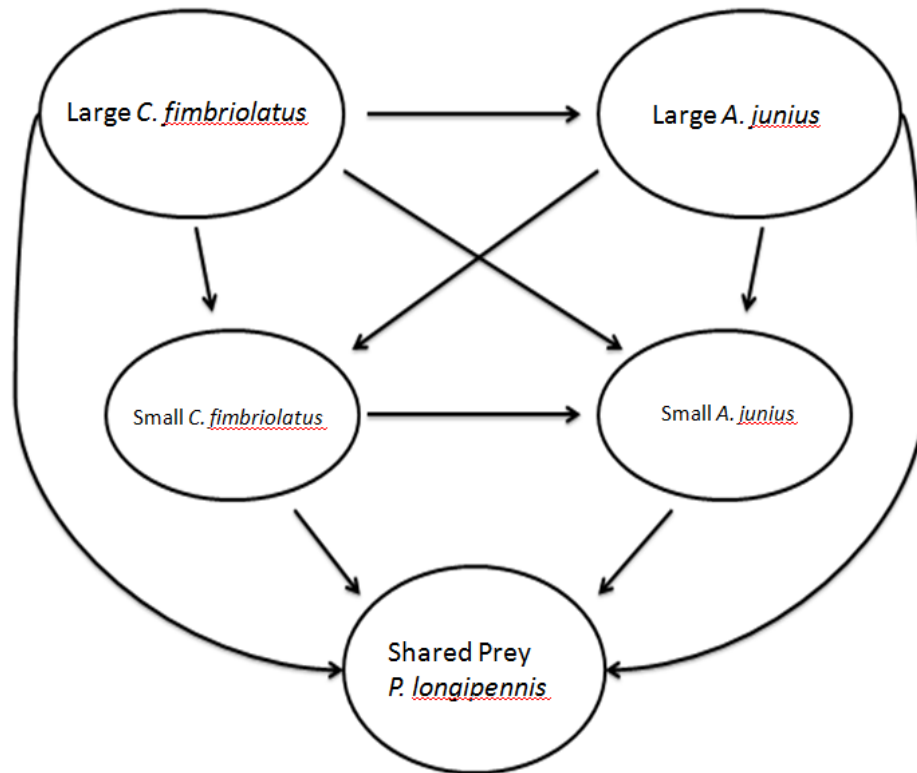


Figure 2: The size-structured community promotes intraguild predation and cannibalism.

The experiment was conducted in plastic mesocosms (22 cm L x 15 cm W x 7 cm D) covered with screen mesh, filled with filtered pond water, and maintained at ambient temperature and light in the Oak Grove at Blandy Experimental Farm. Ambient plankton in the pond water supported the prey items. To determine its instar, each predator was initially photographed and head widths measured in NIH ImageJ. Each trial was

initialized with ten prey and one individual of each appropriate predator species and size. These predator and prey densities reflected natural conditions (Corbett 1999; Crumrine personal observation). Each trial lasted three days. Surviving predators and prey were counted twice each day at 9:00 am and 4:00 pm. Predators that molted out of the appropriate instar were replaced, but predators that were eaten were not replaced. Predator and prey survival data from these trails was used in three separate experimental analyses, with specific procedures and statistical tests outlined in the text below.

Treatment	Grouping 1	Grouping 2	Grouping 3	Grouping 4	Grouping 5	Grouping 6
High Habitat Complexity	Large <i>C. fimbriolatus</i>	Large <i>C. fimbriolatus</i>	Large <i>C. fimbriolatus</i>	Large <i>A. junius</i>	Large <i>A. junius</i>	Small <i>C. fimbriolatus</i>
	Large <i>A. junius</i>	Small <i>A. junius</i>	Small <i>C. fimbriolatus</i>	Small <i>A. junius</i>	Small <i>C. fimbriolatus</i>	Small <i>A. junius</i>
Low Habitat Complexity	Large <i>C. fimbriolatus</i>	Large <i>C. fimbriolatus</i>	Large <i>C. fimbriolatus</i>	Large <i>A. junius</i>	Large <i>A. junius</i>	Small <i>C. fimbriolatus</i>
	Large <i>A. junius</i>	Small <i>A. junius</i>	Small <i>C. fimbriolatus</i>	Small <i>A. junius</i>	Small <i>C. fimbriolatus</i>	Small <i>A. junius</i>

Table 1. Treatments designed to elucidate effects of habitat complexity on intraguild predation and cannibalism in *C. fimbriolatus* and *A. junius*.

Analysis 1.1 Survival of shared prey P. longipennis. Prey were counted twice a day and percent prey survival across all predator groupings and habitat complexity treatments was analyzed using 2-factor ANOVA. Tukey’s HSD test separated means among the significantly different predator treatments.

Analysis 1.2 Comparing predation by each predator. Predation was apparent by examining residual carcasses of consumed prey, and the predator of each consumed prey was determined. *C. fimbriolatus* and *A. junius* utilize different feeding methods, and the condition of prey remains reveals the identity of the predator. *C. fimbriolatus* leaves an empty but complete exoskeleton, while *A. junius* leaves a torn exoskeleton.

I analyzed how the consumption of shared prey by each predator was affected by the presence of each size class of the other predator using T-tests. For example, I compared the proportion of prey consumed by small *A. junius* in the presence of small *C. fimbriolatus* to the proportion of prey consumed by small *A. junius* in the presence of large *C. fimbriolatus*. In these analyses, I only included data from replicates with both predators surviving. This allowed me to focus on patterns of prey mortality caused by size difference between predators and not a reduction in predator density.

Analysis 1.3 Predator survival. Consumed predators were noted at each observation. In replicates with two predator species (i.e. *C. fimbriolatus* and *A. junius*), predation was noted at IGP. In replicates with the same predator species, predation was noted as cannibalism. The proportion of replicates that resulted in IGP or cannibalism was determined and analyzed using G-tests and comparisons were made as a function of predator treatment and habitat complexity.

Experiment 2

After examining results from Experiment 1, different experimental trials were designed to compare the frequencies of cannibalism and IGP by large *A. junius* and large *C. fimbriolatus*. One large size-class predator was placed in each of 18 mesocosms with one small size-class conspecific predator and one small size-class heterospecific predator offered as prey (Table 2). Mesocosms were maintained in the lab and only low nylon stem density mesocosms were used. The mouth parts of the two small predators were removed to ensure all predation was by the large top predator. Prey survival in each mesocosm was recorded every 2 h until each predator had consumed one prey. Nine replicates were performed in two temporal blocks. Differences in consumption patterns of the large top predators were analyzed with G-tests and a binomial test was used to examine which small predator was consumed first.

Treatment	Predator	Prey
1	Large <i>C. fimbriolatus</i>	Small <i>C. fimbriolatus</i>
2	Large <i>A. junius</i>	Small <i>A. junius</i>

Table 2. Treatments designed to reveal the relative strength of IGP and cannibalism in *C. fimbriolatus* and *A. junius*.

CHAPTER THREE

Results

Experiment 1

Analysis 1.1 Prey survival

Survival of prey *P. longipennis* depended on habitat complexity (Figure 3). Mean percent prey survival was significantly greater (ANOVA $p = 0.004$) in the high density habitat for all predator treatments (Figure 4). Percent prey survival in the high density treatments ranged from a low of 3.02 (SE = 0.33) for low stem density to a high of 4.24 (SE = 0.31) for high stem density.

Prey survival varied among top and intermediate predator combinations (ANOVA $p = 0.001$). Percent prey survival was highest (56%) in the small *C. fimbriolatus*/small *A. junius* treatment (Figure 5). Interaction between predator treatments and habitat complexity for shared prey survival was not significant (ANOVA $p = 0.284$), nor was the effect of temporal block (ANOVA $p = 0.684$).

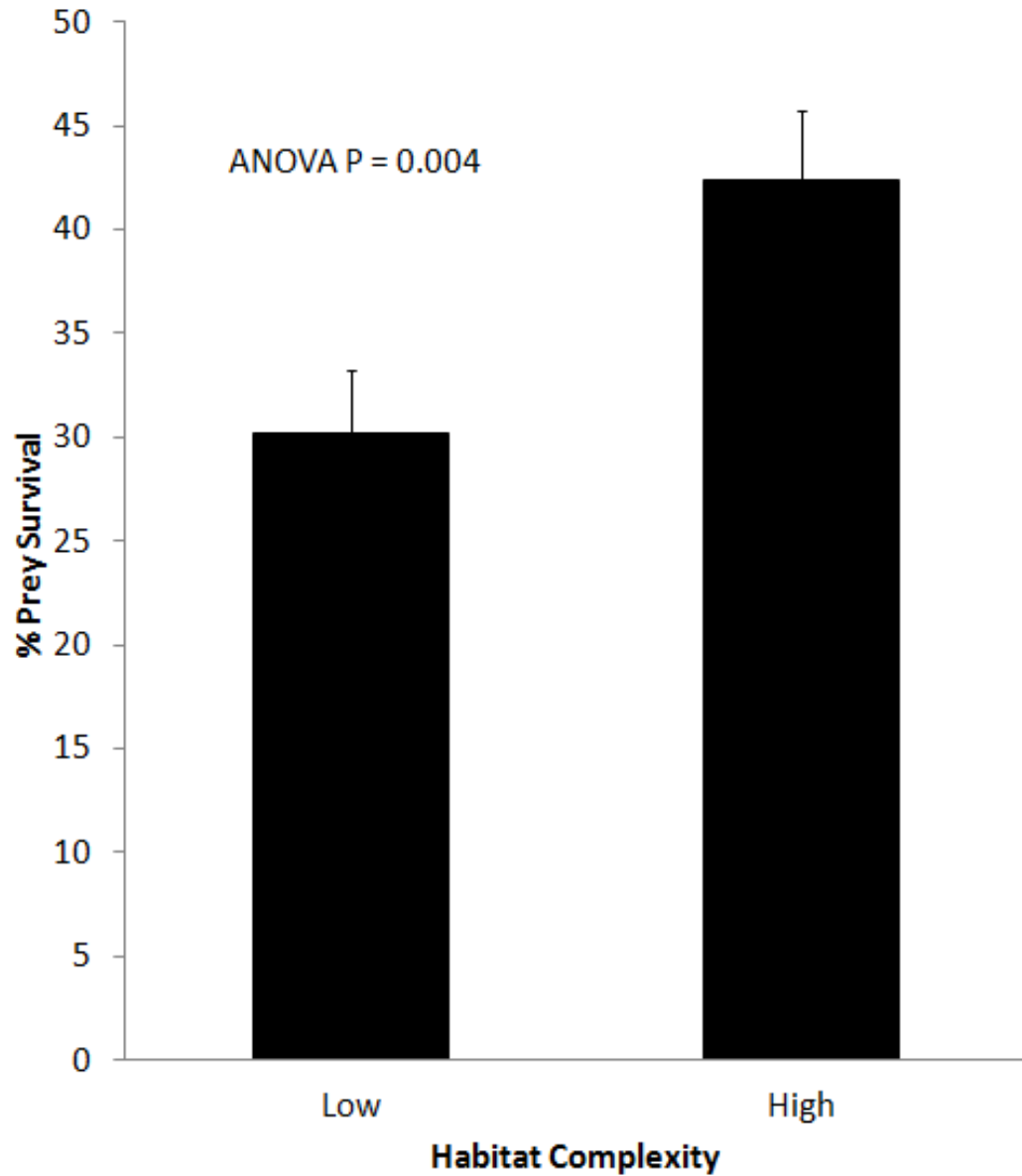


Figure 3. Prey survival was significantly higher at high habitat complexity, where prey could take refuge from predators. Error bars represent ± 1 SE.

Large size classes of both *A. junius* and *C. fimbriolatus* were more effective predators on *P. longipennis* than were small size classes. Large *A. junius* consumed more *P. longipennis* in the presence of small *C. fimbriolatus* than did small *A. junius* (Student's

T test $p < 0.001$). Additionally, large *A. junius* consumed significantly more *P. longipennis* in the presence of large *C. fimbriolatus* than did small *A. junius* (Student's T test $p = 0.004$). Similarly, large *C. fimbriolatus* consumed significantly more *P. longipennis* than did small *C. fimbriolatus*. Large *C. fimbriolatus* consumed more *P. longipennis* in the presence of large *A. junius* than did small *C. fimbriolatus* (Student's T test $p = 0.05$). Large *C. fimbriolatus* consumed more *P. longipennis* in the presence of small *A. junius* than did small *C. fimbriolatus* (Student's T test, $p = 0.033$).

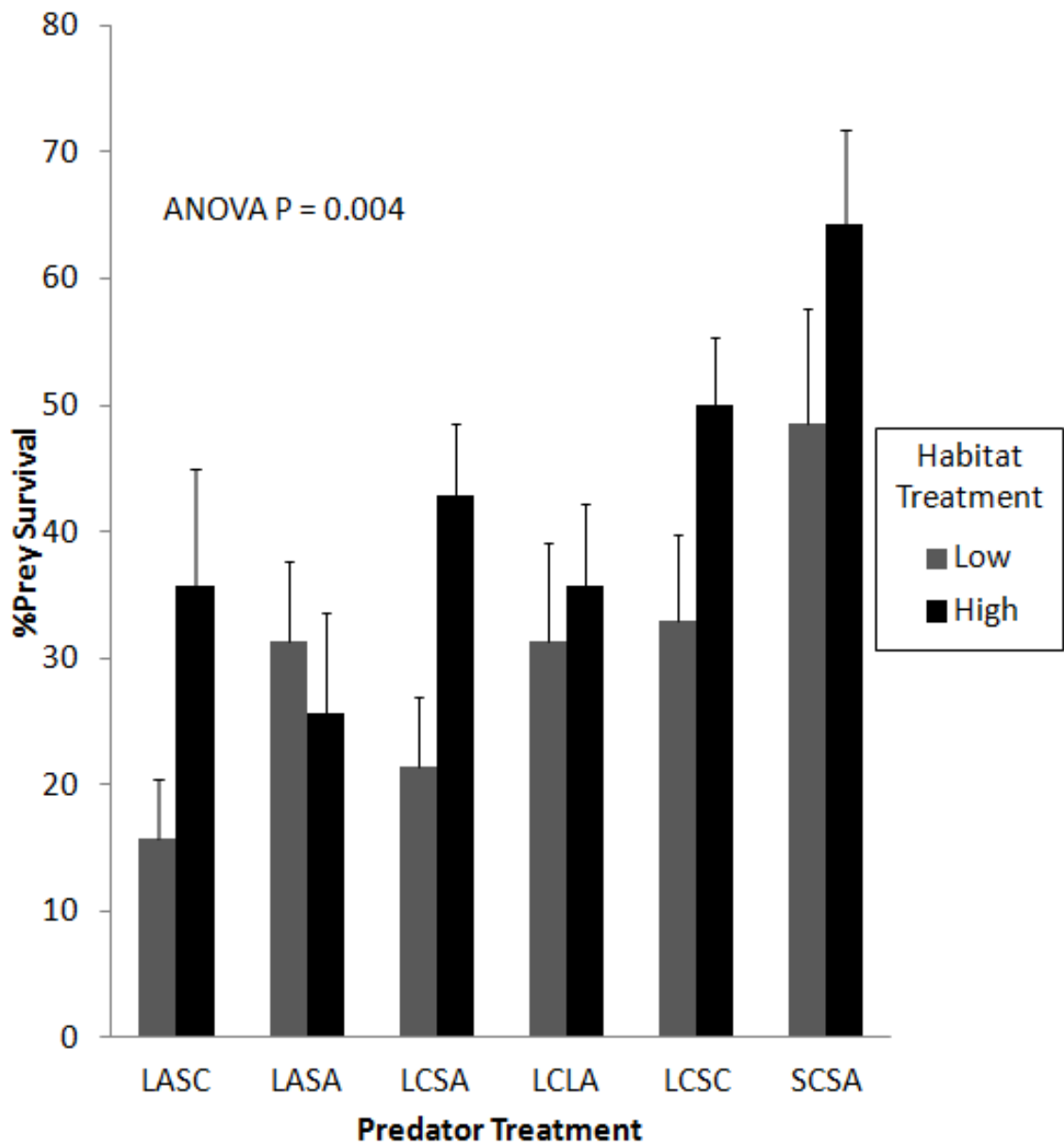


Figure 4. Prey survival was higher at high habitat complexity for all predator treatments except large *A. junius*/small *A. junius* (listed LASA, shorthand used throughout figures). Error bars represent ± 1 SE.

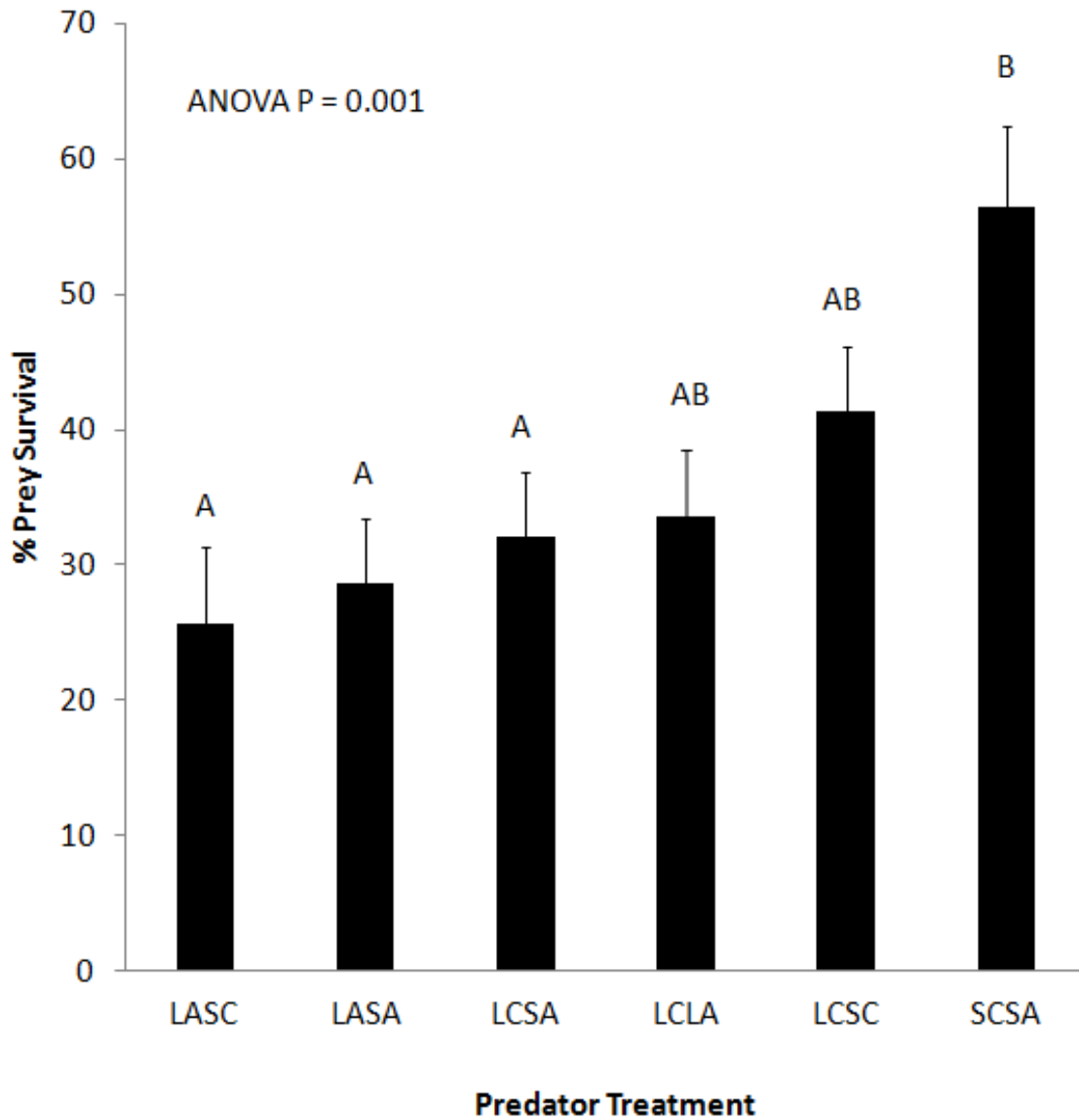


Figure 5. Predator combinations differed in their impact on prey survival. Highest prey survival occurred with small *C. fimbriolatus*/small *A. junius*, because these small organisms have lower energetic demands. Error bars represent ± 1 SE.

Analysis 1.2 Comparing predation by each predator

For some predator combinations, one predator's prey consumption depended on the size of the other predator (Figure 6). Small *C. fimbriolatus* consumed significantly more *P. longipennis* in the presence of small *A. junius* than in the presence of large *A. junius* (Student's T test, $p = 0.044$). Likewise, large *A. junius* consumed significantly more *P. longipennis* in the presence of small *C. fimbriolatus* than in the presence of large *C. fimbriolatus* (Student's T test, $p = 0.05$). However, both small *A. junius* and large *C. fimbriolatus* consumed the same percent of *P. longipennis* in the presence of both size classes of the heterospecific predator (Student's T test $p = 0.259$, $p = 0.094$ respectively).

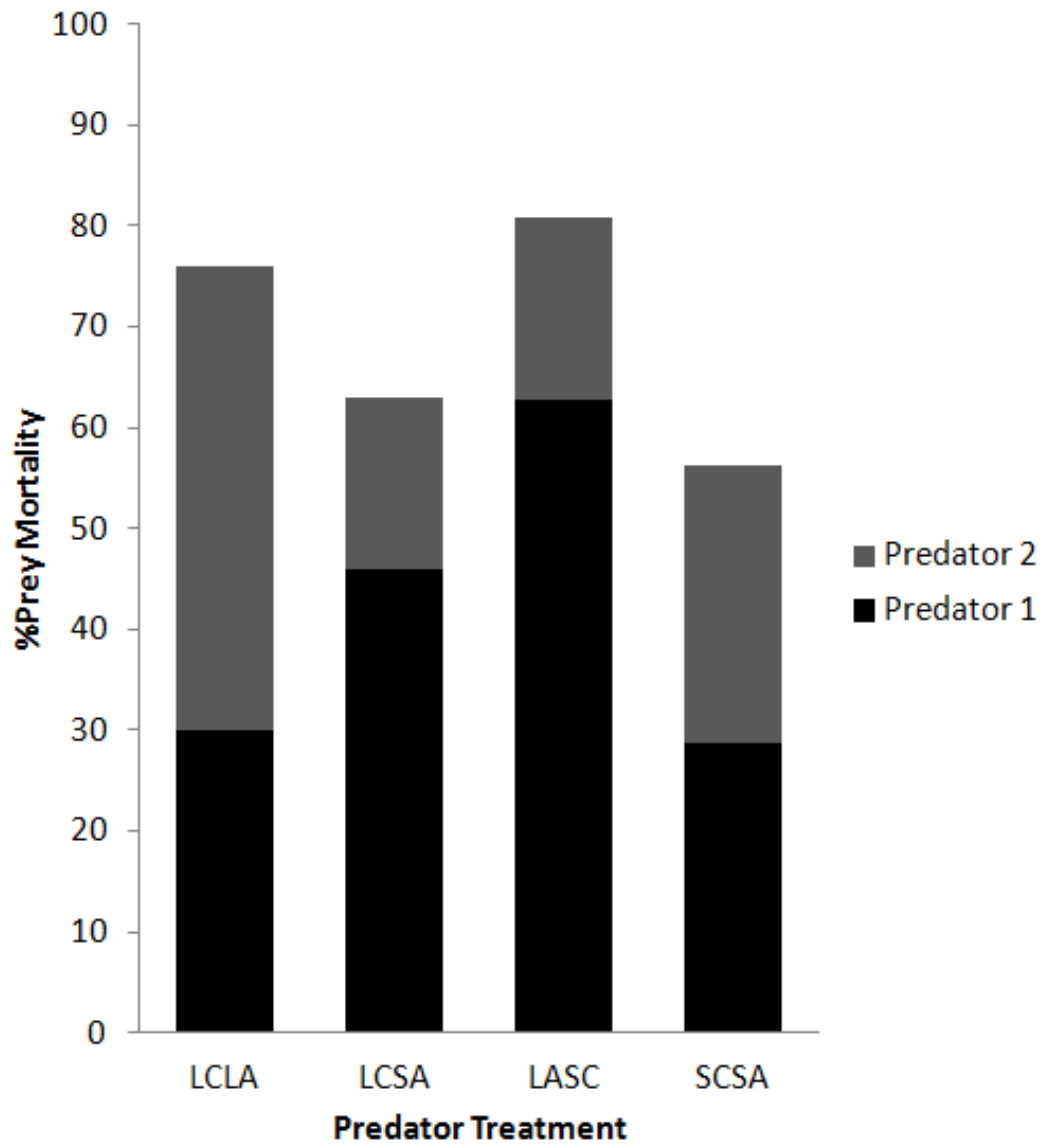


Figure 6. Large *A. junius* and small *C. fimbriolatus* consumed less prey in the presence of large heterospecifics relative to small heterospecifics.

Analysis 1.3 Predator survival

Habitat complexity had no significant effects on the frequency of cannibalism or IGP (Figure 7). Large *C. fimbriolatus* survival was 100%, regardless of habitat treatment or the identity of the other predator. Although survival of small *A. junius* and small *C. fimbriolatus* was greater at high habitat complexity, the differences were not significant (G-test $p > 0.1$). Survival of large *A. junius* was greater at low habitat complexity, but the difference was not significant (G-test $p > 0.2$).

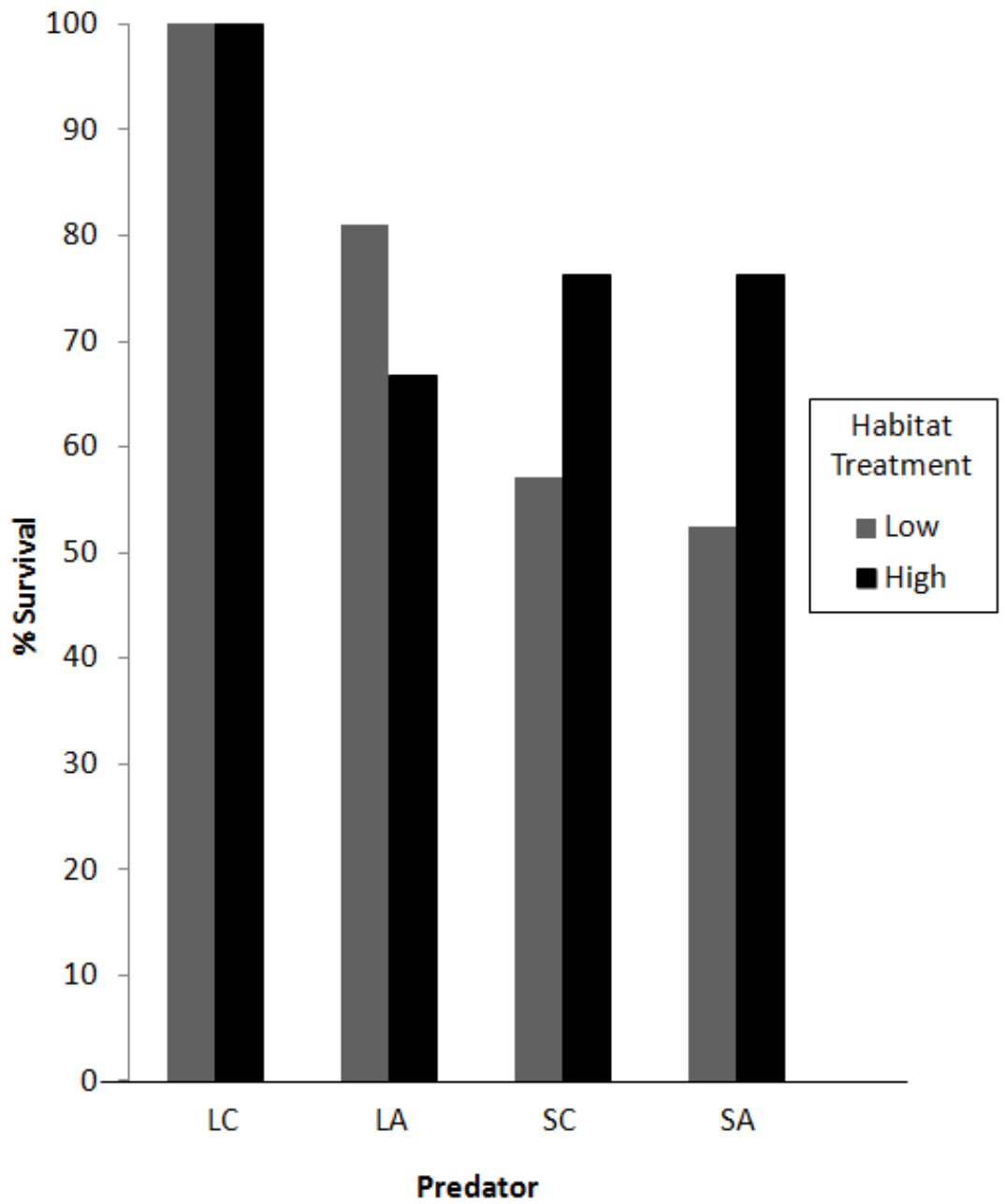


Figure 7. Habitat complexity did not significantly affect survival of any predators in our study.

Predator treatment influenced frequency of cannibalism and IGP (Figure 8).

Survival of small *A. junius* was significantly greater than survival of small *C.*

fimbriolatus in the presence of large *C. fimbriolatus* (G-test $p < 0.01$). Additionally,

survival of small *C. fimbriolatus* was greater than survival of small *A. junius* in the

presence of large *A. junius* (G-test $p < 0.05$).

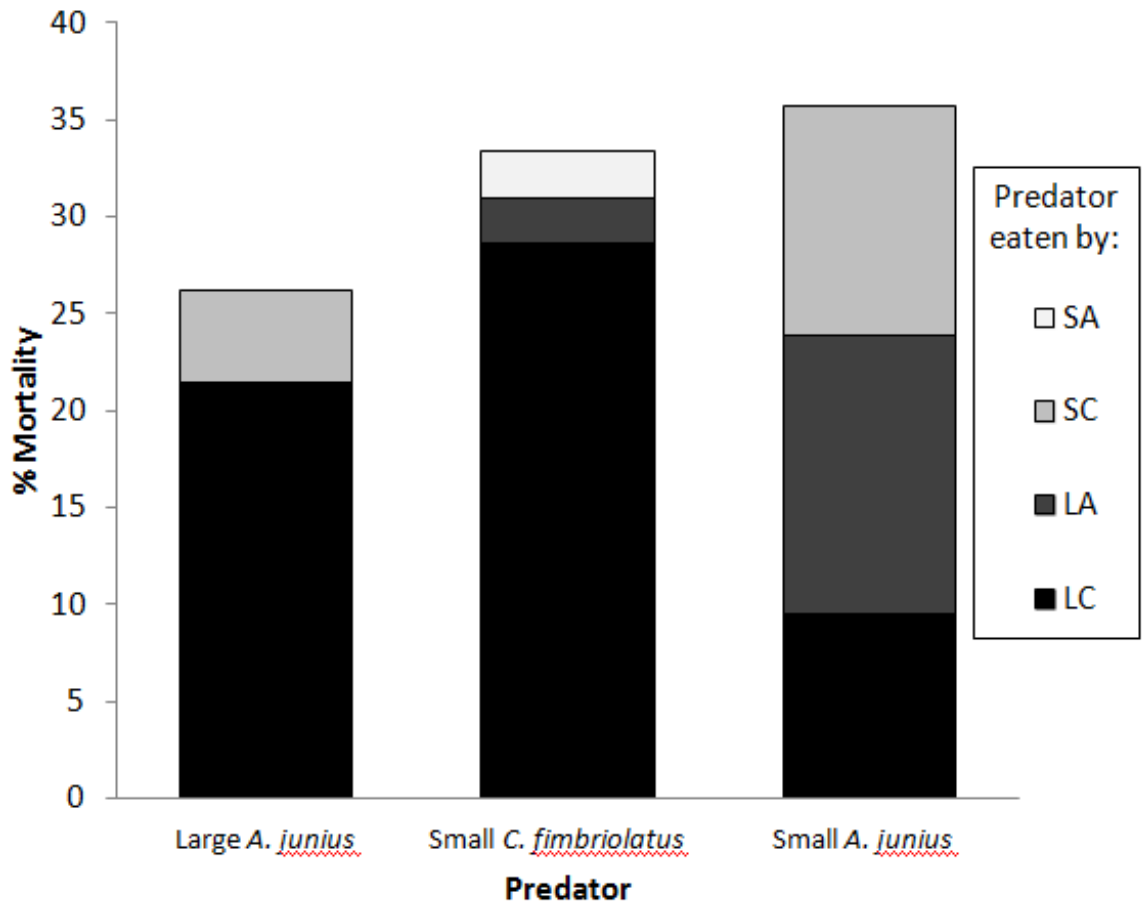


Figure 8. Breakdown of all predator deaths. Large *A. junius* was eaten most often by large *C. fimbriolatus*. Small *C. fimbriolatus* was eaten most often by large *C. fimbriolatus*. Small *A. junius* was equally preyed on by all other predators. Large *C. fimbriolatus* is not included because it was never eaten. Results confirm *C. fimbriolatus* as the top predator and *A. junius* as the intermediate predator.

Experiment 2

In the choice test, there was no difference in which prey was consumed first between large *A. junius* and large *C. fimbriolatus*. Both large predators consumed small *C. fimbriolatus* first 8 out of 9 times, each only consuming small *A. junius* first in 1 replicate (G-test $P > 0.9$). Prey consumed first was significantly different for small *A. junius* versus small *C. fimbriolatus*. Small *C. fimbriolatus* were consumed first significantly more frequently (Binomial test $p = 0.001$) (Figure 9). The amount of time for *A. junius* to feed was not significantly different from the amount of time for *C. fimbriolatus* to feed (Student's T-test $p = 0.28$), but the trend was for *A. junius* to eat sooner than *C. fimbriolatus* (13 hours versus 23 hours).

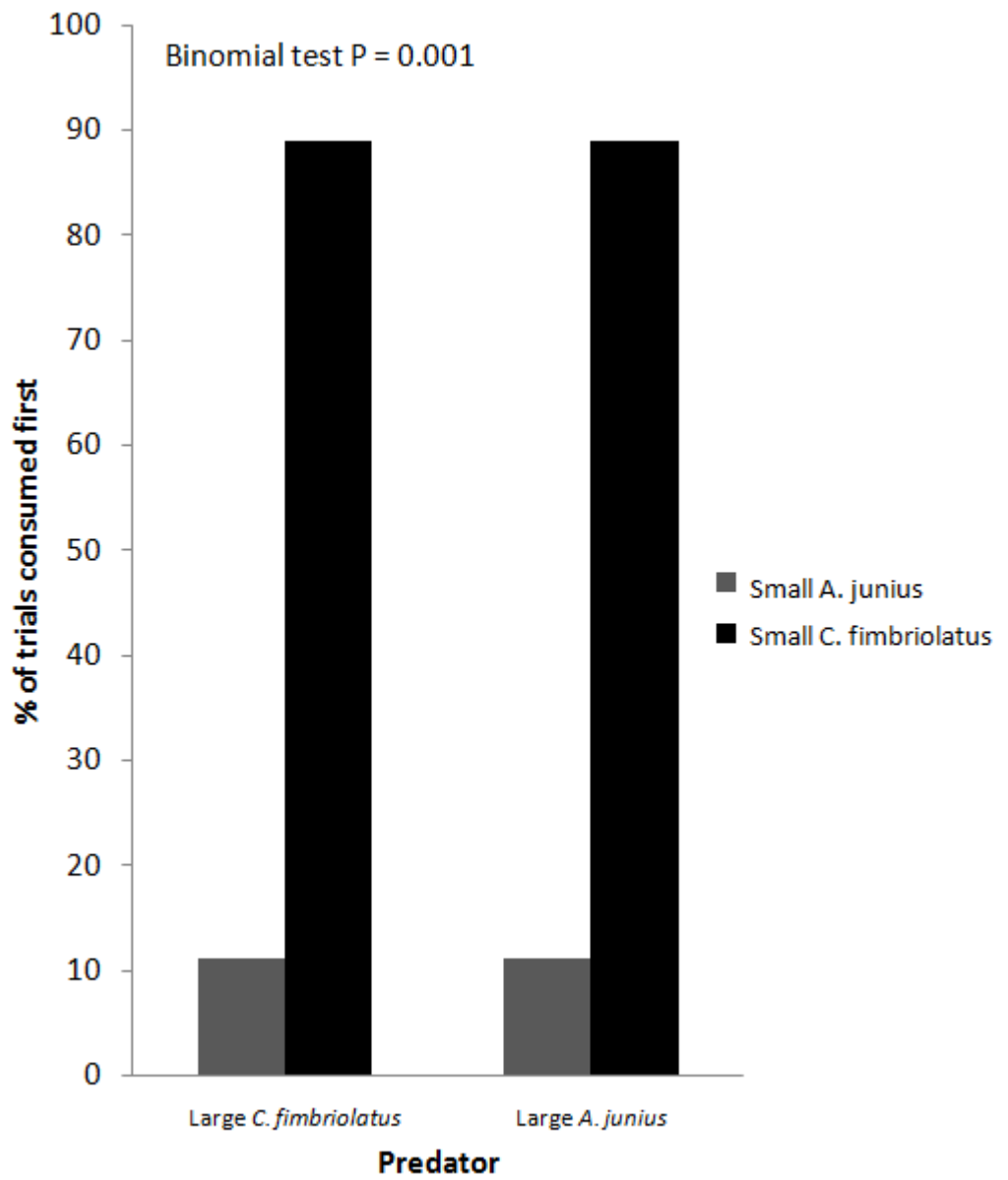


Figure 9. Small *C. fimbriolatus* is preyed on more often than small *A. junius* because its active behavior exposes it to larger predators more frequently.

CHAPTER FOUR

Discussion and Conclusions

This study provides evidence that both habitat complexity and variation in size structure among predators promotes survival of intermediate predators in an IGP system. High rates of cannibalism (86%) were observed between the large and small size classes of *C. fimbriolatus*. Of the six observed predaceous combinations, cannibalism among *C. fimbriolatus* occurred most frequently (Figure 10). This is likely because *C. fimbriolatus* is an active, voracious, generalist predator. All instars of *C. fimbriolatus* are highly active predators with high encounter rates between different size classes of *C. fimbriolatus* (Norwood 2012). Since *C. fimbriolatus* is such a voracious generalist predator, encounters often result in predation (Hall *et al.* 1970, Polis *et al.*, 1989, Crumrine *et al.*, 2008). Frequent cannibalism among *C. fimbriolatus* could limit the number of *C. fimbriolatus* developing to final instar and promote the survival of the intermediate predator, *A. junius* (Crumrine 2005).

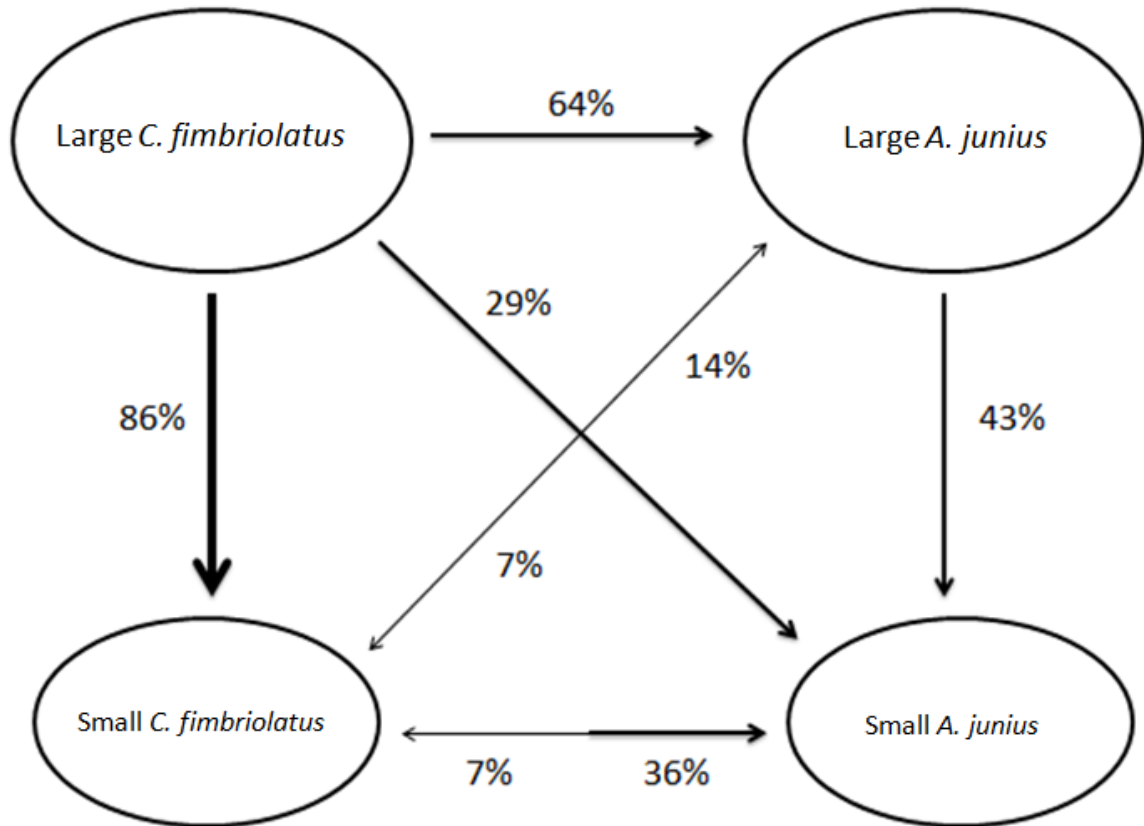


Figure 10. Arrows represent all observed IGP and cannibalism. Percentages include replicates at high and low habitat complexity since habitat complexity did not impact predator survival. These relationships confirm *C. fimbriolatus* as the top predator and *A. junius* as the intermediate predator.

Cannibalism by *A. junius* was less frequent, occurring in 43% of replicates. *A. junius* is a sit-and-wait predator so encounters with conspecific rates are likely lower than those among *C. fimbriolatus*. Behavioral studies could confirm this speculation. Still, *A. junius* more frequently acted as a cannibal than an IG predator; *A. junius* only consumed *C. fimbriolatus* in 3.5% of the replicates where the two species were together (Figure 10). Large *A. junius* never ate large *C. fimbriolatus* and ate small *C. fimbriolatus* in only one of fourteen trials. In treatments pairing large *A. junius* with either size class of *C.*

fimbriolatus, *A. junius* more effectively preyed on the shared prey *P. longipennis* (see Figure 6). The superior ability of the intermediate predator, *A. junius*, to exploit the shared prey resource is another factor supporting the sustained survival of the intermediate predator in an IGP system (Holt and Polis 1997). IGP was strongest between large *C. fimbriolatus* and large *A. junius*, with large *C. fimbriolatus* consuming large *A. junius* in 64% of replicates. Previous evidence indicates that large *C. fimbriolatus* prefers larger bodied prey, explaining its high predation rate on large *A. junius* (Kawecki 2010).

Habitat complexity may also influence the coexistence of top and intermediate predators in an IGP system. High habitat complexity promoted prey survival averaged across all predator size and species combinations. Likely high habitat complexity, provided additional refuge from predators, thus lowering encounter rates and subsequent predation. However, habitat complexity had no significant impact on IGP or cannibalism. Likely, the predators did not utilize the refuge spots provided by habitat complexity as effectively as the smaller bodied prey, *P. longipennis*. *P. longipennis* often took refuge in the fray of the nylon ropes or wedged under the glue anchoring ropes to the mesocosm. These spaces were too tight for *A. junius* and *C. fimbriolatus* but not for small prey. Natural systems likely mirror this pattern: smaller bodied prey can elude potential predators by taking refuge in small spaces.

Another hypothesis which could explain the ubiquity of IGP in communities is the possibility of predator-predator facilitation (Soluk 1997). Highly active behavior by *C. fimbriolatus* may cause *P. longipennis* to avoid predation by frequently relocating, and thereby facilitate the sit-and-wait feeding strategy of *A. junius* by causing encounters that

wouldn't otherwise occur. This behavioral mechanism could support the survival of intermediate predators in an IGP system. This hypothesis could be tested by comparing *A. junius*'s predation rates in the presence and absence of *C. fimbriolatus*.

Size and species combinations of predators also affected prey survival. Prey survival was highest in the small *C. fimbriolatus*/small *A. junius* predator combination. This may be due to the lower energetic needs of the two small predators; both small predators consumed significantly less shared prey than did the conspecific large predator. High prey survival in the small *C. fimbriolatus*/small *A. junius* predator combination could also be attributed to the fact that in 43% of trials one predator consumed the other, thus eliminating possible predator-predator facilitation and limiting the number of predators present to consume prey. Low levels of prey survival occurred among large *A. junius*/small *C. fimbriolatus*, large *A. junius*/small *A. junius*, and large *C. fimbriolatus*/small *A. junius*. IGP was low (21%) in the large *A. junius*/small *C. fimbriolatus* treatment so both predators were present and consumed prey throughout the observation time. The high predation rates in the large *A. junius*/small *A. junius* treatment can likely be attributed to feeding by large *A. junius*, since large *A. junius* was shown to be a more effective predator than small *A. junius*. In the large *C. fimbriolatus*/small *A. junius* treatment, IGP was low (large *C. fimbriolatus* consuming small *A. junius* 29% of the time), likely because *C. fimbriolatus* prefers larger bodied prey (Kawecki 2010). Again, with both predators remaining alive a significant amount of time, prey survival was low.

Large *C. fimbriolatus* was the most common predator on other predators. Of the 11 deaths of large *A. junius*, 9 were predation by large *C. fimbriolatus*. Similarly, 12 of

the 14 deaths of small *C. fimbriolatus* deaths were cannibalism by large *C. fimbriolatus*. However, predation on small *A. junius* was equally divided between all other predators (Figure 8). One likely reason predation on small *A. junius* was not biased towards predation by large *C. fimbriolatus* is because *C. fimbriolatus* prefers larger bodied prey. In treatments of large *C. fimbriolatus*/small *A. junius*, *C. fimbriolatus* was equally inclined towards eating either small *A. junius* or *P. longipennis*, and thus preyed on small *A. junius* less frequently.

Experiment 2 tested the relative frequencies of IGP and cannibalism between large *A. junius* and large *C. fimbriolatus*. Large *C. fimbriolatus* was highly cannibalistic while large *A. junius* was much more frequently an intraguild predator. Both large predators consumed small *C. fimbriolatus* first in 8 out of 9 trials. This strong relationship is likely attributable to the high activity level of small *C. fimbriolatus*, which results in high encounter rates with potential predators. If such strong feeding relationships exist in nature, this could be another factor which promotes the persistence of IGP. If small *C. fimbriolatus* frequently falls prey to both larger conspecifics and larger heterospecifics, then populations of the top predator *C. fimbriolatus* may be limited and facilitate the survival of an intermediate predator. However, results from Experiment 1 suggest that the presence of alternative prey dampens cannibalism between large *A. junius* and small *C. fimbriolatus*. Removal of mandibles from small *C. fimbriolatus* may make it an easier target for large *A. junius* and thus inflate predation rates.

This study reveals that habitat complexity and size structure are two factors that could allow the top and intermediate predators of an IGP system to coexist in nature. Natural ecological communities are complex and dynamic and it is necessary to adjust

current models to reflect that complexity. Size-structured IGP and cannibalism are common interactions, but their impact on community structure is underappreciated. Our knowledge of predator-prey interactions within a community informs policy regarding agroecosystems and wildlife management, so it is critical that we understand all variables that could influence these relationships. In many cases, our ability to make responsible and informed decisions for a sustainable earth depends on our accuracy in predicting relationships in natural and manufactured communities.

APPENDICIES

APPENDIX A

Images of *C. fimbriolatus*



Clockwise from upper left: Piercing sucking mandibles of *C. fimbriolatus*; *C. fimbriolatus* attacking *A. junius*; adult *C. fimbriolatus*; 3rd instar *C. fimbriolatus* larva

APPENDIX B

Images of *A. junius*



Clockwise from upper left: 12th instar *A. junius* larva; adult *A. junius*; emerging *A. junius*; author with *A. junius*

APPENDIX C

Images of Experimental Design



Clockwise from upper left: Collecting organisms from fishless ponds with Patrick Crumrine, PhD; Organisms separated, photographed, and measured in lab; Organisms assigned to high (left) and low (right) habitat complexity mesocosms; Predator and prey survival measured twice daily for three days

APPENDIX D

Images of Blandy Experimental Farm



Top: Blandy Experimental Farm, researcher housing



Bottom: Cattle tanks filled with pond water for storage of organisms in lab

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