Size-structured cannibalism between top predators promotes the survival of intermediate predators in an intraguild predation system

Patrick W. Crumrine

Department of Biology, University of Kentucky, Lexington, Kentucky 40506-0225 USA
and Department of Biological Sciences and Program in Environmental Studies, Rowan University, Glassboro, New Jersey 08028 USA

Abstract. Individuals in most natural populations of predators vary in size, and size differences among individuals often result in cannibalism. Cannibalism is an extremely common phenomenon in the animal kingdom, particularly among generalist predators that engage in intraguild predation (IGP). However, few studies have specifically addressed the effects of cannibalism on IGP. The aim of my study was to investigate how trophic and behavioral interactions between 2 size classes of an intraguild (IG) predator influenced the survival and behavior of IG prey and a shared prey resource. I tested for these effects with larval odonates by exposing a shared prey resource (Ischnura verticalis) to the presence or absence of IG prey (Pachydiplax longipennis) and 2 size classes of IG predators (small or large Anax junius) in a $2 \times 2 \times 2$ factorial design. Mortality rates of the shared resource in all single-predator treatments were significantly greater than in nonpredator controls, and risk reduction was observed when the shared resource was exposed to combinations of predators. The significant negative effect of large A. junius on P. longipennis survival and activity level was greater than that of small A. junius. Cannibalism occurred between large and small A. junius in size-structured IG predator treatments, and the effects of the size classes were not additive for the survival of IG prey. Cannibalism was not solely responsible for risk reduction in IG prey, and reduced activity level of small A. junius in the presence of larger conspecifics probably had a positive influence on P. longipennis survival. My results demonstrate that cannibalism among IG predators can influence the survival of IG prey and might contribute to coexistence among predators in systems with strong IGP.

Key words: intraguild predation, size structure, cannibalism, community structure, food webs, multiple predators, Anax junius, Odonata.

Intraguild predation (IGP) occurs when species that compete for resources also prey on each other (Polis et al. 1989, Holt and Polis 1997). In its simplest form, IGP includes intraguild (IG) predators that consume IG prey, and both species consume and, thus, compete for a shared resource. IGP is quite common in aquatic, terrestrial, and marine communities (Polis et al. 1989, Arim and Marquet 2004), but initial theoretical studies predicted that predators in IGP systems should coexist only under a limited set of conditions (Polis and Holt 1992, Holt and Polis 1997). Simple models predict that coexistence is most likely when IG prey are superior at exploiting the shared resource, IG predators gain significantly from consuming IG prey, and at intermediate levels of the shared resource (Holt and Polis 1997, Diehl and Feissel 2000, Mylius et al. 2001). To address this discrepancy, several studies explored mechanisms that promote coexistence of predators in IGP systems. Recent theoretical efforts demonstrate that the availability of alternative resources for the IG prey are particularly important (Holt and Huxel 2007). Furthermore, cannibalism in size-structured assemblages of IG predators also can promote the coexistence of IG predators and IG prey (Rudolf 2007b). These models show that coexistence is a function of the relative strength of cannibalism vs intraguild predation (Rudolf 2007b).

IG predator size structure is likely to influence IG prey survival and shared resource survival via a greater number of direct and indirect density-mediated and trait-mediated pathways relative to in systems without IG predator size structure (Fig. 1A, B). Size structure often promotes cannibalism (Fox
1975, Polis 1981, Ebenman and Persson 1988), and cannibalism of small IG predators by large IG predators could decrease overall IG predator density, promoting IG prey survival. This effect could indirectly hinder short-term survival of the shared resource, although antipredator behavior by IG prey could counteract this effect. The threat of cannibalism also could induce behavioral modifications in small IG predators that alter their foraging patterns (Sih 1981, Leonardsson 1991, Biro et al. 2003, Rudolf 2006). The survival of IG prey and the shared resource should ultimately depend on the strength of predation between different size classes of IG predators and IG prey and the shared resource. For example, different size classes of IG predators could pose different levels of risk to IG prey. Small IG predators might impose lower levels of mortality on IG prey and primarily consume the shared resource, whereas large IG predators might consume more IG prey. Mathematical models that include nonpredatory stages of IG predators also predict coexistence under a slightly wider range of conditions relative to nonsize-structured models of IGP (Mylius et al. 2001), but few experimental studies have addressed the effects of IG predator size structure on the survival of IG prey and shared prey (but see Crumrine 2005).

Many populations of organisms engaged in IGP interactions are size structured (Ebenman and Persson 1988, Polis et al. 1989, Polis and Holt 1992). Incorporating within-population size structure as an experimental variable in IGP studies adds significant complexity to empirical studies, but the commonness and potential importance of this feature provide compelling motivation for addressing size structure more realistically. Furthermore, the temporal and spatial variability of population size structure in natural communities (Butler 1984, Wissinger 1988) necessitates an understanding of IGP interactions in communities with different levels of population size structure. To address these issues, I conducted an experiment to quantify the survival and behavior of Ischnura verticalis damselfly larvae (shared resource) in the presence/absence of 2 size classes of IG predators (small and large Anax junius larvae) and IG prey (larvae of the dragonfly Pachydiplax longipennis). I also quantified the survival and behavior of P. longipennis larvae in the presence of the 2 size classes of IG predators. This experiment allowed me to address 3 key questions: 1) Does cannibalism between IG predators promote the survival of IG prey?; 2) Does the threat of cannibalism cause small IG predators to reduce activity level in the presence or larger conspecifics?; and 3) Do conspecific and heterospecific combinations of predators have non-additive effects on prey survival?

Methods

Natural history of study organisms

Ischnura verticalis, P. longipennis, and A. junius larvae coexist in lakes and ponds in eastern North America (Johnson and Crowley 1980, McPeek 1990, 1998) and are 3 of the more common odonates found in fishless ponds in eastern North America (Johnson and Crowley 1980, Wissinger 1989, McPeek 1990, 1998, Hopper 1998). Anax junius assumes the role of top predator in small fishless bodies of water and strongly influences odonate community composition in these habitats (McPeek 1998). Size structure of larval A. junius assemblages is heavily affected by the overlap of phenologically separate migrant and resident cohorts (for a more complete description of migration in A. junius see Corbet 1999 and May and Matthews 2008), but size structure in larval assemblages of A. junius also can arise because of a relatively long breeding season, particularly in the southern extent of its range.

All odonate larvae used in my experiments were collected from fishless ponds at the University of Kentucky’s Ecological Research Facility, northern Fayette County, Kentucky. Small and large A. junius used in the experiments were in the 8th (mean head width: 3.34 mm) and 12th (mean head width: 7.41 mm) instars respectively, as determined by head width and wing pad development (Calvert 1934, Wissinger 1992). Pachydiplax longipennis larvae used in the experiments included a mix of 11th- (mean head width: 3.26 mm)

![Diagram of intraguild predation configurations](image-url)
and 12th-instar animals (mean head width: 4.27 mm), as determined by head width measurement (Wissinger 1992). The head width of some P. longipennis used in the experiment was greater than the head width of some of the small A. junius. Preliminary predation trials revealed that these P. longipennis did not consume small A. junius. However, small A. junius were capable of consuming all sizes of P. longipennis used in the experiment. The stalking foraging mode, flat blade-like labium, and visual acuity of aeshnids, such as A. junius, allow them to capture large prey items, including conspecifics. Ischnura verticalis larvae used in the experiments consisted of individuals in the final 3 instars of development (mean head width: 2.15 mm). Late-instar larvae were most abundant in the field collections, and the size structure of I. verticalis larvae used in the experiment mimicked the natural range of sizes available in field collections. All odonate larvae were collected 1 d before the beginning of experimental trials. Larvae were housed together in single-species tanks under a 13:11 light:dark photoperiod at room temperature (25.5°C). No final-instar larvae were used in the experiment to avoid the onset of emergence.

Experimental design

Trials were conducted in plastic tubs (30 × 42 × 16 cm) divided into 2 heterogeneous habitats, an open-water habitat (30 × 25 × 16 cm) and a vegetated habitat (30 × 17 × 16 cm). Two habitat types were provided to see if larvae altered habitat use in the presence of predators, but larvae were observed almost exclusively in the vegetated habitat during the experiment. To simulate aquatic vegetation, 25 lengths of nylon rope (15 cm tall and 1 cm diameter) were uniformly distributed and anchored to the bottom of each tub in the vegetated habitat. This intermediate level of habitat complexity (490 stems/m²) corresponds to densities of macrophytes found in nature (Sheldon and Boylen 1977). The bottom of each tub was covered with white silica sand to a depth of 0.5 cm and filled with charcoal-filtered tap water to a depth of 15 cm above the sand bottom. To begin the trials, the shared resource was introduced to the tubs 1 h before IG prey and IG predators were introduced.

The experiment consisted of 8 treatments in a 2 × 2 factorial design (n = 5). The presence/absence of P. longipennis and the 2 size classes of A. junius were manipulated (Table 1). Each treatment received 20 I. verticalis, equivalent to 159 individuals (ind.)/m² and similar to densities reported in field studies for larval Ischnura (Corbet 1999, PWC, personal observation). Treatments with P. longipennis received 10 larvae, equivalent to 80 ind./m². Treatments that included 1 size class of the IG predator received either four 8th-instar or four 12th-instar A. junius larvae, equivalent to 31 ind./m². Treatments that included both size classes of the IG predator received four 8th-instar and four 12th-instar A. junius larvae, equivalent to 63 ind./m². Larval odonate densities vary considerably over space and time and range from 0 to 4500 ind./m² (Corbet 1999). The densities used in the experiment were near the upper limit reported for aeshnid larvae (Van Buskirk 1992), well within the range reported for libellulid larvae (Corbet 1999), and comparable to those used in other larval odonate studies (Morin 1984, Robinson and Wellborn 1987). In preliminary experiments, predators were usually able to consume all shared resources in 4 d, so I ended trials after 3 d. Experimental trials were conducted between 20 May 2002 to 10 June 2002.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Ischnura verticalis</th>
<th>P. longipennis</th>
<th>Small A. junius</th>
<th>Large A. junius</th>
</tr>
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<tbody>
<tr>
<td>Control</td>
<td>20</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Pachydiplax longipennis</td>
<td>20</td>
<td>10</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Small A. junius</td>
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<td>0</td>
</tr>
<tr>
<td>Large A. junius</td>
<td>20</td>
<td>0</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>P. longipennis + small A. junius</td>
<td>20</td>
<td>10</td>
<td>4</td>
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<tr>
<td>P. longipennis + large A. junius</td>
<td>20</td>
<td>10</td>
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<tr>
<td>Small A. junius + large A. junius</td>
<td>20</td>
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<td>4</td>
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<tr>
<td>P. longipennis + small A. junius + large A. junius</td>
<td>20</td>
<td>10</td>
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</table>

Response variables and data analysis

Mortality rates (ki) for small IG predators, IG prey, and the shared resource in each replicate of treatment i were determined using the following equation (Crumrine and Crowley 2003, Crumrine 2005):

\[ k_i = -\ln(1 - p_i)/t \]  \hspace{1cm} [1]

where \( p_i \) is the proportion of individuals killed and \( t \) (3 d) is the length of the experimental trial. This representation of the mortality rate is logically
consistent with the multiplicative risk model developed by Soluk and Collins (1988). Shared resource mortality rates were analyzed using 3-way factorial analysis of variance (ANOVA), and IG prey and small IG predator mortality rates were analyzed using 2-way factorial ANOVA.

The movements of all odonates in each tub were recorded using SONY Hi8 video cameras (SONY, Japan). Each tub was videotaped for 30 min between 0800 and 0900 h, and for 30 min between 1600 and 1700 h for a total of 60 min/d. Activity level of odonates was quantified by counting the total number of movements made by each individual in each tub. Number of movements was chosen as a response variable because activity level strongly influences encounters with predators (Gerritsen and Strickler 1977, Anholt et al. 2000). Odonate activity level was reported as number of movements larva\(^{-1}\) h\(^{-1}\) h⁻¹. Odonate mortality was determined at the end of the 3-d trial. Shared resource, IG prey, and small IG predator activity level were analyzed using repeated-measures ANOVA with day as the repeated measure.

**Observed vs expected mortality rates**

Greater-than-expected and lower-than-expected prey mortality rates are termed risk enhancement and risk reduction, respectively, and indicate interactions between predators. Expected mortality rates of IG prey and the shared resource when exposed to combinations of predators were determined based on mortality rates when exposed to only 1 type of predator using mortality rates generated from equation 1 while accounting for background mortality (\(k_0\)) (Rudolf 2008). For example, the shared resource mortality rate in the presence of small \(A.\) junius is \(k_{SA}\), and the shared resource mortality rate in the presence of large \(A.\) junius is \(k_{LA}\). There was background mortality of the shared resource in the nonpredator control. Thus, simply taking the sum of \(k_{SA} + k_{LA}\) to generate the expected shared resource mortality rate in the presence of both size classes of the IG predator would account for this background mortality twice and would overestimate the expected mortality rate. To account for this, the average background mortality rate was determined for the shared resource from the control treatment and subtracted from both \(k_{SA}\) and \(k_{LA}\) to generate \(k_{SA}^1\) and \(k_{LA}^1\). The expected shared resource mortality rate in the presence of both small and large \(A.\) junius is then \(k_{SA}^1 + k_{LA}^1 + k_0\). Nonadditivity is indicated by a significant interaction term in the 2-way ANOVA of large \(A.\) junius and small \(A.\) junius mortality effects. Risk reduction results when \(k_{SA + LA} < k_{SA}^1 + k_{LA}^1 + k_0\), and risk enhancement occurs when \(k_{SA + LA} > k_{SA}^1 + k_{LA}^1 + k_0\).

**Results**

**Shared resource mortality**

Each predator significantly increased \(I.\) verticalis mortality rate. The effects of small \(A.\) junius (ANOVA, \(F = 34.49, \text{df} = 1, 31, \ p < 0.0001\)) and large \(A.\) junius (ANOVA, \(F = 33.21, \text{df} = 1, 31, \ p < 0.0001\)) were similar in magnitude. The presence of \(P.\) longipennis also caused an increase in \(I.\) verticalis mortality rate (ANOVA, \(F = 16.73, \text{df} = 1, 31, \ p < 0.0003\)), but this effect was not as strong as the effects of either of the 2 size classes of \(A.\) junius.

All 2-way interactions for \(I.\) verticalis mortality were significant, a result indicating that the combined predator mortality rates could not be predicted based on the independent effects of each predator (small \(A.\) junius x \(P.\) longipennis: \(F = 5.34, \text{df} = 1, 31, \ p < 0.03\); large \(A.\) junius x \(P.\) longipennis: \(F = 8.77, \text{df} = 1, 31, \ p < 0.005\); small \(A.\) junius x large \(A.\) junius: \(F = 40.26, \text{df} = 1, 31, \ p < 0.00001\)). For each of the three 2-predator combinations, shared resource mortality rate was lower in the presence of the predator combination than it was in the presence of the most dangerous predator alone. Last, the interaction between small \(A.\) junius and \(P.\) longipennis for \(I.\) verticalis survival depended on the presence of large \(A.\) junius (\(F = \))
17.21, df = 1.31, p < 0.002). This result indicates that the presence of a large IG predator caused a change in the interaction between small IG predators and IG prey that influenced the mortality rate of the shared resource.

Observed and expected prey mortality rates were compared with and without accounting for the effects of IGP on shared resource mortality rate to further characterize the nonadditive interactions. A planned contrast revealed that the observed shared resource mortality rate in the P. longipennis + small A. junius treatment was significantly lower than expected (p < 0.005; Fig. 2A). IGP can reduce the density of predators in combined predator treatments. Pachydiplax longipennis densities were reduced on average by 42% at the end of the experiment in the small A. junius + P. longipennis treatment, but the simple null model does not account for this reduction. Mortality rates based on the final density of P. longipennis in small A. junius + P. longipennis were used to account for the reduction in P. longipennis density. After accounting for IGP, a planned contrast revealed that the observed shared resource mortality rate was still significantly lower than expected (p < 0.01; Fig. 2A).

A planned contrast showed that the observed shared resource mortality rate in the large A. junius + P. longipennis treatment was lower than expected (p < 0.0001; Fig. 2B). On average, large A. junius consumed 82% of the P. longipennis by the end of the experiment in the large A. junius + P. longipennis treatment. After accounting for this IGP effect, the observed shared resource mortality rate was still lower than the expected shared resource mortality rate in the large A. junius + P. longipennis treatment (p < 0.02; Fig. 2B). A planned contrast indicated that the observed shared resource mortality rate in the small A. junius + large A. junius treatment also was lower than expected (p < 0.0001; Fig. 2C). On average, large A. junius consumed 25% of the small A. junius in the large A. junius + small A. junius treatment. After accounting for this cannibalism effect, the observed shared resource mortality rate was still lower than the expected shared resource mortality rate in the small A. junius + large A. junius treatment (p < 0.025; Fig. 2C).

Shared resource behavior

Activity level of I. verticalis was lowest in the presence of small and large A. junius (main effect of small A. junius: $F = 4.57$, df = 1.31, p < 0.05; main effect of large A. junius: $F = 14.78$, df = 1.31, p < 0.0006), but I. verticalis did not respond to the presence of P. longipennis ($F = 0.02$, df = 1.31, p > 0.88; Fig. 3). The behavioral response of I. verticalis in the P. longipennis + small A. junius treatment was similar to the mortality response. Activity level of I. verticalis was lower in the presence of only small A. junius than when both P. longipennis and small A. junius were
present \( (F = 6.90, \text{df} = 1.31, p < 0.01) \). Significant interactions occurred between \( P. \text{longipennis} \) and large \( A. \text{junius} \) \( (F = 5.50, \text{df} = 1.31, p < 0.05) \) and between small and large \( A. \text{junius} \) \( (F = 5.64, \text{df} = 1.31, p < 0.05) \). \( I. \text{verticalis} \) decreased their activity level when \( A. \text{junius} \) were present, regardless of their size, but the magnitude of this response was lower in the \( P. \text{longipennis} + \) small \( A. \text{junius} \) combination. The influence of the interaction between \( P. \text{longipennis} \) and small \( A. \text{junius} \) on \( I. \text{verticalis} \) activity level also depended on the presence of large \( A. \text{junius} \) \( (F = 6.45, \text{df} = 1.31, p < 0.01) \). Adding large \( A. \text{junius} \) to a system that already included small \( A. \text{junius} \) and \( P. \text{longipennis} \) caused an additional decrease in \( I. \text{verticalis} \) activity level.

**IG prey mortality**

Large \( A. \text{junius} \) greatly increased the mortality rate of \( P. \text{longipennis} \), but the effect of small \( A. \text{junius} \) on \( P. \text{longipennis} \) mortality rate was not significant (main effect of large \( A. \text{junius} \): \( F = 18.78, \text{df} = 1.15, p < 0.0006 \); main effect of small \( A. \text{junius} \): \( F = 0.003, \text{df} = 1.15, p < 0.95 \); Fig. 4A). The mortality rate of \( P. \text{longipennis} \) was nearly 3-fold greater in the presence of large \( A. \text{junius} \) than in the presence of small \( A. \text{junius} \). Interactions between small and large \( A. \text{junius} \) influenced \( P. \text{longipennis} \) mortality rate in the size-structured \( A. \text{junius} \) treatment \( (F = 4.8, \text{df} = 1.15, p < 0.04) \). The significant interaction between the 2 size classes of \( A. \text{junius} \) indicates that the effects of the 2 predators on IG prey mortality rate were not additive.

The mortality rate of \( P. \text{longipennis} \) in the presence of both size classes of \( A. \text{junius} \) was 33\% lower in the presence of only large \( A. \text{junius} \), the more dangerous predator.

To further explore how IG predator cannibalism influenced the mortality rate of IG prey, planned contrasts were used to compare observed and expected IG prey mortality rates with and without the effect of a reduction in predator density (i.e., the cannibalism effect). A planned contrast indicated that the observed IG prey mortality rate was lower than expected \( (p < 0.025; \text{Fig. 4A}) \). On average, large \( A. \text{junius} \)
junius consumed 25% of the small A. junius in the large A. junius + small A. junius + P. longipennis treatment. After accounting for the reduction in density of small A. junius, the expected IG prey mortality rate was not significantly different from the observed IG prey mortality rate in the small A. junius + large A. junius treatment (p > 0.1; Fig. 4A). This result indicates that cannibalism between IG predators had a significant and positive impact on the survival of the IG prey.

IG prey behavior

Activity levels of P. longipennis were primarily dependent on the presence of large A. junius (F = 20.15, df = 1,15, p < 0.0004; Fig 4B). Pachydiplax longipennis were 78% less active in the presence of large A. junius relative to in control treatments without A. junius, whereas the reduction in activity level in the presence of small A. junius was smaller (33%) and not significant (F = 1.89, df = 1,15, p > 0.18; Fig. 4B). Interactions between small A. junius and large A. junius did not influence P. longipennis activity level (F = 0.96, df = 1,15, p > 0.34; Fig. 4B). The behavioral response of P. longipennis in the size-structured A. junius treatment was similar to its response in the large A. junius treatment. The main effects of small A. junius and large A. junius on P. longipennis activity level were similar to the mortality responses. The main effect of large A. junius on P. longipennis mortality rate was significant, and P. longipennis responded by decreasing their activity level, but small A. junius did not have a significant effect on P. longipennis mortality rate nor on their behavior.

Small and large IG predator mortality and behavior

As noted above, large A. junius decreased the survival of small A. junius (F = 10.37, df = 1,15, p < 0.005). Mortality of small A. junius occurred in both treatments that included the 2 size classes of A. junius, so cannibalism occurred when both types of potential prey were present (i.e., P. longipennis and I. verticalis). The presence of large A. junius also caused small A. junius to reduce their activity level (F = 4.81, df = 1,15, p < 0.04). No large A. junius mortality occurred in the experiment, and large A. junius did not modify their behavior in the presence of P. longipennis (F = 3.72, df = 1,15, p > 0.07) or small A. junius (F = 3.12, df = 1,15, p > 0.09).

Discussion

Size structure has been hypothesized to be a stabilizing feature in IGP systems (Holt and Polis 1997), and several studies indicate that size-dependent cannibalism might promote the coexistence of IG predators and IG prey (Borer 2002, Yasuda et al. 2004, Rudolf 2006, 2007b). However, few IGP studies have integrated within-population size structure as an experimental variable (but see Crumrine 2005, Rudolf 2008). My results demonstrate that IG prey benefit from size structure in the assemblage of IG predators and that interactions between pairs of predators are influenced by the degree of size structure of the IG predator assemblage. In general, the results of my laboratory experiment are supported by results of previous experiments conducted in field enclosures with the same species. Crumrine (2005) used a substitutive design that controlled for overall predator density and demonstrated that the mortality rate of IG prey was lower in the presence of size-structured assemblages of IG predators than when in the presence of a single size class of large IG predators. Cannibalism was not reported in the size-structured IG predator assemblage, so these effects were presumably caused by shifts in diet or behavior by small IG predators (Crumrine 2005). The present study adds some support to this conclusion because small IG predators did reduce activity levels in the presence of large IG predators, but it is likely that both cannibalism and behavioral shifts resulting from the threat of cannibalism promoted the survival of IG prey.

These interactions occurred in a system with IG predators that were more effective competitors for the shared resource than were the IG prey. Simple IGP models without cannibalism (Holt and Polis 1997) would predict the eventual extinction of IG prey under such conditions, but recent theoretical work expanding simple IGP models to include cannibalism in IG predators suggest that coexistence is possible even if IG prey are not more effective exploiters of the shared resource (Rudolf 2007b). Robust tests of these predictions require long-term data (Briggs and Borer 2005), but I contend that the results of my short-term experiment provide some evidence that cannibalism might be an ecological mechanism that promotes coexistence of IG predators and IG prey. Cannibalism essentially weakens the predatory link between large IG predators and IG prey, and theoretical studies have shown a positive relationship between community stability and the presence of weak links among species in food webs (McCann and Hastings 1997, McCann et al. 1998).

In my system, interactions between large and small size classes of A. junius (IG predators) had a significant risk reducing effect on P. longipennis (IG prey). Observed P. longipennis mortality was lower than expected in the presence of both size classes of A. junius, probably because of a combination of canni-
Cannibalism and behavioral avoidance of cannibalism by small *A. junius*. If these short-term changes in behavior affect maturation rates, long-term effects could influence the strength of trophic cascades (Rudolf 2007a). This finding has significant implications for studies addressing IGP. Those conducting such experiments must pay close attention to the degree of size structure in natural populations when designing experiments, and this feature has been largely ignored in IGP studies to date (but see Crumrine and Rudolf 2005); in addition, the behavioral response of the shared resource and IG prey in my system depended on the identity of the predator. In particular, IG prey did not simply respond to the presence of an IG predator but adjusted its response to the level of risk imposed by the 2 size classes of IG predators. A similar pattern of behavior has been reported in a size-structured community of stream salamanders (Rudolf 2006). Some prey species appear to have the capability of fine-tuning behavioral responses based on the size and identity of a predator, and this capability has the potential to influence IGP interactions and longer-term community dynamics. Thus, failing to take size structure into account in systems where it is prevalent could make it difficult to extend results of experimental studies to natural communities. This problem should be of particular importance for practitioners in the field of biological control where natural enemies of crop pests engage in intraguild predation.

IG predator size structure also influenced survival of the shared resource. The interaction between IG prey and small IG predators for shared resource mortality rate depended on the presence of large IG predators. Likewise, the interaction between IG prey and large IG predators for survival of the shared resource depended on the presence of small IG predators. IGP alone did not account for the discrepancy between observed and expected shared resource mortality rates for any of the significant nonadditive interactions between predators. Studies in similar systems indicate that behavioral modifications probably played a significant role in reducing overall risk to prey when faced with multiple predators (Wissinger and McGrady 1993, Schmitz and Suttle 2001, Crumrine and Crowley 2003). In my experiment, IG prey (*P. longipennis*) reduced their activity level in the presence of large IG predators (large *A. junius*), but not small IG predators (small *A. junius*), so this mechanism could be an explanation for the lower than expected shared resource mortality rates in the *P. longipennis* + large *A. junius* treatment.

Alternative prey effects (a reduction in shared resource consumption by IG predators in the presence of IG prey) probably also influenced shared resource mortality rate (Crumrine and Crowley 2003). Given the absence of a significant behavioral response by *P. longipennis* in the presence of small *A. junius*, changes in small *A. junius* foraging and consumption probably promoted the survival of the shared resource in the *P. longipennis* + small *A. junius* treatment.

One confounding factor that must be considered in my experiment is the increase in predator density in combined predator treatments, a shortcoming of many combined predator studies (Relyea 2003). This factor makes it difficult to determine if prey were responding to the combination of predators or an increase in predator density. In systems with IGP, the observed effects of combined predators on shared resource mortality rate are often lower than what one might expect based on the independent effects of the predators. In these cases, increases in predator density actually have positive effects on shared resource survival because IG predators consume IG prey and also induce behavioral shifts in IG prey. Large IG predators also have a similar effect on small IG predators. Cannibalism and the threat of cannibalism can promote prey survival. Both of these types of responses were observed in my study.

IG predator size structure clearly plays an important role in the interaction between species in IGP systems but population size structure also can exhibit considerable spatiotemporal variability (Wissinger 1988). This variation has the potential to influence the intensity of IGP in communities. IG prey might be vulnerable to predation from IG predators during only a fraction of their lifetime and then interact primarily as competitors (Wissinger 1992). This shift could be caused by ontogenetic diet changes in IG predators or through a refuge in size as IG prey grow larger. Thus, they might experience particularly harsh conditions for only short periods of time. This phenomenon has been termed life-history omnivory and is particularly common in aquatic communities (Pimm and Rice 1987). Seasonal and ontogenetic niche shifts are common in communities with IGP (Polis and Holt 1992, Wissinger 1992, Woodward and Hildrew 2002). Such shifts probably reduce competition in size-structured populations, allow species to attain size refuges, and promote species coexistence. The spatially or temporally invariant conditions often assumed in mathematical models might apply only over short periods of time, periods too short for species to be excluded completely from a system. The intensity of IGP might be tempered by the presence of population size structure, a characteristic that might vary predictably over space and time because of seasonal patterns of movement. In cases where IGP is
intense, coexistence might be more likely when organisms are able to adapt their behavior according to the level of risk present in the system (Abrams and Matsuda 1993, Matsuda et al. 1993).

Size structure is common in larval assemblages of *A. junius* in temperate North America, particularly in the central and northern latitudes of the US and the southern latitudes of Canada because of the coexistence of phenologically separate migrant and resident cohorts (May and Matthews 2008). *Anax junius* assumes the role of top predator in fishless ponds (McPeek 1998). Thus, the size-structured interactions described here have the distinct potential to influence strongly community structure in pond ecosystems where *A. junius* is present. During spring, assemblages of larval *A. junius* tend not to be highly size structured (Crumrine 2003). Thus, in spring, IGP might be more intense and *A. junius* might exert a stronger effect on the survival of IG prey species. In contrast, assemblages of *A. junius* during late summer can be highly size structured and present many opportunities for cannibalism. In late summer, the effect of *A. junius* as an IG predator might decrease and release IG prey species from some predation.

These types of interactions are not restricted to odonate communities. They play a role in species coexistence in other systems where stage or size structure is important. Theoretical and empirical studies (reviewed in Persson and De Roos 2006) with roach, perch, and pike in lake ecosystems in Europe have demonstrated the importance of size-structured interactions for population dynamics and community structure. Size-structured interactions also are prevalent among terrestrial arthropods. In desert scorpions, large dominant species, such as *Paruroctonus mesaensis*, often consume smaller conspecifics and experience significant mortality from cannibalism (Polis 1980). *Paruroctonus mesaensis* also cause high mortality in smaller heterospecific scorpions (Polis 1980, Polis and McCormick 1987). Thus, cannibalism by *Paruroctonus mesaensis* (IG predators) might positively affect densities of smaller scorpion species (IG prey).

Recent modeling studies have demonstrated that stage/size structure and cannibalism can influence species coexistence (Mylius et al. 2001, Rudolf 2007b). The results of my study indicate that cannibalism and size structure influence the outcome of IGP in ways that should promote coexistence based on these theoretical studies. However, the conditions in my study were much simpler than those found in most natural communities, and I addressed only the effects of IG predator size structure on IGP interactions. In natural communities, all species engaged in IGP probably are size-structured to some extent. More work must be done to further elucidate the role of size structure in predator–prey systems particularly among prey species (Rudolf 2008). Addressing the complexity that size structure adds to IGP interactions experimentally will be a challenge, but doing so will help us refine our theoretical predictions concerning the coexistence of species in these systems.

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**Literature Cited**


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