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Life Cycle Complexity Influences Intraguild Predation and Cannibalism in Pond Communities

Thomas L. Anderson[1,2], Cy L. Mott[3], Todd D. Levine[2,4,5], and Howard H. Whiteman[2,6]

Predation risk is an important contributor to community structure that varies in response to abiotic and biotic factors. In aquatic habitats, predation risk is often linked to hydroperiod as the latter directly influences predator identity within these ecosystems. For pond-breeding salamanders, intraguild predation (IGP) and cannibalism are prevalent interactions in larval communities, but the frequency of each type of agonistic interaction, as well as changes in their pervasiveness along hydroperiod gradients are not well understood. Size-structured populations of aquatic life stages (paedomorphic adults and overwintered larvae) of mole salamanders (*Ambystoma talpoideum*) have the potential to be dominant IG predators and cannibals in permanent ponds because of large size advantages over successive cohorts, but the species exists as only a single larval cohort in temporary ponds with reduced predatory abilities on guild members. Thus, both the potential for and intensity of predation by this species is linked to hydroperiod; yet, the predatory abilities of aquatic life stages of mole salamanders have not been evaluated. This study examined the extent to which larger size classes (paedomorphs and overwintered larvae) of mole salamanders preyed upon conspecifics and a congeneric competitor, the spotted salamander (*Ambystoma maculatum*). Predation trials occurred in indoor microcosms and were executed under two habitat treatments that included pseudo-natural conditions containing alternate prey and refugia, as well as simplified environments (no alternative food or cover). Embryos or hatchlings of mole and spotted salamanders were exposed either separately or concurrently to paedomorphic and overwintered larval mole salamanders in each habitat treatment. Additionally, overwintered larvae were offered as prey to paedomorphic adults. No significant differences in mortality were observed between habitat treatments (complex versus simple) for either embryo or hatchling predation experiments. Mortality of mole and spotted embryos did not differ when they were offered separately or together, but paedomorphs caused significantly higher mortality among mole embryos compared to spotted embryos. Hatchlings of both species were heavily preyed upon (nearly 100% in all trials), but overwintered larvae exhibited 100% survival with paedomorph predators, indicating size-thresholds of predation risk that were not species specific. Paedomorphs and overwintered larvae therefore are most likely generalist predators that feed equally and effectively on hatchlings of co-occurring species, but are more likely to consume egg masses that do not incur significant handling costs. When present, paedomorphs or overwintered larvae have the potential to alter population dynamics of both guild members and conspecifics by being dominant predators on early life stages. As the prevalence of overwintering and paedomorphosis varies along hydroperiod gradients, predation risk from this species is likely to occur discontinuously and thereby may be an important, yet variable, structuring force.

GRADIENTS in abiotic and biotic components of an ecosystem can be crucial in determining community structure (Wellborn et al., 1996; Mylius et al., 2001). Often, variation in these two components is linked, such that biotic gradients directly reflect abiotic gradients. In freshwater ecosystems, the gradient along which a body of water remains permanent (e.g., hydroperiod) often influences species composition, which causes temporary aquatic habitats (e.g., ephemeral ponds) to consist of different species assemblages than permanent aquatic habitats (e.g., lakes; Wellborn et al., 1996). In particular, predator identity, presence, and/or density varies in direct response to the duration that the aquatic habitat persists (Wellborn et al., 1996; Stoks and McPeek, 2003). As predator guild structure shifts along hydroperiod gradients, concomitant changes occur in lower trophic levels in response to the attributes of different predators (e.g., Wissinger et al., 1999; Stoks and McPeek, 2003); thus, the structuring effects of predation on communities are directly tied to habitat permanence.

Two specific types of predation that are important in structuring aquatic communities are intraguild predation (IGP) and cannibalism (Polis and Myers, 1989; Wissinger et al., 1999; Stoks and McPeek, 2003). The pervasiveness of these strategies depends upon the cost: benefit ratios of pursuing such behavior; for example, IGP and cannibalism reduce competitor densities and provide higher-quality nutritional content to the predator, but leave the attacker more susceptible to injury from the attempted predation (Polis and Myers, 1989). A preference for IGP over cannibalism, or vice versa, by a single predator would be highly influential on community structure, and the cost: benefit ratio (e.g., differences in energy assimilation or inclusive fitness) of employing each strategy may determine their relative occurrence (Crump, 1990; Hawley, 2009).

Cannibalism and IGP are especially prevalent in larval stages of pond-breeding ambystomatid salamanders, and these behaviors are often the consequence of variability in larval density, breeding phenology, and the length of the larval period, all of which result in size-structured communities (Semlitsch and Reichling, 1989; Cortwright and Nelson, 1990; Boone et al., 2002, Yurewicz, 2004; Wissinger et al., 2010). Such size patterns terminate as

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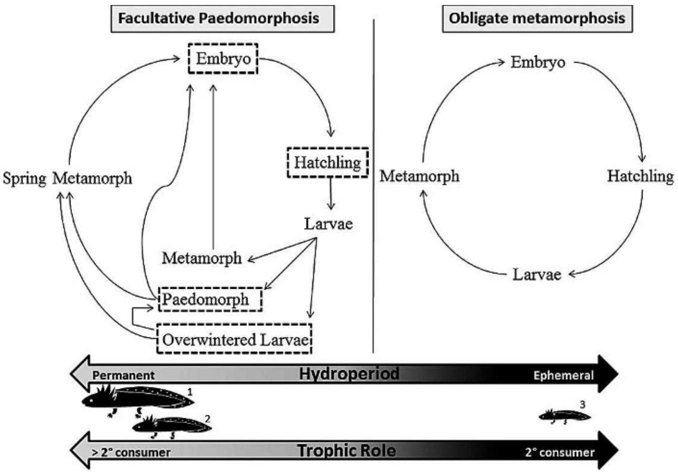

Fig. 1. Variation in the life cycle of *Ambystoma talpoideum* along a hydroperiod gradient, which changes their trophic position. The left diagram demonstrates facultative paedomorphosis, including potential outcomes of overwintered larvae and paedomorphs, which can occur in ponds of semi-permanent to permanent hydroperiod. The right diagram shows the life cycle of non-paedomorphic populations of mole salamanders that undergo obligate metamorphosis, the only possible scenario in ephemeral ponds. The right diagram is also representative of some congeneric pond-breeding species, such as *A. maculatum*. Dashed boxes represent life history stages that potentially overlap in increasingly permanent ponds, creating size-structured populations, and are the stages used in the current study. Cartoon salamanders represent where 1) paedomorphs, 2) overwintered larvae, and 3) larvae in non-overlapping age cohorts are predicted to exist along hydroperiod and trophic level gradients.

individuals metamorphose, or as size differences between predator and prey become minimized to where predation is precluded by gape limitations (Morin, 1983; Mylius et al., 2001). Most studies that have explored IGP among ambystomatids have examined species exhibiting obligate metamorphosis, and the associated IGP risk between single cohorts of different species (e.g., Brodman, 2004; Yurewicz, 2004). Additionally, cannibalism has primarily been explored in simple pond ecosystems, where only one species of salamander predator exists in size-structured populations (e.g., Wissinger et al., 2010; but see Nyman et al., 1993). Variation in hydroperiod may directly alter the prevalence of IGP and cannibalism in both of these systems by influencing the development of size-structured populations, thus linking hydroperiod with predation potential.

At least three size classes of the mole salamander (*Ambystoma talpoideum*) can temporally overlap in permanent fish-free ponds, two of which may be dominant interspecific and intraspecific (i.e., cannibalistic) predators (Patterson, 1978; Fig. 1). The largest size class includes sexually reproductive, gilled adults (i.e., paedomorphs) that remain in aquatic environments rather than undergo metamorphosis (facultative paedomorphosis; Whiteman, 1994). Additionally, *A. talpoideum* can overwinter as immature larvae (middle size class) and metamorphose or become paedomorphic the following year (Doyle and Whiteman, 2008; Anderson, unpubl.). The third size class consists of progeny of both metamorphic and paedomorphic adults that hatch from egg masses in early spring. This group is potentially vulnerable to cannibalism from older age cohorts of mole salamanders and IGP from several guild members (e.g., *Ambystoma opacum*; Boone et al., 2002), while still in the egg mass and in the free-swimming hatchling stage. Paedomorphosis in *A. talpoideum* has been well-studied experimentally in some ecological contexts (e.g., Semlitsch, 1987a; Ryan and Semlitsch, 2003; Doyle and Whiteman, 2008), yet the functional role paedomorphs play as a top predator via cannibalism or IGP on either smaller classes of conspecifics or guild members, has not been addressed despite their importance in community dynamics (Fauth, 1999a, 1999b). Overwintering ecology of larval mole salamanders has also received little attention, although such individuals have the potential to be superior IG predators and cannibals, similar to other ambystomatid species (Wissinger et al., 1999, 2010). As the prevalence of paedomorphosis (and thus the degrees of population size-structure) is affected by hydroperiod (Semlitsch, 1987a), the ecological role of *A. talpoideum* may fluctuate among ponds of different hydroperiod from top predator to secondary consumer (Fig. 1).

This study examined the extent to which paedomorphic and overwintered larval mole salamanders act as predators on early life history stages (embryos and hatchlings) of conspecifics and a known congeneric competitor, *Ambystoma maculatum* (spotted salamander). Intraguild predation and cannibalism are often examined between developed larvae (e.g., Brodman, 2004), bypassing the egg and hatchling stages which often exhibit high mortality (Shoop, 1974). Foraging on embryos and hatchlings constitutes preferable, higher quality prey sources compared to some other food items (Polis and Myers, 1989; Burley et al., 2006) that could result in subsequent impacts on population dynamics. Differential rates of cannibalism versus IGP were expected to occur in this system, due to physical and ecological differences within each stage of prey. Specifically, because spotted salamanders have a considerably thicker gelatinous matrix covering their embryos, we predicted that conspecific embryos would be targeted by predators over congeneric masses. For hatchlings, high mortality was expected for both species, but we predicted that congeners should be targeted due to their slightly larger size (i.e., increased gains per predation attempt), and demonstrated naivety of larvae of *A. maculatum* to intraguild predators (Walls, 1995).

MATERIALS AND METHODS

All experiments were performed at Hancock Biological Station (Murray, Kentucky) in March 2011. Indoor microcosm experiments were conducted in two types of containers due to availability (see sections below for details), but all were filled with aged well-water and separated by opaque material to minimize external visual stimuli. Water temperature was constant (~18°C), and windows allowed a natural photoperiod (approximately 12 L: 12 D). Predators (paedomorphs and overwintered larvae) came from a previous competition experiment (Anderson, 2011), and all were measured for snout–vent length (SVL) prior to adding to microcosms. A subset of individuals was also measured for total length, mass, and head width (HW). Egg masses of *A. talpoideum* and *A. maculatum* were collected from three natural ponds in Calloway and Trigg Counties, Kentucky, and were held in environmental chambers at 14°C until used in predation trials. Egg masses not used in embryo predation trials were allowed to continue development, and resulting hatchlings were held in environmental chambers until

Table 1. Mean Sizes (±SE) in Snout–Vent Length (SVL, in cm) and Head Width (HW, in cm) for Predators and Mean (±SE) Initial Embryo Numbers in Embryo Predation Experiments in (A) "Simple" and (B) "Complex" Habitat Treatments, with Three and Five Replicates of Each Type, Respectively. Mole only, Spotted only, and Mixed refer to the embryo treatment applied within the simple/complex treatments.

(A) SIMPLE

Treatment	Mole only	Spotted only	Mixed
Predator SVL	5.5±0.33	5.2±0.38	5.4±0.17
Predator HW	1.0±0.03	1.1±0.08	1.1±0.08
Mole embryos	13.0±1.53	NA	20.0±1.15
Spotted embryos	NA	23.7±3.66	14.3±0.66

(B) COMPLEX

Treatment	Mole only	Spotted only	Mixed
Predator SVL	5.3±0.20	5.0±0.07	5.1±0.15
Predator HW	1.0±0.03	1.0±0.03	1.0±0.03
Mole embryos	19.8±4.04	NA	22.0±5.54
Spotted embryos	NA	18.4±1.86	15.2±1.32

enough were available for experimentation. Mean hatchling total length was calculated from digital photographs for each species ($n = 50$) using ImageJ software (Mott et al., 2010).

As the availability of paedomorphs, larvae, and hatchlings was asynchronous, replicates of each experiment were not equal, and trials were performed when individuals became available. However, all trials of a single experimental test were conducted simultaneously. Sex-specific predation rates by paedomorphs were not analyzed as the sex ratios were not equal, and for some predators, sex was uncertain; individuals that were equal to or larger in SVL than some mature paedomorphs were classified as paedomorphs (see Tables 1 and 2 for size class information). Each individual was used in only one trial, after which they were preserved.

Egg mass predation.—Experiments were conducted to assess predation on conspecific and congeneric embryos by paedomorph predators under two habitat complexity and three embryo treatments. Nine aquaria (9.5 L; 30 × 15 × 20 cm) were filled with eight liters of water, and had no refuge or alternative food available (hereafter, "simple" treatment). To increase realism of the experimental conditions ("complex" treatment), 15 aquaria (38 L; 51 × 25 × 30 cm) were completely filled with water and contained a thin layer of leaves from experimental mesocosms (Anderson, 2011). These leaves contained alternate invertebrate prey such as midge larvae (not quantified, but homogenized among containers) and provided habitat heterogeneity. Egg masses of either *A. talpoideum* or *A. maculatum,* or both species ("mixed") were added to all aquaria, resulting in three and five replicates for each embryo treatment in the simple and complex habitat treatments, respectively (Table 1). Egg masses of *A. maculatum* were split apart to parallel the size and match roughly the initial number of embryos of *A. talpoideum*, which were counted for each species prior to addition; overall egg density was not held constant between mixed and single species treatments and therefore mixed treatments contained roughly twice as many eggs as single species treatments. All paedomorphs were held in environmental chambers for 48 hours to standardize hunger and given 24 hours to acclimate in their aquaria before adding egg masses.

All tanks were observed every 24 hours for seven consecutive nights. Additionally, *ad hoc* checks were performed during the day, resulting in a minimum of approximately three aquaria checks per day. Embryonic mortality was determined at the end of the experiment by the equation: $[(1-E_{\text{final}}/E_{\text{initial}}) \times 100]$, where E = embryos.

Size-structured predation.—To test for palatability of conspecific or congeneric hatchling prey ("simple"), eight aquaria (9.5 L; 30 × 15 × 20 cm) were filled with eight liters of water with no cover or alternative food with four predator–prey combinations and two replicates of each treatment. Both paedomorphs and overwintered larvae were used as predators in these trials. Predators were placed into aquaria and allowed to acclimate for one hour prior to addition of hatchling prey. Four hatchlings of either *A. talpoideum* or *A. maculatum* were added to each aquarium and checked 24 hours later to determine mortality in each treatment.

Predation experiments under a pseudo-natural setting (i.e., "complex") were set up to assess both predation on hatchlings of *A. maculatum* and size-structured cannibalism in *A. talpoideum* in five treatments with six replicates of each treatment (Table 2). Plastic containers (4.3 L; 32 × 19 × 11 cm) were filled with two liters of water and leaves from a filled but loosely packed 500 mL beaker that contained alternate invertebrate prey. Concentrated zooplankton (50 mL) was added to each container as an additional food source. Two treatments consisted of five hatchlings of *A. talpoideum* and either a paedomorph or overwintered larvae as a predator. One treatment had five overwintered larvae of *A. talpoideum* that were combined with a paedomorph predator. Hatchling and overwintered larvae control treatments were also set up that contained only equal-sized individuals of *A. talpoideum* to compare survival rates with treatments that had larger predators. No objects were introduced to act as a surrogate predator in our control treatments, as our focus was primarily on prey consumption rather than avoidance behavior (e.g., Walls, 1995). Finally, a congeneric predation trial was set up with five hatchlings of *A. maculatum* and a paedomorph predator. No control was conducted for this treatment due to unavailability of hatchlings, and thus this treatment was not statistically analyzed; only the mean (±SE) of the six replicates is presented. The experiment was maintained for seven days, after which the leaves were removed and carefully searched

Table 2. Mean Sizes (±SE) in Snout–Vent Length (cm) for Predators and Prey for "Complex" Hatchling Predation Experiments. Hatchling predation treatments are as follows: (1) *A. talpoideum* hatchling control; (2) *A. talpoideum* hatchling prey with paedomorph predator; (3) *A. talpoideum* hatchling prey with overwintered larvae predator; (4) Overwintered larvae control; (5) Overwintered larvae prey with paedomorph predator; (6) *A. maculatum* hatchling prey with paedomorph predator. Hatchling sizes represent total length and are a mean value for each species. Predator values for both size classes are mean values based on five replicates for each treatment. * indicates treatments that had significantly higher mortality.

HATCHLING PREDATION IN COMPLEX TREATMENT						
Treatment	1	2*	3*	4	5	6
Control	1.2±0.01	NA	NA	3.6±0.03	NA	NA
Predator	NA	5.3±0.09	3.7±0.05	NA	5.4±0.07	4.8±0.11
Prey	NA	1.2±0.01	1.2±0.01	NA	3.7±0.03	1.3±0.01

for surviving prey. Hatchling mortality was calculated similarly to embryo mortality.

We also assessed whether paedomorphic mole salamanders exhibited a preference for conspecific or congeneric hatchlings. Five aquaria (9.5 L; 30 × 15 × 20 cm) were filled with eight liters of water, with no refugia or alternative food added. A paedomorph predator was introduced to each tank and allowed to acclimate for one hour; five hatchlings of both mole and spotted salamanders were then added. Aquaria were checked every 30 minutes for four hours, and the number of hatchlings remaining of each species was recorded at each time point and percent mortality calculated.

Analysis.—All statistical analyses were conducted using R (ver. 2.13.0, R Core Development Team, 2012). Data could not be transformed to meet assumptions of normality, and thus, non-parametric analyses were performed. Kruskal-Wallis tests were conducted to assess all treatment differences for each species separately in both hatchling and egg predation trials, as well as to assess potential bias in the initial number of embryos offered of each species. Response variables for the Kruskal-Wallis tests included percent embryonic survival and hatchling/larval survival.

General additive models (GAM) that incorporated non-parametric smoothers (regression splines) as the estimation method were used to assess non-parametric relationships of continuous variables, including HW and SVL with survival (Faraway, 2006). Due to low sample sizes, "complex" and "simple" treatments were combined in this analysis. The GAM approach was also used to model prey survival with the size ratio between prey and predator, which was calculated by dividing the mean SVL of prey by the respective predator SVL in that container (% size difference). For control treatments (i.e., no specified predator), mean SVL of all individuals was divided by the largest individual length in that container. Percent mortality of each species in hatchling preference predation trials were analyzed using repeated measures analysis of variance with a rank transformation of mortality (Conover and Iman, 1981).

RESULTS

The mean initial number of spotted embryos was significantly higher in the spotted only versus spotted in mixed treatments (Kruskal-Wallis $\chi^2 = 5.71$, df = 1, $P = 0.02$), but not significant for mole embryos in the mole only compared to mixed treatments ($\chi^2 = 0.47$, df = 1, $P = 0.5$; Table 1). No significant differences existed for initial embryo number between the two species when offered together (i.e., mixed; Table 1); no differences in initial embryo numbers were detected between the palatability trials ("simple") versus natural ("complex") treatments for either species (Table 1). Mean values for initial predator HW and SVL were also not significantly different between either the "simple" or "complex" conditions, or the embryo treatments (Table 1).

No significant differences existed in embryo mortality between "complex" versus "simple" treatments for either species; embryo mortality data within each treatment was pooled thereafter for further analyses. Embryonic mortality was not significantly different between tanks with a single species' embryos and the mixed treatment for either *A. talpoideum* or *A. maculatum* (Fig. 2). Complexity and embryo treatments were then both pooled to test for overall species differences in susceptibility to predation. Mole salamander embryos were preyed upon by paedomorphs significantly more than embryos of spotted salamanders ($\chi^2 = 5.3912$, df = 1, $P = 0.02$; Fig. 2). Mean mortality (±SE) was 51±11% and 10±3% for embryos of mole and spotted salamanders, respectively, regardless of complexity or embryo treatment combinations. Neither paedomorph HW nor initial SVL were significant predictors of embryo mortality for either species, indicating predator size did not influence embryo predation rates.

Hatchling palatability trials ("simple") resulted in 100% mortality for both species, and with both types of predators (paedomorphs and overwintered larvae). For predation in "complex" treatments, hatchlings of *A. talpoideum* that were paired with larger predators had significantly higher mortality compared with the hatchling control treatments ($\chi^2 = 25.2$, df = 4, $P < 0.001$; Fig. 3). Predation was nearly 100% on hatchlings of both *A. maculatum* and *A. talpoideum* (only one and two hatchlings remained overall, respectively), and both predators caused equivalent mortality. There were no significant differences in mortality for overwintered larvae when they were prey compared to the larval control that had no predator (0% in all replicates; Fig. 3). The GAM analysis that modeled size difference between predator to prey with percent mortality of prey produced a smoothed relationship that showed mortality increased in a near-logistic pattern that had a predation size threshold of approximately 40% (adj. $r^2 = 0.97$, $F_4 = 195.3$, $P < 0.0001$; Fig. 4). In species-preference trials, paedomorphs exhibited no significant preference overall or through time for a particular species, as hatchlings of both species were consumed readily (Fig. 5). On average, approximately one hatchling of *A. maculatum* remained after four hours of observation in each of the five trials, whereas all five hatchlings of *A. talpoideum* were consumed in every trial.

DISCUSSION

Most studies that have examined cannibalism and IGP among pond-breeding amphibians used species that complete

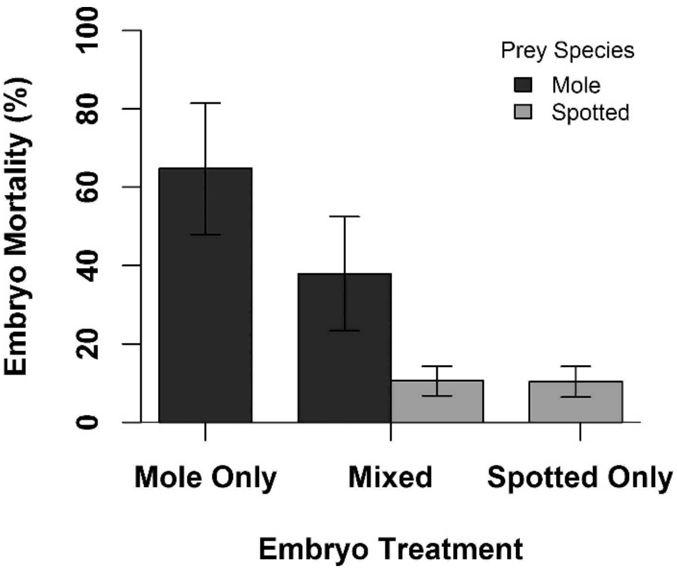

Fig. 2. Mean embryonic mortality (±SE) of *Ambystoma talpoideum* (Mole) and *A. maculatum* (Spotted) by paedomorphic mole salamanders in "complex" and "simple" conditions. "Mixed" treatment included egg masses of both species simultaneously, and "Mole Only" and "Spotted Only" had only that species' embryos present.

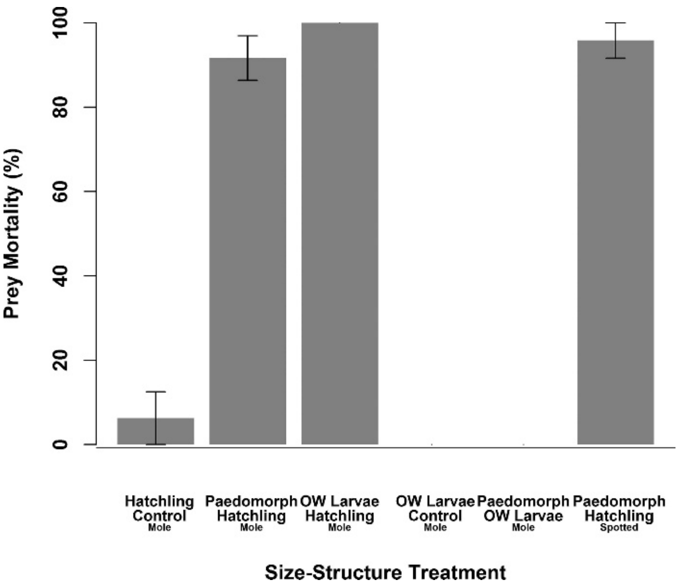

Fig. 3. Mean mortality (±SE) of hatchling and larval mole (*A. talpoideum*), and hatchling spotted (*A. maculatum*) salamanders in the "complex" treatment. Predators are indicated in the top row, and prey in the bottom row of the x-axis, respectively, except for control treatments where one size class was used. No bar exists for Paedomorph-OW Larvae (overwintered larvae) and OW Larvae Control treatments as 100% survival occurred. No error bars exist in the OW Larvae-Hatchling treatment due to 100% mortality.

metamorphosis annually (but see Morin, 1983; Fauth, 1999b; Wissinger et al., 2010). In regions where multiple species co-occur in ponds, such as the southeastern United States, few studies have examined IGP and cannibalism across age cohorts, though the importance of these interactions has been documented for some species (e.g., Morin, 1983; Fauth, 1999b). In this study we assessed how predation by two larger size classes of mole salamanders that are also an older age cohort affected the survival of early life history stages of conspecific and congeneric prey, which were predicted to be highly susceptible to predation by guild members. Paedomorphs and overwintered larvae significantly preyed upon hatchlings of both prey species, but with no species preference. Significant embryo predation by paedomorphs was only observed on conspecific embryos. These results indicate that, at least under experimental conditions, paedomorphs and overwintered larvae: 1) are highly effective predators of hatchlings, regardless of species; 2) consume conspecific embryos more than a congeneric competitor, and consequently; 3) may be opportunistic consumers on low-cost/high-reward prey items (Pyke, 1984; Crump, 1990), even when such foraging choices favor cannibalism.

Susceptibility of embryos to predation likely depends on the structural integrity of each species' egg mass and associated energetic costs of foraging. Embryos of *A. talpoideum* are laid in loosely clustered masses (Semlitsch and Walls, 1990), and had five times higher mortality than embryos of *A. maculatum*, which are laid in structurally thicker masses that likely deter paedomorphs, as well as other predators such as fish (Walters, 1975; Semlitsch, 1987b; Petranka, 1998). Conspecific embryo consumption has been observed in natural populations of paedomorphic mole salamanders, though its importance to or prevalence in their diet is unclear (McCallister and Trauth, 1996). The ecological consequences of this behavior are also currently unknown, but as paedomorph presence is determined by hydroperiod, the potential for cannibalism would increase in permanent ponds (Semlitsch, 1987a; Fig. 1). Harsh winter conditions may limit food resources, such that the availability of embryos in permanent ponds provides a substantial boost to energetic stores and potentially allows for metamorphosis of overwintered/paedomorphic individuals. Splitting apart egg masses of *A. maculatum* in this study did expose the egg mass interior and/or individual embryos, providing the opportunity for paedomorphs to prey upon the few embryos that were loosened from splitting the masses (indicated by the 10% mortality; Fig. 2), but it is unlikely that paedomorphs could extract intact embryos within the mass (Walters, 1975). Direct observations of this behavior were not conducted to support this hypothesis, however.

Size differences between predator and prey appeared to be the main factor that determined survival in the size-structured predation experiments. Recent hatchlings have limited swimming abilities and minimal defensive mechanisms, resulting in higher vulnerability of both prey species to larger, faster predators (Anderson et al., 1971; Hawley, 2009). In contrast, overwintered larvae of *A. talpoideum*, which are larger and more mobile, had 100% survival when matched with a paedomorph predator. Corresponding decreases in mortality with diminished size differences between predator and prey observed in this study match similar predator–prey size thresholds observed in other studies on salamanders, where prey susceptibility is reduced when they reach approximately 50% of a predator's size, presumably due to gape limitation or increased mobility (Rudolf, 2006; Wissinger et al., 2010). Unsuccessful predation attempts resulting in non-lethal injuries (e.g., limb/tail damage; Semlitsch and Reichling, 1989) could have occurred in treatments of low mortality (i.e., paedomorph with overwintered larvae), but such injuries were not quantified in this study. Often, a trade-off in IGP and cannibalism is that attempted predation, while

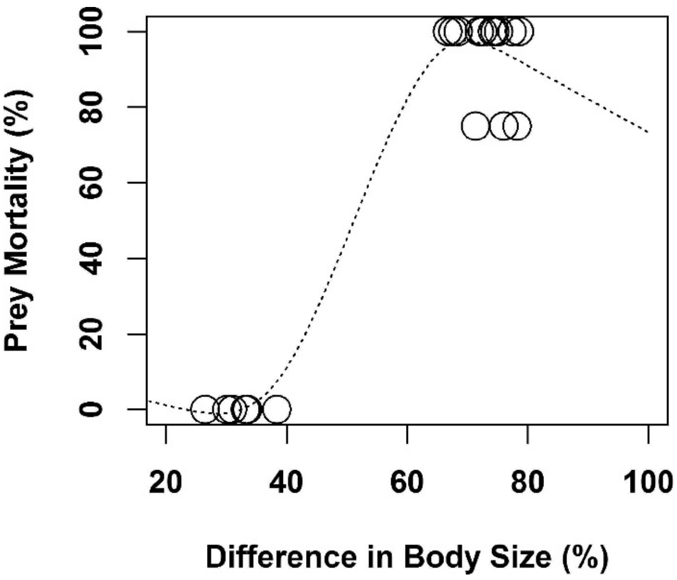

Fig. 4. Relationship of prey mortality with prey to predator size difference using a generalized additive model. Dashed trendline indicates smoothed estimation of prey mortality (%) using regression splines (adj. $r^2 = 0.97$, $P < 0.001$). Predator–prey size differences were calculated as (predator SVL–prey SVL)/predator SVL.

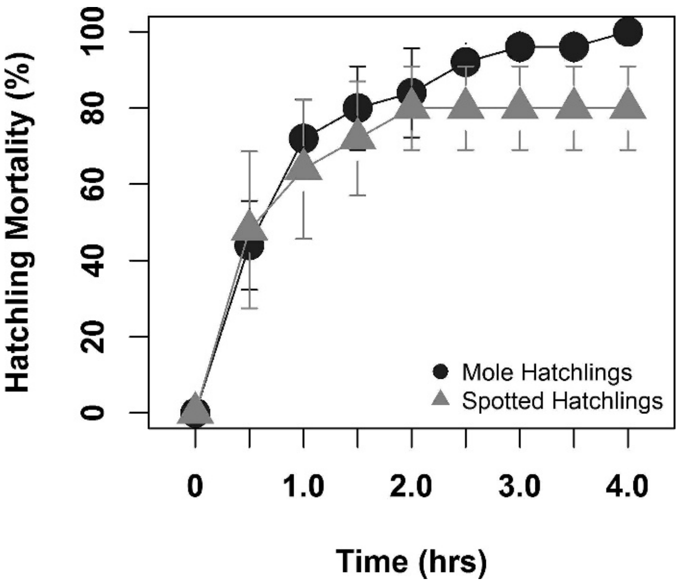

Fig. 5. Mean mortality (±SE) of hatchling mole (*A. talpoideum*) and spotted (*A. maculatum*) salamanders when offered simultaneously to paedomorphic mole salamander predators.

energetically beneficial, may result in injury from reciprocal predation attempts (Walls and Semlitsch, 1991; Brodman, 2004; Mott and Maret, 2011). Paedomorphs and overwintered larvae may circumvent these negative effects, however, by preying upon future guild members as embryos or hatchlings before they are able to present a competitive or reciprocal predatory threat.

Changes in pond community structure due to predators are predicated by hydroperiod, which also determines the suite of predators occupying those habitats, including paedomorphs (Semlitsch, 1987b; Wellborn et al., 1996). Ponds that remain filled for several years are more likely to contain paedomorphs and overwintered larvae (Semlitsch, 1987b), that in turn increases their potential to act as predators on early life stages such as hatchlings. Additionally, metamorphic mole salamanders may re-colonize semi-permanent ponds after drying events, and restart the cycle of paedomorphosis, allowing them to exist at higher trophic levels in these semi-permanent habitats compared to top predators that cannot cross terrestrial barriers (e.g., fish). In annually ephemeral habitats, only a single size class of *A. talpoideum* could occur, and their role would be that of a secondary consumer with limited predatory abilities on conspecifics and congeners because of reduced size differences (Fig. 1). Thus, population dynamics for both *A. talpoideum* and congeners may be influenced by climatic patterns (i.e., rainfall or drought) that affect hydroperiod, which in turn influences the prevalence of paedomorphs or overwintering larvae in *A. talpoideum*, both of which have the potential to limit recruitment via predation on early life stages and alter guild structure by preying upon other dominant IG predators (e.g., *A. opacum*; Boone et al., 2002). Alternatively, predation by paedomorphs may reduce larval densities such that larval competition is decreased and the fitness of surviving larvae is increased (Morin, 1981). Paedomorph occupancy could also influence oviposition by metamorphic adults of conspecifics and other guild members given a landscape of ponds with varying hydroperiod: laying eggs in permanent ponds increases the risk of cannibalism and IGP from paedomorphs but ephemeral ponds increase the risk of drying prior to completing the larval stage. Fauth (1999a) discussed the implications of spatial variation in *A. talpoideum* as a keystone species, but including temporal variation of paedomorphoic predators that are influenced by hydroperiod regimes provides additional context to its keystone role.

Despite their potential importance, the impacts of IGP and/or cannibalism by *A. talpoideum* on community structure in natural ponds are still limited to this experiment and few natural observations (McCallister and Trauth, 1996). Additional field-based data on guild member and community dynamics from habitats along hydroperiod gradients are needed to understand the impacts of paedomorph predation on natural systems. Information on interactions with other non-fish predators (e.g., odonates), or competition among size classes/age cohorts of mole salamanders, as well as variation in other abiotic factors that may influence predation by paedomorphs are also needed (e.g., Rudolf, 2006; Kishida et al., 2011). Continued investigation of other predators that exhibit plasticity in the size- and age-structure of their populations would be valuable, including those which vary widely in density or presence/absence along abiotic gradients (Wissinger, 1989). Such studies would provide greater insight into how differences in predation risk due to life cycle complexity impacts aquatic communities.

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