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Ontogenetic Shift in Efficacy of Antipredator Mechanisms in a Top Aquatic Predator, *Anax junius* (Odonata: Aeshnidae)

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Abstract

The ability of prey to escape predation often lies in the occurrence and efficacy of their predator avoidance and antipredator behaviors, which are often coupled with specialized morphology. How the use and efficacy of these behaviors change throughout ontogeny may be indicative of the vulnerability and ecological roles these animals experience throughout their lives. We examined the antipredator behavior of a large dragonfly nymph, *Anax junius*, from a historically fishless pond where these animals have traditionally been classified as top predators. These dragonfly nymphs displayed a series of distinct aggressive antipredator behaviors when grasped that involved stabbing with lateral and posterior spines and seizing with labial hooks. Larger (older) nymphs displayed these aggressive behaviors significantly more than smaller (younger) animals in simulated predation trials. During encounters with live larval salamander predators (*Ambystoma tigrinum*), all large nymphs, but only 12.5% of small nymphs successfully escaped predation attempts by the amphibians through the use of antipredator behavior. Large nymphs were also significantly more active than smaller nymphs in the presence of salamander larvae. Despite often being considered top predators in fishless ponds, our study demonstrates that their true role is more complex, depending on ontogeny and body size, and that effective antipredator behavior is likely necessary for survival in these systems.

Introduction

During a predatory encounter, prey experience a variety of situations that limit their ability to forage, reproduce, or otherwise contribute to enhancing fitness (Lima & Dill 1990). These interactions typically involve a series of stages that escalate in intensity, ultimately resulting in the death or escape of the prey (Endler 1986; Lima & Dill 1990). As the encounter escalates, the risk of injury to the prey increases and the probability of escape decreases.

Prey possess a host of behaviors that can be utilized during each stage of the predation event to decrease their risk of predation. These behaviors can be loosely classified as predator avoidance and antipredator behaviors (Brodie et al. 1991). Predator avoidance mechanisms are utilized before the prey enters the perceptual field of the predator and typically provide the greatest reduction in predation risk because the predatory encounter is deterred prior to the detection and identification of the prey as such. In contrast, antipredator behaviors are typically utilized after the organism has been detected and identified as prey and function to aid the prey's escape after being captured.

While predator avoidance and antipredator behaviors are important to the survival of most animals, their occurrence and efficacy may change with ontogeny (Johnson 1968; Dixon & Baker 1988; Corbet 1999; Crumrine 2006). For example, there is some evidence that behavior in dragonfly nymphs may change with developmental stage and size

(Johnson 1968; Dixon & Baker 1988; Corbet 1999; Crumrine 2006). This change may be indicative of the differing vulnerability and trophic role that some animals may experience throughout ontogeny.

In fishless aquatic ecosystems, predator–prey systems are dominated by large carnivorous invertebrates. These organisms have traditionally been classified as 'top aquatic predators' (Hopper 2001), and numerous studies have examined their ecology and behavior in this role (e.g., Hopper 2001; Crumrine 2006; Ferris & Rudolf 2007). For example, insects from the orders Coleoptera, Hemiptera, and Odonata possess voracious predatory species that can consume invertebrate or vertebrate prey larger than the predator itself (e.g., Brodie & Formanowicz 1983, 1987). These predators are particularly detrimental to small amphibians and fishes, which are often mobile, lack morphological or chemical defenses, and are present in high densities (Walker 1953; Duellman & Trueb 1986; Brodie & Formanowicz 1987). Moreover, these top predators are typically considered 'safe' in predator–prey interactions in these communities because of the absence of any large vertebrate predator (Hopper 2001).

Large, late-instar dragonfly (Odonata: Anisoptera) nymphs of the family Aeshnidae are an example of 'top predators' in fishless aquatic habitats (Walker 1953; Johnson 1991; Hopper 2001; Mikolajewski et al. 2006; Ferris & Rudolf 2007). The common green darner, *Anax junius*, is a large aeshnid, which, in its nymph stage, has traditionally been classified in this role (Crumrine 2006; Ferris & Rudolf 2007). In aquatic habitats, it is a known predator of a variety of organisms, ranging from invertebrates (Hopper 2001) to small fish (Walker 1953) and amphibian larvae (e.g., Walker 1953; Caldwell et al. 1980; Brodie & Formanowicz 1987; Skelly & Werner 1990; Petranka & Hayes 1998; Storfer & White 2004). Recent work (Crumrine 2010a,b) has described small, earlier-instar *A. junius* as cannibalistic prey of larger, late-instar nymphs. This age/size-structured intraspecific and intraguild predation can influence ecosystem dynamics and allow large and small dragonfly nymphs to fill niches as both predators and prey (Crumrine 2010a,b), respectively. Only two published studies (Godley 1980; Crumrine 2006), however, have examined *Anax junius*' role as interspecific prey in aquatic systems. Crumrine (2006) examined *A. junius*' predator avoidance behavior in response to fish. Godley (1980) reports that striped crayfish snakes (*Regina alleni*) tried to prey on *A. junius*, but were unable to swallow the nymphs because of their ability to seize the snakes with the labial hooks.

The purpose of our study was to examine the occurrence and efficacy of predator avoidance and antipredator behaviors of *Anax junius* from a fishless aquatic ecosystem, against both simulated and natural (larval salamander) predators. Although amphibian larvae have primarily been considered prey of large aeshnids (e.g., Walker 1953; Caldwell et al. 1980; Skelly & Werner 1990; Petranka & Hayes 1998; Storfer & White 2004), our study placed them in the opposite trophic position. While *A. junius* will readily eat young larval tiger salamanders (*Ambystoma tigrinum*) (Storfer & White 2004), large tiger salamander larvae are present at our study site and are likely predators to most invertebrates, including *A. junius*. To help address questions of ecological role switching and the importance of size and developmental stage, we examined large and small dragonfly nymphs to determine whether the occurrence and efficacy of this species' antipredator behaviors changed with ontogeny.

Materials and Methods

Experimental Animals

All dragonfly nymphs (*Anax junius*) used in this study were collected from a pond near Preston, Idaho, USA. Dragonfly nymphs were housed in individual 10.5-cm-diameter, 4.0-cm-deep glass bowls, with a small rock (approximately 3 cm diameter) for perching, and 200 ml of filtered tap water. These bowls were placed in an environmental chamber (17°C) with a 12-h light:12-h dark cycle. Larval tiger salamanders (*Ambystoma tigrinum*) ($\bar{x}$ mass ± SE = 16.2 ± 1.0 g; $\bar{x}$ Snout-Vent Length ± SE = 7.2 ± 0.2 cm) were caught at the same pond as the dragonfly nymphs. Each tiger salamander was housed in a plastic container (34.9 cm × 20.3 cm × 12.7 cm) with 3.5 l of filtered tap water and an aerator and kept in the same environmental chamber as the dragonfly nymphs. Dragonfly nymphs and larval salamanders were fed blackworms (*Lumbriculus variegatus*) *ad libitum* for the approximately 2 wk that elapsed between field collection and start of experiments.

Anax junius ranged from 9–13th instars. Instar was determined through measurements of head width and total length (Calvert 1934; Crumrine 2006). Dragonfly nymphs were classified as 'small' in the 9–11th instars (total N = 10: 9th instar N = 2, 10th instar N = 6, 11th instar N = 2; $\bar{x}$ head width ± SE = 5.6 ± 0.2 mm; $\bar{x}$ total length ± SE = 24 ± 1 mm), whereas 'large' nymphs were in the 12th and 13th instars (total N = 12: 12th instar N = 5, 13th instar

N = 7; x̄ head width ± SE = 7.9 ± 0.3 mm; x̄ total length ± SE = 38 ± 1 mm). A similar differentiation was used by Crumrine (2006, 2010a). Odonates in imminent stages of emergence decrease activity, and we did not use 13th-instar nymphs with swollen wing pads in our experiments (Mikolajewski & Johansson 2004).

Simulated Predation

A randomly chosen *A. junius* was placed into a plastic experimental arena (33 cm long × 18.4 cm wide × 10.8 cm high), with 0.8 cm of gravel, one small rock (diameter = 3.2 cm), and 2.0 l of filtered tap water. Animals were placed in the arena by pouring them from their holding container into the arena; animals were handled in this manner to prevent acclimation to the simulated predation event.

After a 5-min acclimation period, blunt forceps were brought toward the abdomen of the dragonfly at an angle of 45°, until the tip was next to, but not touching the animal. At this point, there was a 1- to 2-s pause to see whether the animal would flee. The forceps were then lightly brushed against the side of the animal, and a second observer noted whether *A. junius* swam away from the forceps. Lightly tapping on nymphs in this manner has been used to simulate a generic predation event (Hopper 2001). After the presence or absence of this behavior was noted, the nymph was grasped around the posterior portion of the thorax, so as to not interfere with the use of abdominal spines. The second observer recorded the sequence of antipredator behaviors exhibited by the nymph (see Results). When the animal was not immobile, these behaviors generally occurred immediately and all nymphs were grasped for <5 s. This procedure was repeated for each dragonfly nymph, and the total number of times a behavior was observed was summed for each age class. Dragonfly nymphs were tested only once and not reused for any other experiments. The occurrence of each antipredator behavior was compared among age classes using a two-tailed Fisher's exact test ($\alpha = 0.05$) in GraphPad Instat® (GraphPad Software Inc. 2003).

Natural Predators

Three days before the start of the experiment, the water in each salamander's holding container was changed. To standardize hunger level, each animal was fed 1.3 g of blackworms (all blackworms were typically consumed within 1 h). Remaining food was removed and withheld for 72 h before the predation trials began. The water in each holding container was changed 24 h prior to the commencement of trials. Food was never withheld from dragonfly nymphs.

At the start of the predation trials, a salamander was randomly selected, the aerator was removed from the container, and white plastic blinds were set up around three sides of the container to reduce visual stimuli from adjacent test containers. A dragonfly nymph was placed into the salamander's container by pouring it in without physically grasping it. The moment the nymph entered the water, a stopwatch was started, and detailed behavioral observations of the dragonfly and salamander were recorded. These included the time the dragonfly was active, the number of predatory attacks by the salamander, and the occurrence and efficacy of any antipredator behavior by nymphs. Lunges by a salamander without physical contact were distinguished from attacks that resulted in physical contact. Each trial lasted 20 min.

During the first set of trials, each salamander was randomly assigned either a small (9–11 instars, n = 5) or large (12–13 instars, n = 6) dragonfly nymph. At the conclusion of testing, all salamanders were fed bloodworms *ad libitum* for 2 d. The second set of trials was identical to the first except that the salamanders that were initially offered large dragonflies were now offered small, and vice versa, for a total of 11 predator–prey encounters per age class. Survival was treated as a binomial response variable and was compared between large and small nymphs using logistic regression ($\alpha = 0.05$) in R (R Development Core Team 2008). The amount of time small vs. large *A. junius* nymphs spent immobile vs. active in the presence of larval salamander predators was compared using an unpaired *t*-test ($\alpha = 0.05$) in GraphPad Instat® (GraphPad Software Inc. 2003).

Results

Morphological Adaptations

Anax junius possess three morphological features used to facilitate escape when attacked by a predator: lateral spines, posterior spines, and labial hooks. The lateral spines are rearward facing acute projections located on the lateral portions of abdominal segments 7, 8, and 9 (Fig. 1A). The posterior spines are lance-like projections composed of the epiproct and two paraprocts (Fig. 1B,C). A smaller posterior spine (modified cerci) is located immediately dorsal

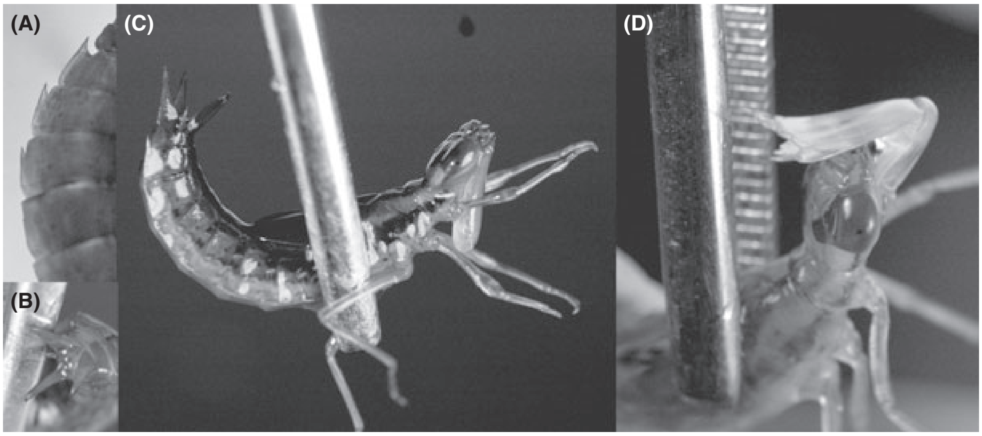

Fig. 1: Morphological antipredator adaptations of *Anax junius* nymphs. (A) Close-up view of 'lateral spines' on the 7th, 8th, and 9th abdominal segments. (B,C) Epiproct, paraprocts, and cerci spread to form the 'posterior spines' that are arched dorsally toward the simulated predator (forceps). (D) The labium is projected backwards over the head, toward the simulated predator (forceps), with biting grasping hooks outstretched. The hooks gripped onto (bit) the forceps moments after this photograph was taken.

to each paraproct (Fig. 1B,C). The posterior spines are located on the posterior portion of abdominal segment 10. When grasped by a predator, the posterior spines are spread apart forming a triangle, increasing the effective area of the spines. The final morphological adaptation is typically used in food capture, but also functions as an antipredator mechanism. The labium in aeshnids is folded and can be projected forward to capture prey. Two hinged palpal lobes are located at the anterior end of the labium and terminate in movable labial hooks (Fig. 1D).

Antipredator Sequence

The antipredator mechanisms of *A. junius* to both simulated and natural predators consisted of a sequence of behavior that progressively increased in aggressive magnitude (Fig. 2). After being captured, these behaviors typically occurred in succession until either (1) a behavior succeeded in gaining release of the *A. junius* or (2) no single behavior resulted in release and all behaviors were utilized collectively.

When approached, or more often touched by a predator, *A. junius* often responded by 'jetting' away from the stimulus (Table 1, Fig. 2). *Anax* store water in a specialized chamber inside the rectum. By rapidly contracting the muscles surrounding the chamber, nymphs eject the water out the anus producing forward momentum at 10 cm/s (Mill & Pickard 1975).

After an *A. junius* was physically restrained by a predator (or grasped by forceps), three mechanisms were used to facilitate escape (Fig. 2). When grasped on the thorax, *A. junius* flexed the abdomen beginning with the first abdominal segment and wrapped the abdomen toward the predator. The three lateral spines on abdominal segments 7, 8, and 9 were then forced into the predator (Stage 1, Fig. 1A). If the lateral spines were unsuccessful in procuring release, the nymph immediately positioned the abdomen such that one or more of the posterior spines struck the predator (Stage 2, Fig. 1B,C). Although stage two often occurs immediately after stage one, nymphs may forgo striking with lateral spines and immediately utilize the posterior spines. *Anax junius* nymphs can rotate the abdomen 360° to strike a predator holding them by the thorax (Fig. 1C). If the previous two mechanisms failed to result in the release of the nymph, the head was positioned toward the predator. The nymph then struck by extending the labium and imbedding the labial hooks into the predator (Stage 3, Fig. 1D). The head is less flexible than the abdomen and many unsuccessful strikes may occur before contact with the predator. When a strike was successful, nymphs often continued grasping the predator until released.

If all three of these behaviors failed to facilitate release, the nymph repeatedly performed all three

Table 1: Percent of small (9–11th instars) and large (12–13th instars) *Anax junius* nymphs exhibiting different behavioral responses to simulated attack with large forceps

Behavior	% Small (n = 10)	% Large (n = 12)
Swam	50	41.7
Lateral spines	40	91.7
Posterior spines	40	91.7
Grasp	40	91.7
Immobile	60	8.3

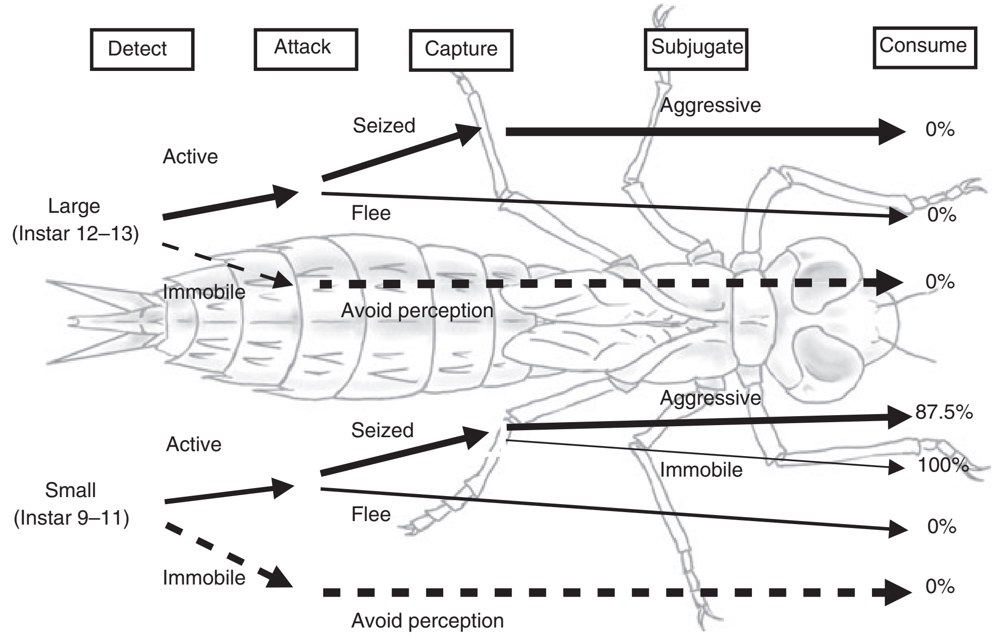

Fig. 2: Behavioral flowchart showing interactions between small (9–11th instars) and large (12–13th instars) *Anax junius* nymphs and tiger salamander larvae (*Ambystoma tigrinum*) and their result. The headings in boxes indicate the five stages of a typical predator–prey encounter as outlined by Endler (1986) and Lima & Dill (1990), and the actions of the prey dragonfly nymphs corresponding to each stage are found below. Solid arrows indicate antipredator behavior by nymphs, and dashed arrows indicate predator avoidance behavior. Thickness of arrows is indicative of the percent of animals exhibiting each behavior in each stage of attack. Illustration of nymph in background by Bronwyn McIvor.

behaviors until it was released or apparently reached exhaustion. There was typically little delay between the use of lateral and posterior spines. There may, however, be a short delay between the use of posterior spines and seizing with the labial hooks. If a nymph successfully seized the predator, but was not released, the other two mechanisms may be simultaneously and continuously utilized until released.

Simulated Predation

Anax junius nymphs exhibited all aspects of antipredator behavior when grasped with forceps, although there was a significant difference in the occurrence of each behavior among age classes (p = 0.02, Fisher's exact test; Table 1). Nearly all (91.7%) large dragonfly nymphs performed the full sequence of aggressive antipredator behaviors (as described earlier), with one individual remaining immobile when grasped (Fig. 3). In contrast, only 40% of small nymphs performed the full sequence of antipredator behavior, with the majority remaining immobile (Fig. 3).

Natural Predators

Nine of 11 large and all eleven small *A. junius* nymphs were lunged at by salamanders (Table 2, Fig. 2). All attacks by salamanders occurred when the nymphs were moving. When nymphs were lunged at but not grasped, all individuals jetted away. Of the dragonflies that were lunged at, sala-

Table 2: Results of behavioral interactions between *Anax junius* nymphs (small = 9–11th instars; large = 12–13th instars) and larval tiger salamanders (*Ambystoma tigrinum*) in predation trials

	Small (n = 11)	% Small	Large (n = 11)	% Large
Lunged at	11	100.0	9	81.8
Seized	8	72.7	8	72.7
Antipredator behavior when seized	7	87.5	8	100.0
Immobile when seized	1	12.5	0	0.0
Survived when seized	1	12.5	8	100.0
Consumed	7	87.5	0	0.0
% Time immobile ($\bar{x}$ ± SE)	60.56 (±7.6)		19.42 (±7.4)	
% Time moving ($\bar{x}$ ± SE)	39.44 (±7.6)		80.58 (±7.4)	

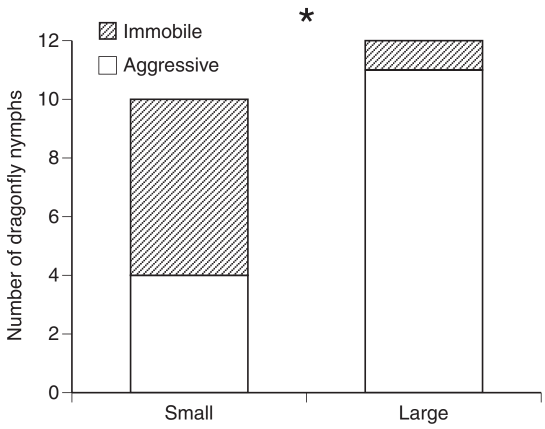

Fig. 3: The number of small (9–11th instars; n = 10) and large (12–13th instars; n = 12) *Anax junius* dragonfly nymphs exhibiting the suite of aggressive antipredator behaviors (open area) (stabbing with the lateral and posterior spines and biting) vs. remaining immobile (shaded area) when grasped by forceps in simulated predation trials. Asterisk denote a significant difference between occurrence of aggressive behavior between small and large nymphs ($p < 0.05$).

manders physically grasped eight nymphs in each age class (Table 2, Fig. 2).

All of the large *A. junius* nymphs and 87.5% of the small nymphs grasped by predators exhibited the antipredator response as described earlier (one small individual remained immobile when grasped; Table 2, Fig. 2).

One hundred percent of large dragonfly nymphs survived the predation trials, which is significantly more than small nymphs ($F_{21,20} = 14.4$, $p < 0.0001$).

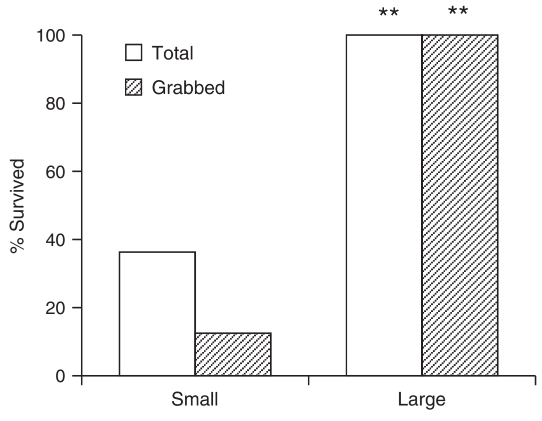

Fig. 4: Percentage (%) of small (9–11th instars) and large (12–13th instars) *Anax junius* nymphs that survived predation trials with tiger salamander larvae (*Ambystoma tigrinum*). Open bars indicate the total percentage that survived trials, and shaded bars indicate the percentage of individuals that survived that were physically grasped by salamander predators. Asterisks denote significant differences in survival between small and large nymphs ($p < 0.001$).

All of the large dragonfly nymphs attacked and grasped by salamanders survived the predation encounter by utilizing antipredator behavior (Table 2; Figs 2 and 4). Small nymphs had a 12.5% survival rate when grasped by salamanders, despite 87.5% of these animals performing antipredator behavior (Table 2; Figs 2 and 4), which was significantly less than the survival rate of large nymphs that were grasped ($F_{15,14} = 6.03$, $p < 0.0001$). Salamanders consumed the majority of small nymphs after the initial attack. One small nymph survived the initial attack but was consumed on the second attack. While 36.6% of small nymphs survived the trials (Figs 2 and 4), most of these animals exhibited reduced mobility and were never physically grasped by salamanders. Small nymphs remained immobile significantly longer on average (60.6 ± 7.6% of the 20-min trial) than large nymphs (19.4 ± 7.4% of the 20-min trial) ($t_{20} = 3.22$, $p = 0.004$, Table 2, Fig. 2).

Discussion

Anax junius nymphs, a top predator in fishless aquatic environments (Crumrine 2006; Ferris & Rudolf 2007), exhibited distinct antipredator behaviors when threatened by both artificial (forceps) and natural (salamander) predators. Nymphs jetted away when approached. If seized by the predator, they rotated their abdomen to stab the predator with their lateral and posterior spines and seize it with their labial hooks. In addition, to avoid detection by predators, some nymphs reduced their activity and remained immobile in the presence of predators. While all of these strategies have been reported for a variety of odonate nymphs, most literature has focused on small dragonfly species and predator avoidance (Peckarsky 1982; Dixon & Baker 1988; Corbet 1999; Wohlfahrt et al. 2006; Ferris & Rudolf 2007). This approach has helped categorize larger dragonfly species as predators in fishless aquatic systems. Nevertheless, these 'top predators' possess and utilize a suite of antipredator behavior that can be extremely effective at deterring predation.

Every predator–prey encounter involves several basic steps: detection, attack, capture, subjugation, and consumption (Endler 1986; Lima & Dill 1990; Fig. 2). Potential prey can take actions to prevent predation at each of these stages, yet previous studies of predatory encounters with odonates have primarily focused on strategies used to avoid the detection and identification (stages 1–2), as opposed to antipredator behavior (stages 3–5) (dashed vs. solid lines in Fig. 2) (Peckarsky 1982; Dixon & Baker

1988; Corbet 1999; Wohlfahrt et al. 2006; Ferris & Rudolf 2007). Decreasing activity level in the vicinity of predators, as was observed in small nymphs in our study, is a successful predator avoidance mechanism because the probability of being detected decreases, and thus a predation encounter never takes place (Brodie et al. 1991; Wohlfahrt et al. 2006). Amphibians are predominantly visual hunting predators that respond to movement of prey (Freed 1980), and attacks on both size classes of *A. junius* nymphs in this study occurred only when the nymphs were moving. On the other hand, reducing activity level in response to predator presence can also reduce foraging, and this could have fitness costs in reduced growth and rate of development (Dixon & Baker 1988; Lima & Dill 1990).

When predator avoidance and escape behavior (i.e., jetting away or fleeing) are unsuccessful in escaping capture, prey typically rely on antipredator behaviors that are coupled with morphological defenses (Mikolajewski & Johansson 2004). The presence and length of abdominal spines in odonate nymphs have been demonstrated to be enhanced by fish predation (Johansson & Samuelsson 1994; Mikolajewski & Rolff 2004) and may be lost in fishless systems with heavy invertebrate predation (Mikolajewski et al. 2006). These results are interesting to note in light of our study, where the presence of spines seems to be necessary for survival in a historically fishless ecosystem when large amphibian predators are present. In addition, where others have found the backward-facing spines of odonate nymphs to be effective only when attacked from behind (Mikolajewski & Rolff 2004), *Anax junius* in our study were able to twist and wrap their abdomen forward, allowing for protection from a predatory attack in most directions. *Anax junius* nymphs also seized attacking salamander larvae with their labial hooks, an antipredator behavior that has been reported to be effective against foraging striped crayfish snakes (Godley 1980). The antipredator use of the labium is arguably more risky, however, as the labium is an essential feeding adaptation (Corbet 1999). Risking damage to the labium should be used as a last resort, as our results indicate.

In large *A. junius* nymphs, the use of distinctive aggressive antipredator behaviors proved 100% effective against larval salamander predators, but this was certainly not the case for small nymphs. The majority (87.5%) of small nymphs displayed the aggressive antipredator behaviors when grasped by salamanders; however, only one individual (an 11th instar) survived the encounter by using these behaviors. The use of antipredator behaviors is energetically costly and should be used only when reliably effective (Dixon & Baker 1988; Johansson & Samuelsson 1994; Ferris & Rudolf 2007); this may explain the lack of preference of aggressive behavior over immobility in simulated predation trials with small nymphs (Fig. 3). In light of these results showing a stark difference in survival between large and small nymphs when in physical contact with a predator, it would thus seem logical that small nymphs try to avoid detection by predators significantly more than large nymphs, and this is indeed what we found. Small nymphs were significantly less active than large nymphs, which correspond to previous work (Crumrine 2006, 2010a). These results showing an ontogenetic shift in efficacy of antipredator mechanisms in *Anax junius* also represent an ontogenetic niche shift from prey to predator in fishless aquatic environments. This ontogenetic niche shift has been demonstrated before in an intraguild setting with *Anax junius* (Crumrine 2010a,b), but not to our knowledge in any interspecific relationships. Interspecific niche shifts have been shown to have profound ecological consequences with other organisms in piscivorous environments (e.g., Olson 1996), and our results open the door for future work on possible community-level effects in fishless habitats.

In historically fishless systems where large, late-instar dragonfly nymphs are thought of as 'top predators,' these animals retain antipredator behavior and associated morphological adaptations that are effective at repulsing attackers during a predation event. The nature and efficacy of these behaviors change with ontogeny, allowing *Anax junius* to succeed in environments where it plays a dynamic role as both predator and prey.

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