

# Macroinvertebrate Foraging on Larval *Ambystoma maculatum* across Ontogeny

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**Understanding community interactions, such as predator–prey dynamics, is vital for determining species viability. Outside of larger macroinvertebrate predators, such as crayfish and dragonfly larvae, there is a paucity of information regarding the effectiveness of other macroinvertebrate predators in consuming larval amphibians, especially caudate larvae, during aquatic life-stages within pond communities. In this study, we tested the ability of a suite of macroinvertebrate predators to consume Spotted Salamander larvae (*Ambystoma maculatum*) at two points during larval development. We tested the ability of macroinvertebrate predators belonging to the genera *Belostoma*, *Lestes*, *Notonecta*, and *Ranatra*, the families Aeshnidae, Dytiscidae, Gomphidae, Gyrinidae, Hirudinae, Libellulidae, and Notonectidae, or order Trichoptera, as well as larvae of *Rana clamitans*, to consume *A. maculatum* immediately after hatching and several weeks into their larval period across four separate experiments. We tested for significant differences in percent survival of *A. maculatum* among predator treatments using ANOVA. Across all trials, we found a significant effect of predator treatment. Both hatchling and larval *A. maculatum* were susceptible to predation by Aeshnidae and Notonectidae. In all other treatments, we observed low or zero mortality of hatchlings of *A. maculatum* and 100% survival of larvae of *A. maculatum*. As Aeshnidae and Notonectidae are both gape unconstrained predators, the increase in larval size did not appear to increase survival of *A. maculatum* due to increased escape performance. Overall, rates of predation are low for *A. maculatum* for most macroinvertebrates during the tested life stages, suggesting that predation by only a handful of invertebrate taxa and vertebrates contribute to high mortality rates within this system.**

UNDERSTANDING food web dynamics is vital for determining species persistence and viability. Deconstructing how these dynamics function in species-rich communities can be difficult, however, because of the myriad of interaction types (e.g., competition, predation) and strengths that occur within them (Preston et al., 2018). Interaction strengths or types can also change through time as ontogeny proceeds (Yang and Rudolf, 2010). Therefore, developing baseline information on how, whether, or when species interact can help develop a greater understanding of the role of species interactions in structuring community patterns.

Freshwater ponds are taxonomically diverse ecosystems, consisting of numerous vertebrate and invertebrate species that require water for one or more life stages (Wellborn et al., 1996; Wilbur, 1997; Urban, 2004). Amphibians in particular exploit these ecosystems, using ponds for reproduction and subsequent larval development (Wells, 2007). While several factors can influence community structure and demographic rates of amphibians, predation has been repeatedly identified as an important factor for both aspects of this ecosystem (Relyea, 2007). Much of the extensive work on predator–prey dynamics with amphibians has focused on a select group of taxa which are known have strong effects on the community (Relyea, 2007). For example, numerous types of fishes strongly limit recruitment and influence breeding efforts of amphibians (Hecnar and M'Closkey, 1997; Boone et al., 2007; Shulse et al., 2013). In addition, several macroinvertebrates, including larval odonates (e.g., *Anax* or *Tramea*) and coleopterans (e.g., *Dytiscus*), also induce strong consumptive and non-consumptive predatory effects on larval amphibians (Van Buskirk, 1988; McCollum and Leimberger, 1997; Urban, 2007; Davenport et al., 2014).

There are numerous other, less well-studied, macroinvertebrates that are secondary consumers in ponds that co-occur with larval amphibians, encompassing several taxonomic orders (Schneider and Frost, 1996; Urban, 2004). Several of these taxa have been reported to prey on larval amphibians, including crayfishes (Decapoda; Gamradt and Kats, 1996), giant water bugs (Belostomatidae; Formanowicz and Brodie, 1982; Babbitt and Jordan, 1996; McCoy et al., 2011), and backswimmers (Notonectidae; Ramos and Van Buskirk, 2012). However, anuran tadpoles have been the focal prey group studied, leaving ambiguity as to whether aquatic stages of pond-breeding salamanders (Ambystomatidae) are equally susceptible to these and other predators. Although an array of invertebrates are documented predators of caudate eggs (reviewed in Gunzburger and Travis, 2005), the only invertebrates documented to consume caudate larvae are larval Aeshnidae (Davenport and Chalcraft, 2012; Anderson and Semlitsch, 2016), caddisfly (Trichoptera) larvae (Rowe et al., 1994), crayfishes (Decapoda; Gamradt and Kats, 1996), and dytiscid beetle larvae (Urban, 2010). Furthermore, many predaceous macroinvertebrates, such as water scorpions (Nepidae) or damselfly larvae (*Lestes*), have received little attention at all in their ability to consume caudate larvae. Therefore, a systematic test of the foraging abilities of different macroinvertebrates on aquatic stages of caudates is needed to understand whether they suffer similar mortality rates to more commonly studied anuran tadpoles. Such information would be particularly valuable to derive empirically based predation risk indices in ponds, similar to Van Buskirk (2005), for each amphibian group.

In this study, we tested whether a variety of predatory macroinvertebrate taxa, as well as one vertebrate predator, could consume larval Spotted Salamanders (*Ambystoma maculatum*). We specifically tested whether consumption

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rates differed at two ontogenetic time points during the larval stage, right after hatching and several weeks into the larval period. We predicted that predators that readily consume anuran tadpoles (e.g., Aeshnidae, Belostomatidae, and Notonectidae) would also inflict strong mortality on larval salamanders.

## MATERIALS AND METHODS

**Study species.**—*Ambystoma maculatum* is a widely distributed species throughout the Eastern United States and Canada (Savage and Zamudio, 2005). It has aquatic egg and larval stages, and terrestrial juvenile and adult life stages (Savage and Zamudio, 2005). Breeding in Missouri, where this study occurred, typically occurs from February–April, and metamorphosis occurs from June–October (Semlitsch and Anderson, 2016). Several predators of the larval stage have been documented, including other ambystomatids, Red-Spotted Newts, aeshnid dragonfly larvae, caddisfly larvae, and dytiscid beetle larvae (Rowe et al., 1994; Urban, 2007; Drake et al., 2014; Anderson et al., 2016).

**2017 hatchling and larval predation trials.**—We collected late-stage egg masses of *A. maculatum* from Fort Leonard Wood Military Training Facility in Pulaski County, Missouri, USA on 30 March 2017 and reared hatchlings in approved animal care facilities at the University of Missouri in Columbia, Missouri, USA. We collected macroinvertebrate predators on 9 April 2017 from the University of Missouri's Baskett Research Center in Boone County, Missouri, USA. The taxa used as macroinvertebrate predators belonged to the genera *Belostoma*, *Notonecta*, *Ranatra*, or the families Dytiscidae, Gomphidae, Gyrinidae, and Libellulidae. After collection, all predators were housed individually and starved for three days prior to each trial.

We conducted all trials within a temperature- and humidity-controlled animal care space (12–15°C; 30–50% RH) and a 12:12 light:dark cycle. Our arenas were 38 L glass aquaria filled with 19 L of dechlorinated water to which we added Prime<sup>®</sup> water conditioner (Seachem Laboratories, Madison, GA) to remove chloramine. To minimize the influence of outside stimuli, we covered the sides with blinders. Further, we added six strips of gray window screen (20 × 5 cm; 1.6 mm pore size) in the shape of bowties, as described by Drake et al. (2014), to be used as cover for the salamander larvae and perches for “sit and wait” predators.

To assess whether the tested suite of macroinvertebrate predators could consume *A. maculatum* across their ontogeny, we conducted predation experiments at three days and three weeks post-hatching. All three-week post-hatching larvae were reared in outdoor mesocosms (114 L, 76 cm diameter, polyethylene watering tank). We established mesocosms on 1 April 2017 by adding dechlorinated tap water, 0.30 kg deciduous leaf litter, and zooplankton. We added hatchlings to mesocosms on 14 April 2017 and recaptured them on 29 April 2017 for use in the larval trial.

We conducted the hatchling trial on 12 April 2017. We randomly assigned predator and no predation (control) treatments ( $n = 4$ ) to each of 51 aquaria. Predator treatments were *Belostoma* ( $n = 5$  replicates), *Notonecta* ( $n = 7$ ), *Ranatra* ( $n = 7$ ), Dytiscidae ( $n = 7$ ), Gomphidae ( $n = 7$ ), Gyrinidae ( $n = 7$ ), and Libellulidae ( $n = 7$ ). Predators were not measured during these trials. We added 12 hatchlings (total length [TL] =  $15.3 \pm 1.72$  mm [mean  $\pm$  SD]) per aquarium and allowed them

to acclimate for one hour prior to predator addition. We counted the number of hatchlings remaining at 24 hours to determine survival for each macroinvertebrate predator treatment.

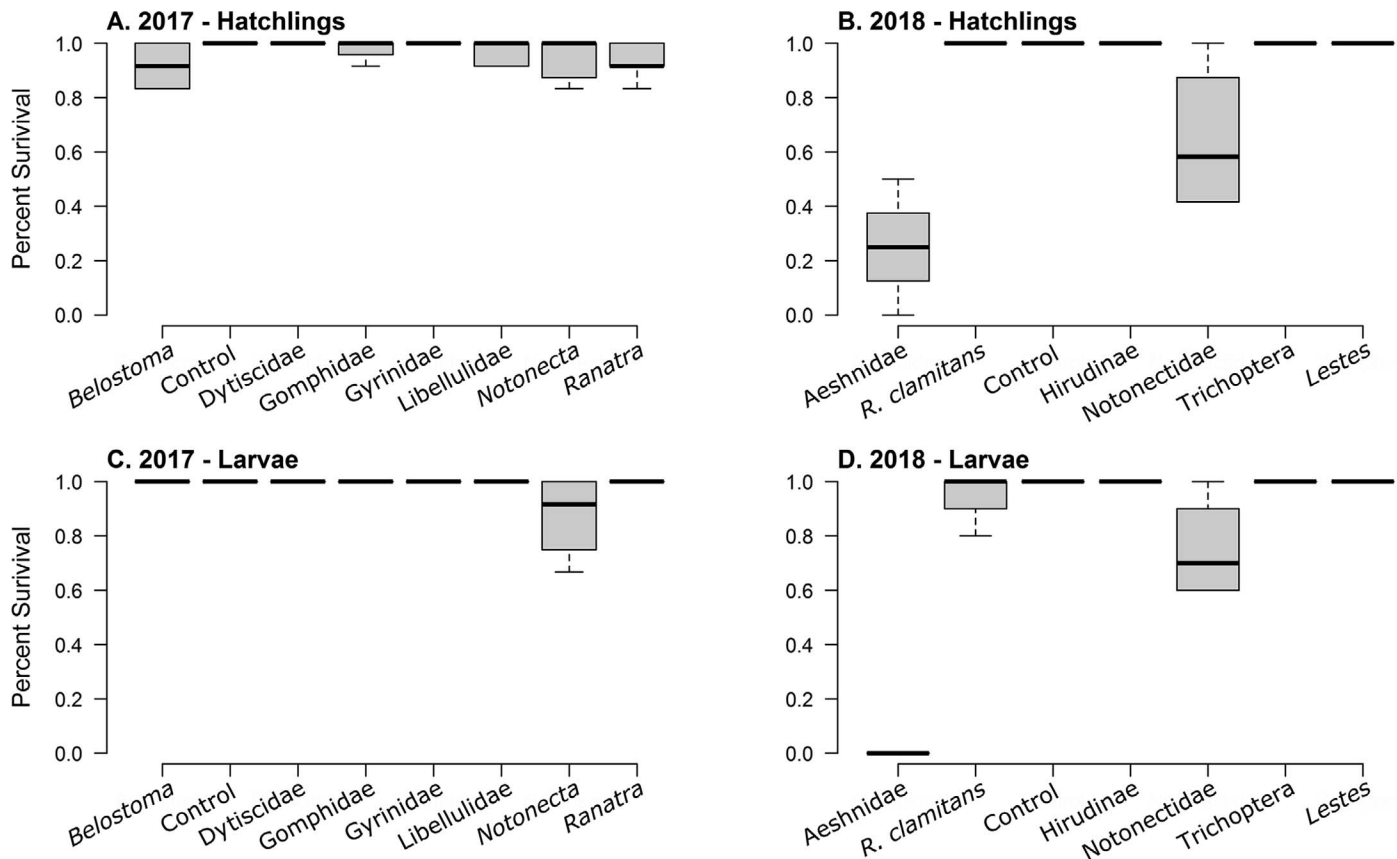
The larval trial commenced on 30 April 2017. This trial included two tanks acting as experimental controls and four replicates of each predator treatment outlined above for a total of 30 aquaria. Six larvae (TL =  $27.6 \pm 3.16$  mm) were randomly assigned to each tank and given one hour to acclimate before adding the predators. The number of surviving larvae were counted at 48 hours to determine survival for each treatment instead of 24 hours because of low consumption rates.

**2018 hatchling and larval predation trials.**—We conducted this set of predation trials in the same room and under the same environmental conditions as the 2017 trials. However, we used plastic containers (30 × 20 × 12 cm) instead of aquaria as the experimental chamber. As in previous trials, we placed blinders around all containers to minimize the influence of outside stimuli, filled with dechlorinated water, and used Prime<sup>®</sup> water conditioner as an amendment to remove chloramine.

We collected eggs of *A. maculatum* from Baskett Wildlife Research Area on 28 March 2018 and hatched them in the lab. The predator treatments in these trials included adult Notonectidae (TL =  $11.2 \pm 0.39$  mm) and Hirudinae (no size data available), as well as larval Aeshnidae (TL =  $39.7 \pm 4.69$  mm), *Lestes* sp. (TL =  $27.4 \pm 2.53$  mm), *Rana clamitans* (TL =  $66.1 \pm 3.87$  mm), and Trichoptera (TL =  $38.4 \pm 3.73$  mm). We had four replicates of each predator treatment. We also had four replicates of a no predation (control) treatment. We added the remaining hatchlings to the same 114 L outdoor mesocosms used for the previous year's experiment that had been filled with water, leaf litter, algae, and zooplankton several weeks prior, where they remained prior to being used in the larval trials.

We added 12 hatchlings of *A. maculatum* (TL =  $13.2 \pm 1.30$  mm) and collected predators on 11 April 2018. We housed predators individually overnight to standardize hunger levels and added them on 12 April 2018. Predator sizes were as follows: adult Notonectidae (TL =  $12.4 \pm 1.33$  mm) and Hirudinae (no size data available), as well as larval Aeshnidae (TL =  $56.5 \pm 1.85$  mm), *Lestes* sp. (TL =  $34.5 \pm 0.37$  mm), *Rana clamitans* (TL =  $81.4 \pm 7.14$  mm), and Trichoptera (TL =  $37.0 \pm 3.44$  mm). For the larval trials, we used five larvae (TL =  $20.4 \pm 2.28$  mm) per container. Larvae were removed from mesocosms and added to the trial arenas on 12 May 2018 to acclimate before predators were added on 13 May 2018 after a 24-hour period to standardize hunger. We counted the number of hatchlings or larvae remaining after 48 hours to determine survival for each predator treatment.

**Statistical analyses.**—We analyzed logit-transformed percent survival of *A. maculatum* (Warton and Hui, 2010) and analyzed whether there were treatment differences using ANOVA in R v3.5.2 (R Core Team, 2018). If the predator escaped the trial arena during the study period, as occurred once with Hirudinae, the replicate was dropped from our analyses. If the overall *F*-statistic was significant, we then investigated which treatments were different using Tukey's pairwise comparisons, adjusted for the overall number of comparisons. We conducted separate analyses for each life stage and year because of the methodological differences between each set up.



**Fig. 1.** Percent survival of *A. maculatum* after all four predation trials in 2017 (A, C) and 2018 (B, D). There was a significant effect of predator treatment on percent survival of *A. maculatum* across all trials. Percent survival was significantly lower in the Notonectidae treatments of the 2017 larval trials (C) as well as in the Aeshnidae and Notonectidae treatments of the 2018 hatchling (B) and larval (D) trials. Black lines indicate the median, the box extends to the first and third quartiles, and the error bars extend to the minimum and maximum data limits.

## RESULTS

**2017 hatchling and larval predation trials.**—In the hatchling trial, there was a significant effect of predator treatment on survival of *A. maculatum* ( $F_{7,43} = 2.532$ ,  $P = 0.040$ ; Fig. 1A). Over the 24-hour trial period, average survival of *A. maculatum* was high across all treatments (Table 1).

In the larval trial, there was a significant effect of predator treatment on survival of *A. maculatum* ( $F_{7,22} = 2.588$ ,  $P = 0.042$ ; Fig. 1C). Over the 48-hour trial period, survival of *A. maculatum* was 100.0% in all treatments except *Notonecta* where average survival of *A. maculatum* was 87.5% (Table 1).

**2018 hatchling and larval predation trials.**—In the hatchling trial, there was a significant effect of predator treatment on survival of *A. maculatum* ( $F_{6,21} = 19.07$ ,  $P < 0.001$ ; Fig. 1B). Across all treatments, average survival of *A. maculatum* over the 48-hour trial period was 100.0% in all treatments except for Aeshnidae (25.0%) and Notonectidae (64.6%; Table 1). When looking at pairwise contrasts, survival was significantly lower in the Aeshnidae and Notonectidae treatments than in all other treatments, and survival in Aeshnidae treatments was significantly lower than in the Notonectidae treatments (Fig. 1B).

In the larval trial, there was a significant effect of predator treatment on survival of *A. maculatum* ( $F_{6,21} = 54.401$ ,  $P < 0.001$ ; Fig. 1D). Over the 48-hour trial period, average survival of *A. maculatum* was 100.0% in all trials except for *Rana clamitans* (95.0%), Notonectidae (75.0%), and Aeshnidae (0.0%). As with the hatchling trial, survival of *A.*

*maculatum* was significantly lower in the Aeshnidae and Notonectidae treatments than in all other predator treatments, with survival being significantly lower in Aeshnidae treatment than in Notonectidae treatment (Table 1).

## DISCUSSION

Amphibians co-occur with numerous invertebrate and vertebrate taxa in pond ecosystems, many of which are predators of their larval stages. Many of these predators have only been identified to consume larval anurans, but they were previously unknown in their ability to eat larval salamanders. We tested whether a large suite of common vertebrate and macroinvertebrate predators can consume larval *A. maculatum* at two different ontogenetic stages, hatchlings or larvae. Overall, we found that many of these macroinvertebrates have very low consumption rates of either life stage or did not prey on them at all (Fig. 1). The only predators we observed to readily consume *A. maculatum* were Notonectidae and Aeshnidae, both of which have been identified as major predators of anurans. These findings have important implications for studies of pond community structure, as our results help define predatory threats to larval salamanders across ontogeny.

Both hatchling and later-stage larval *A. maculatum* were susceptible to predation by species of Notonectidae and Aeshnidae, but the two predators used different tactics to capture their prey. Aeshnidae have a stiff, grasping mouth part (labium) that helps them subdue large prey prior to consuming them. This permitted Aeshnidae to capture and

**Table 1.** Summary of the remaining *Ambystoma maculatum* at the conclusion of each trial period by macroinvertebrate predator treatment.

Treatment	Mean	S.D.	Median	Min	Max	Initial #	Survival	Replicates
A) Trial 1—2017 hatchlings								
Control	12.00	0.00	12.00	12	12	12	100.0%	4
<i>Belostoma</i>	11.00	1.00	11.00	10	12	12	91.7%	5
Dytiscidae	12.00	0.00	12.00	12	12	12	100.0%	7
Gomphidae	11.71	0.49	12.00	11	12	12	97.6%	7
Gyrinidae	12.00	0.00	12.00	12	12	12	100.0%	7
Libellulidae	11.57	0.53	12.00	11	12	12	96.4%	7
<i>Notonecta</i>	11.29	0.95	12.00	10	12	12	94.0%	7
<i>Ranatra</i>	11.29	0.76	11.00	10	12	12	94.0%	7
B) Trial 2—2017 larvae								
Control	6.00	0.00	6.00	6	6	6	100.0%	2
<i>Belostoma</i>	6.00	0.00	6.00	6	6	6	100.0%	4
Dytiscidae	6.00	0.00	6.00	6	6	6	100.0%	4
Gomphidae	6.00	0.00	6.00	6	6	6	100.0%	4
Gyrinidae	6.00	0.00	6.00	6	6	6	100.0%	4
Libellulidae	6.00	0.00	6.00	6	6	6	100.0%	4
<i>Notonecta</i>	5.25	0.96	5.50	4	6	6	87.5%	4
<i>Ranatra</i>	6.00	0.00	6.00	6	6	6	100.0%	4
C) Trial 3—2018 hatchlings								
Control	12.00	0.00	12.00	12	12	12	100.0%	5
Aeshnidae	3.00	2.45	3.00	0	6	12	25.0%	4
<i>R. clamitans</i>	12.00	0.00	12.00	12	12	12	100.0%	4
Hirudinae	12.00	0.00	12.00	12	12	12	100.0%	3
Notonectidae	7.75	3.40	7.00	5	12	12	64.6%	4
Trichoptera	12.00	0.00	12.00	12	12	12	100.0%	4
<i>Lestes</i>	12.00	0.00	12.00	12	12	12	100.0%	4
D) Trial 4—2018 larvae								
Control	5.00	0.00	5.00	5	5	5	100.0%	5
Aeshnidae	0.00	0.00	0.00	0	0	5	0.00%	4
<i>R. clamitans</i>	4.75	0.50	5.00	4	5	5	95.0%	4
Hirudinae	5.00	0.00	5.00	5	5	5	100.0%	3
Notonectidae	3.75	0.96	3.50	3	5	5	75.0%	4
Trichoptera	5.00	0.00	5.00	5	5	5	100.0%	4
<i>Lestes</i>	5.00	0.00	5.00	5	5	5	100.0%	4

consume even three-week old larvae of *A. maculatum*. In contrast, Notonectidae have a piercing mouth part (proboscis) that they used to stab *A. maculatum*, and extract body fluids, another strategy that is not reliant on body size differences. This method was evident, as the carcasses of consumed individuals remained in the container bottom after they were eaten. Both foraging tactics do not rely on gape limitation, which may explain why increases in larval body size did not increase survival rates, despite larger sizes increasing escape abilities (Landberg and Azizi, 2010).

The remaining potential predators had low consumption rates of *A. maculatum* (non-aeshnid dragonflies, *Belostoma*, *Ranatra*) or did not eat them at all (Gyrinidae, Hirudinae, *Lestes* sp., *R. clamitans*, Trichoptera); all mortality within these predator treatments occurred at the hatchling stage. Either these predators do not typically consume larvae, or have difficulty capturing them, despite some of them being documented as anuran predators (e.g., *Belostoma*; Formanowicz and Brodie, 1982; Babbitt and Jordan, 1996; McCoy et al., 2011). There may be functional differences in escape response behavior or abilities between anuran tadpoles and salamander larvae that leave each group more or less susceptible to predators, which could be related to morphology and/or ontogeny (Landberg and Azizi, 2010). The size of the tail relative to the body in hatchling salamanders is larger than hatchling anurans, which may aid their ability to avoid

predators. However, larger, older tadpoles and larvae in many species exhibit plasticity in tail shape that aids in escaping predators (McCullum and Leimberger, 1997; Van Buskirk et al., 2003; Davenport and Chalcraft, 2013; Shaffery and Relyea, 2015).

We only recorded *ad hoc* behavioral observations as to how predators were foraging which was typically after prey were captured. *Belostoma* has been noted as a strong predator of anuran tadpoles (Formanowicz, 1982; Babbitt and Jordan, 1996; Relyea, 2001; McCoy et al., 2011), but we did not observe similar results here. Some individuals within Hirudinae climbed out of the containers, and thus assessment of their impacts was limited in this study. The non-aeshnid dragonflies killed hatchlings at low levels and never consumed the entire hatchling; when mortality occurred, either the tail or head of a hatchling remained in the tank. Although *Ranatra* did not appear to eat hatchlings, they caused mortality through handling which resulted in larvae being left dead and contorted into a zig-zag shape. Thus, the apparent lack of consumption by *Ranatra* may have been a result of handling difficulties rather than lack of palatability. Finally, we observed one instance of mortality within a replicate of the *Rana clamitans* treatment during the 2018 larval trials. Given that *Rana clamitans* was not previously documented as an amphibian predator and we observed a corpulent *A. maculatum* that was of a larger body size than

other larvae within this replicate, it is likely that the mortality within this treatment was actually an incidence of cannibalism in *A. maculatum* rather than predation by *Rana clamitans*. Thus, cannibalism could be an additional, albeit minor, source of mortality.

Larvae typically show exponential mortality over the course of the larval period in ponds, with very few survivors relative to reproductive effort (<1%, Shoop, 1974; Semlitsch et al., 2014; Semlitsch and Anderson, 2016). A large component of this mortality is often attributed to predation by the numerous invertebrate and vertebrate predators found within these communities (Relyea, 2007). Based on our results, however, it seems likely that only a handful of invertebrate species contribute to these mortality patterns. Although this study focused on pond communities from Missouri and community composition of predators is variable throughout the range of *A. maculatum*, our study suggests that few macroinvertebrates may function as predators of larval *A. maculatum*. Additionally, differences in predator densities may also play a role in determining their relative impacts: adults of Notonectidae may have a lower consumption rate than larval Aeshnidae but could inflict greater total mortality due to higher relative densities, which we observe in ponds in Missouri (unpubl. data). Vertebrate predators, including other salamanders, may play a larger role as predators than invertebrates (Cortwright and Nelson, 1990; Anderson et al., 2016). As such, these data suggest that, barring a handful of invertebrate taxa, less importance can be placed on many invertebrate taxa when developing predation risk indices (Van Buskirk, 2005) or estimating factors that influence abundance and/or occupancy of salamanders.

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