

Agonistic Behavior and Resource Defense among Sympatric Juvenile Pond-Breeding Salamanders

SARAH E. NUSSBAUM, BRITTANY H. OUSTERHOUT,¹ AND RAYMOND D. SEMLITSCH

Division of Biological Sciences, University of Missouri, Columbia, Missouri USA

ABSTRACT.—Interference competition is frequently observed in sexually mature adults as they defend breeding territories. However, it remains unclear in many taxa whether juveniles respond aggressively to other juveniles or if they defend resources. To test whether postmetamorphic juveniles of a pond-breeding amphibian were aggressive towards other juveniles or were defending resources, we staged terrestrial encounters between three species of sympatric *Ambystoma* salamanders. We observed biting and other aggressive behaviors by juvenile Spotted (*Ambystoma maculatum*) and Marbled Salamanders (*Ambystoma opacum*). However, we did not observe aggressive behaviors by Ringed Salamanders (*Ambystoma annulatum*). In addition to species-level variations in aggression, these three species also differed in whether aggression was targeted primarily intra- or interspecifically. This study suggests that juveniles of pond-breeding amphibians of some species may defend essential habitat with agonistic behavior.

Interference competition is one factor that may regulate population densities and ultimately species assemblages (Gur-evitch et al., 1992). Interference competition occurs when one individual directly affects the ability of another to consume resources. Such direct negative interactions are ubiquitous in nature and can arise from an array of behaviors including chemical competition such as allelopathy, physical interactions including predation or aggression, or combinations of both, as is the case with territoriality (Amarasekare, 2002; Gherardi and Cioni, 2004). Territoriality is the advertisement and defense of a fixed area by an individual to maintain sole occupancy (Wilson, 1975). Territoriality is predicted to occur when individuals encounter each other frequently and compete with con- and heterospecifics for a limited resource (e.g., a refuge) (Walls, 1990). This form of interference competition is commonly observed in sexually mature adults when defending breeding territories and offspring rearing space and has been extensively studied in many taxa including mammals (Grant et al., 1992), song birds (Krebs et al., 1978), and terrestrial salamanders (Mathis et al., 1995; Toll et al., 2000). Agonistic territorial defense of feeding sites also can occur among immature juveniles (Stamps, 1984; Wolff, 1997); however, the role of aggressive and territorial behaviors in regulating the juvenile life stage and structuring species assemblages as a whole remains poorly understood.

Although aggressive and territorial behavior have been observed in postmetamorphic juveniles (Ducey, 1989; Walls, 1990; Ducey et al., 1994; Smyers et al., 2001, 2002), these tests have been limited to a few species and general patterns are still being discerned for pond-breeding salamanders of the family Ambystomatidae. Considerable effort has been directed toward investigating agonistic interactions between aquatic larvae and the potential effects of these aggressive interactions on community assemblages (Stenhouse et al., 1983; Walls and Jaeger, 1987; Walls and Semlitsch, 1991; Nyman et al., 1993; Mott and Maret, 2011; Anderson et al., 2013). The role of aggressive interactions among terrestrial juveniles and adults, however, has received less attention (Ducey, 1989; Walls, 1990; Ducey et al., 1994; Smyers et al., 2001, 2002). This is troubling, because amphibian population dynamics are thought to be more

sensitive to the vital rates of juvenile (Vonesh and De la Cruz, 2002) and adult stage classes (Messerman and Semlitsch, unpubl.) than to the vital rates of larvae. Therefore, the outcome of agonistic interactions among adults and juveniles may have a disproportionate effect on population dynamics and community structure.

Terrestrial juvenile and adult *Ambystoma* salamanders are fossorial, occupying small mammal and insect burrows. These burrows are essential refuges, protecting individuals from predators and environmental fluctuations, and are limited in availability (Kroese et al., unpubl. data), so it is expected that residents would aggressively defend burrows against intruders. Such intrusions likely occur, as the terrestrial life stages are concentrated near breeding ponds (Rittenhouse and Semlitsch, 2007). Among *Ambystoma*, there is support for agonistic behavior in some species (Martin et al., 1986; Smyers et al., 2001, 2002). There also is evidence of territorial behavior (Ducey and Ritsema, 1988; Walls, 1990) in instances where individuals display site tenacity, advertisement, and defense of an area, and individuals can exclude competitors (Jaeger et al., 1982). The extent to which juveniles display agonistic behavior, however, not to mention territorial behavior, remains poorly resolved.

To begin determining if juveniles of *Ambystoma* are territorial, we tested whether juveniles of three sympatric species of pond-breeding salamanders defended an area, a first step towards testing for territorial behavior (Jaeger and Gergits, 1979). We staged laboratory encounters among and between juvenile Spotted (*Ambystoma maculatum*), Marbled (*Ambystoma opacum*), and Ringed Salamanders (*Ambystoma annulatum*) to test whether they displayed intra- or interspecific aggression and whether aggression differed among species. We also tested whether juveniles aggressively defended an area from intruders and if aggression differed among resident and intruder salamanders. Because of the ecological similarity of the three species and their sympatry, we hypothesized that aggressive behaviors would occur. We additionally predicted that the amount of aggression displayed and the relative strength of con- and heterospecific aggression would differ among species. In this salamander assembly, larvae of Marbled and Ringed Salamanders are competitively superior to larvae of Spotted Salamanders, and intraguild predation can occur when size asymmetries are large (Urban, 2007; Anderson and Semlitsch, 2014). Intraguild predation also has been observed between larvae of Ringed

¹Corresponding author. E-mail: BOusterhout@gmail.com
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and Marbled Salamanders (Doll, pers. comm.). Because these three salamander species can be congeners, we predicted that competitive asymmetries during the juvenile life stage that differ from those in the larval life stage would facilitate coexistence (Ducey, 1989; Walls, 1990; Smyers et al., 2001).

MATERIALS AND METHODS

Study System.—The Spotted Salamander (*A. maculatum*), Marbled Salamander (*A. opacum*), and Ringed Salamander (*A. annulatum*) occur in sympatry in the central interior highlands (i.e., Ozark and Ouachita mountains) (Petranka 1998). *Ambystoma* salamanders have a complex life cycle, with an aquatic larval stage and postmetamorphic terrestrial juvenile and adult stages. Ringed and Marbled Salamander adults migrate to ponds to breed in the fall. Larvae overwinter in the ponds and metamorphose in May and June. Spotted Salamanders breed at ponds in March and metamorphose June–November (Hocking et al., 2008). Larvae of all three species can co-occur in the same pond (Ousterhout et al., 2015). Juveniles of all three species have similar body lengths at metamorphosis (Anderson, unpubl. data). Adults and juveniles are fossorial and utilize passive burrowing, enlarging pre-existing cracks or small-mammal burrows in which to move underground during hot and dry weather (Semlitsch, 1983).

Salamander Maintenance.—We reared salamanders from hatchlings (Ringed and Spotted Salamanders) and midstage larvae (Marbled Salamanders) in 1,000-L cattle tank mesocosms in the same manner as similar studies (e.g., Ousterhout et al., 2014). We initiated mesocosms in late September 2013 for Ringed Salamanders ($n = 10$ mesocosms), and mid-March 2014 for Spotted and Marbled Salamanders (Spotted Salamanders: $n = 19$ mesocosms, Marbled Salamanders: $n = 2$ mesocosms). We filled mesocosms with tap water and allowed the water to stand and dechlorinate over 14 d. To each mesocosm we added 1 kg of air dried leaf litter (primarily *Quercus* spp. and *Acer* spp.) and a 1-L concentrated aliquot of plankton from natural ponds. Water levels were maintained at approximately 50 cm during larval rearing.

We collected Ringed and Spotted Salamander egg masses by hand and we dip-netted Marbled Salamanders larvae from natural ponds at Fort Leonard Wood, Pulaski County, Missouri. We randomly assigned hatchlings and larvae to mesocosms with each mesocosm containing a single species. Mesocosms were randomly assigned to a density treatment (6, 18, or 36 larvae/mesocosm). We checked mesocosms nightly for metamorphosing salamanders (gills reduced to <2 mm) beginning 7 May 2014. Individuals used in this experiment metamorphosed 13 May–8 July 2014 (Marbled Salamanders 13 May–29 June; Ringed Salamanders 19 May–26 June; Spotted Salamanders 10 June–July 8), and at least 7 d elapsed between metamorphosis and behavioral testing (time between metamorphosis and tests [mean \pm SD]: Marbled Salamanders 42 ± 11 d; Ringed Salamanders 36 ± 11 d; Spotted Salamander 20 ± 8 d). Metamorphosed salamanders were placed individually in plastic containers (15 \times 10 \times 7 cm) and housed at a secure facility at the University of Missouri (25–28°C, 12 : 12 h light : dark cycle). The plastic containers had a substrate of moist sphagnum moss that had been soaked in pond water and wrung out. We fed each salamander two small Red Wiggler Worms (*Eisenia fetida*) weekly.

Experimental Procedure.—To test whether juvenile salamanders were aggressive and if aggression was associated with the defense of an area, we scored behavior during staged intra- and

interspecific encounters between a resident and an intruder. We conducted behavioral observations 20 June to 23 July 2014 at the University of Missouri, Columbia, Missouri. We placed salamanders in 9-cm diameter petri dishes lined with moistened coffee filters as a substrate. Because all species tested were fossorial, each test chamber had an opaque burrow made of PVC pipe (4.5 cm long, 2 cm diameter) cut in half longitudinally (Ducey and Ritsema, 1988). We placed one salamander in each petri dish and gave individuals 7 d to establish a residency (Walls, 1990).

We conducted all staged encounters between 2000 h and 0130 h in a dark laboratory illuminated with dim red light (Semlitsch and Pechmann, 1985) and made observations from behind a blind to minimize observer effects (Ducey and Ritsema, 1988). At the start of each trial, we picked up the resident and placed it under a small opaque cup adjacent to the burrow within the petri dish it had occupied for the previous 7 d (hereafter, test chamber). We removed the intruder from the petri dish it had occupied for the previous 7 d and placed it in the test chamber underneath a different opaque cup, farthest from the burrow. We followed the same protocol with controls, which were a rolled-up, moistened paper towel the size of a salamander (Walls, 1990), similarly placing the control under an opaque cup in the resident's test chamber. After a 3-min acclimation period, we removed the cups and recorded aggressive behaviors for 20 min. We recorded behaviors as a count of the number of times that behavior occurred or the cumulative time the animal spent doing that particular behavior. We scored the following postures and behaviors thought to be aggressive in ambystomatid salamanders (as defined in Walls, 1990 and Ducey, 1989): counts of bites, movements toward the other salamander, looks toward the other salamander (turning head in the direction of the other salamander), and the proportion of time individuals displayed all raised trunk (ATR, elevated head and trunk). We also recorded two submissive behaviors: the count of movements away from the other salamander and the proportion of time when the salamander was flat (entire ventral surface of body in contact with the substrate). All behaviors were recorded using JWatcher (Blumstein et al., 2000). After 20 min, we returned salamanders to their original plastic containers. We cleaned test chambers with hydrogen peroxide between trials to remove any scent and used new coffee filters for each trial.

Our experiment was fully factorial, with individuals in a trial randomly designated as a resident or intruder and randomly paired with a conspecific, a heterospecific, or a control. The temporal order of trials was haphazard so as to avoid temporal pseudoreplication. To minimize the potential effect of size on interactions, we size-matched all salamanders (mean \pm SD difference in snout–vent length [SVL]: 2.41 ± 1.69 mm; SVL range: 27–34 mm). The greatest difference in size between paired animals in our study was 7 mm. Size matching also minimized the differences in larval density between resident and intruder because size is strongly correlated with larval density (Ousterhout and Semlitsch, 2016). We measured aggression in 104 trials (72 observations of residents, 104 observations of intruders) with at least 6 replicates for each treatment combination (Table 1). In this experiment we used 45 Spotted Salamanders, 36 Ringed Salamanders, and 35 Marbled Salamanders. No salamander was tested under the same condition twice ($n = 72$ tested once, $n = 33$ tested twice, $n = 9$ tested three times, and $n = 3$ tested four times), and all salamanders had at least 7 d between trials.

Data Analysis.—Resource defense and intruder submission behavior.—To explicitly test the hypothesis that resident

TABLE 1. Replication of experimental treatments.

Resident	Intruder	Replicates
Spotted	Spotted	11
	Ringed	9
	Marbled	6
	Control	12
Ringed	Spotted	6
	Ringed	8
	Marbled	7
	Control	12
Marbled	Spotted	8
	Ringed	8
	Marbled	9
	Control	8

juvenile salamanders displayed aggression, we modeled aggression by residents and tested whether this varied among species with a multivariate analysis of covariance (MANCOVA) in the package 'car' (Fox and Weisberg, 2011). For that analysis, the response simultaneously considered resident aggressive behaviors (number of bites, moved toward, looked toward, and proportion of trial displaying raised trunk) and the predictor was resident species. We likewise modeled whether intruders were submissive by simultaneously considering the responses proportion of trial "flat" and number of "move away." As in the previous analysis, we included the covariate of intruder species to account for species-level differences. The residuals of these models met all assumptions of normality and homoscedasticity. If resident or intruder, respectively, was a significant predictor, we conducted planned contrasts using 'linearHypothesis' in the package 'car' (Fox and Weisberg, 2011) to compare species. All statistical analyses were performed using R version 3.0.2 (R Core Team, 2015) and descriptive statistics were expressed as mean \pm SD.

Species and residency dependent differences.—We also tested whether species differed in their aggressive or submissive behavior or whether behavior was context dependent with a model containing two, 2-way interactions: 1) between focal individual species (Ringed, Spotted, or Marbled Salamander) and residency status (resident or intruder), and 2) between focal animal species and experimental treatment (conspecific, heterospecific, or control). We modeled this using generalized estimating equations (GEE) using 'geeglm' in package 'geepack' (Yan, 2000; Yan and Fine, 2004; Højsgaard et al., 2006). The GEEs allowed us to use a generalized linear model (GLM) approach while accounting for the potential correlation between the behavior of a resident and an intruder in the same trial. This made it possible to test predictions regarding differences between intruders and residents in a single model rather than fitting separate models for each group. Additionally, GEEs perform better than mixed effects models when there are numerous subjects and few observations per subject (Zuur et al., 2009; Hocking, 2012), as was the case in our experiment. We converted count data to a presence/absence binary and assumed a binomial error distribution for all response variables (presence/absence or proportion). Unlike with GLMs and mixed effects models, GEEs have an inherent overdispersion parameter, making the use of a negative binomial error structure unnecessary (Zuur et al., 2009). We used an exchangeable correlation structure, otherwise known as compound symmetry correlation structure, which assumes that only individuals within a trial are correlated. Preliminary

analyses indicated that individual identity accounted for little variation, so we did not include it in the final covariance matrix.

RESULTS

Resource Defense Behavior.—When all potential aggressive behaviors were considered as a response, aggressive behaviors by residents differed by species (MANOVA: $F_{12,256} = 5.90$, $P < 0.001$). Biting (ANOVA: $F_{3,100} = 3.05$, $P = 0.03$), look toward ($F_{3,100} = 42.962$, $P < 0.001$), and move toward ($F_{3,100} = 13.39$, $P < 0.001$), but not ATR ($F_{3,100} = 1.14$, $P = 0.34$), were predicted by species. While all species were aggressive (test for aggression being non-zero: Ringed Salamander $F_{4,97} = 7.91$, $P < 0.001$; Marbled Salamander $F_{4,97} = 6.07$, $P < 0.001$; Spotted Salamander $F_{4,97} = 6.57$, $P < 0.001$), none differed in pairwise comparisons (Spotted vs. Marbled $F_{4,97} = 0.66$, $P = 0.62$; Spotted vs. Ringed $F_{4,97} = 0.75$, $P = 0.56$; Ringed vs. Marbled $F_{4,97} = 1.24$, $P = 0.30$). When only biting was considered as the response, Spotted and Marbled Salamander residents were aggressive toward intruders whereas Ringed Salamander residents were not (Spotted Salamander $F_{1,100} = 4.78$, $P = 0.03$; Marbled Salamander $F_{1,100} = 4.37$, $P = 0.04$; Ringed Salamander $F_{1,100} = 0.00$, $P = 1.00$).

Intruder Submissive Behavior.—We observed species-level differences in submissive behavior (MANOVA: $F_{3,138} = 12.85$, $P < 0.001$), for both move away (ANOVA: $F_{3,70} = 11.06$, $P < 0.001$) and all flat behaviors (ANOVA: $F_{3,70} = 11.06$, $P < 0.001$). While intruders of all species displayed submissive behavior (test for submission being non-zero: Ringed Salamander $F_{4,97} = 7.91$, $P < 0.001$; Marbled Salamander $F_{4,97} = 6.07$, $P < 0.001$; Spotted Salamander $F_{4,97} = 6.57$, $P < 0.001$), there were no pairwise differences between species.

Species and Residency Dependent Differences.—The ATR behavior was displayed in 9.1% of trials ($n = 16$ trials). When individuals displayed ATR, they spent $3.9 \pm 4.7\%$ of the trial in this posture. The ATR was predicted by an interaction between focal species and treatment (Fig. 1c, $\chi^2 = 1,889$, $P < 0.001$). While Ringed Salamanders displayed ATR similarly regardless of what species the intruder was, Spotted and Marbled Salamanders displayed ATR more frequently to conspecifics and heterospecifics, respectively (Table 2; Fig. 1a). The ATR also was predicted by an interaction between focal species and residency status (Fig. 1b, $\chi^2 = 9$, $P = 0.014$). Ringed and Spotted Salamander juveniles spent more time in ATR as intruders whereas Marbled Salamander residents assumed the ATR posture more than did intruders (Table 2; Fig. 1b).

Eleven percent of juvenile salamanders bit during a trial ($n = 19$). In trials where biting was observed, there were 2.82 ± 3.03 bites and in trials where salamanders bit, only one of the two individuals bit, with two exceptions. These two trials also had the most biting (11 and 9 bites, respectively). Whether biting occurred during an encounter was predicted by the interaction between focal animal species and experimental treatment (Fig. 1c, $\chi^2 = 269$, $P < 0.001$). While Spotted Salamanders bit more frequently when they were paired with conspecifics, Marbled Salamanders exclusively bit heterospecifics (Fig. 1c). We never observed biting by Ringed Salamanders or by any salamander in the presence of the control (i.e., the simulated salamander). Bites were also predicted by the interaction between focal species and intruder/resident status (Fig. 1d, $\chi^2 = 13$, $P = 0.002$): Spotted Salamander residents bit in more trials than did intruders, but there was no difference between the number of

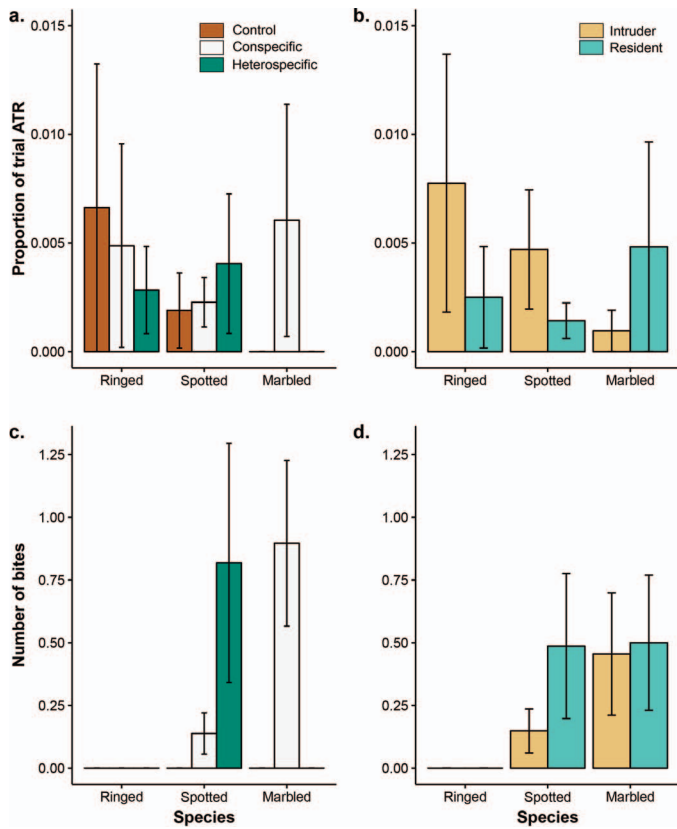


FIG. 1. Aggressive behaviors displayed by juvenile Ringed Salamanders (*Ambystoma annulatum*), Spotted Salamanders (*A. maculatum*), and Marbled Salamanders (*A. opacum*) during 20-min staged encounters. Bars represent means and error bars \pm SD.

trials where bites were observed by Marbled Salamander residents and intruders (Table 2).

Focal animal species, experimental treatment, intruder/resident status, or the interactions we tested were not predictors of look toward or move toward actions (Table 2).

Submissive Behavior.—We did not observe a significant effect of focal animal species, experimental treatment, intruder/resident status, or their interactions on move away or flat (Table 2).

DISCUSSION

Our study supports the hypothesis that juvenile salamanders respond aggressively when encountering another salamander. The behavioral response depended on the focal species and whether the other salamander was a conspecific or heterospecific. Additionally, residents of some species were aggressive, indicating resource defense among juvenile salamanders; however, our findings did not support the prediction that residents of all species would be more aggressive than would intruders. Additionally, we did not find support for intruders being more submissive than the residents.

Aggressive behavior by juvenile *Ambystoma* depended on the focal species and context. The Marbled Salamander was the most unambiguously aggressive species in our study, biting more frequently than Spotted or Ringed Salamanders. This behavior was context dependent: Marbled Salamanders responded aggressively (ATR and biting) only when paired with a heterospecific. Smyers et al. (2001) observed a similar pattern, although bites were far less frequent in their study. While juvenile Marbled Salamanders appear to be selectively aggressive towards heterospecifics, conspecific aggression has been observed among adults (Ducey, 1989; Ducey and Heuer, 1991). However, whether Marbled Salamander adults are aggressive toward heterospecifics, and whether their aggression is context dependent, remains to be tested.

Unlike Marbled Salamander juveniles, Spotted Salamanders responded aggressively toward both conspecifics and heterospecifics. Spotted Salamanders displayed ATR more when encountering heterospecifics but bit more often when paired with conspecifics. The elevated biting of conspecifics has been documented in other experiments with juvenile Spotted Salamanders (Walls, 1990) and adults (Ducey and Ritsema, 1988). While Marbled and Spotted Salamanders were aggressive, Ringed Salamanders were not more aggressive toward

TABLE 2. Count (*n*) and percent (%) of trials in which behaviors were displayed. Numbers under Treatment and Residency columns represent counts of trials in which the behavior was observed.

Response	Species	%	<i>n</i>	Treatment			Residency	
				Control	Conspecific	Heterospecific	Resident	Intruder
Aggressive								
ATR	Marbled	4.4	2	0	0	2	1	1
	Spotted	17.3	9	2	2	5	5	4
	Ringed	10.0	5	1	2	2	2	3
Bite	Marbled	22.2	10	0	0	10	5	5
	Spotted	17.3	9	0	6	3	6	3
	Ringed	0.0	0	0	0	0	0	0
Look toward	Marbled	60.0	27	5	8	14	18	9
	Spotted	61.5	32	3	14	15	17	15
	Ringed	66.0	33	7	10	16	22	11
Moved toward	Marbled	40.0	18	2	4	12	11	7
	Spotted	63.5	33	7	12	14	17	16
	Ringed	62.0	31	8	9	14	18	13
Submissive								
Move away	Marbled	42.2	19	2	5	12	8	11
	Spotted	59.6	31	4	9	18	17	14
	Ringed	50.0	25	5	9	11	15	10
Flat	Marbled	73.3	33	4	13	16	20	13
	Spotted	80.8	42	8	15	19	26	16
	Ringed	54.0	27	5	9	13	14	13

salamanders than toward the control. Additionally, Ringed Salamanders never bit. Martin et al. (1986) found similar support for the null hypothesis when testing for territoriality in adult Smallmouth Salamanders (*Ambystoma texanum*). We observed the full spectrum of aggression among the three study species (interspecific, intraspecific, and none).

Biting is an unambiguous aggressive behavior and we observed it at a much higher frequency than in another experiment with juveniles of *Ambystoma* (Walls, 1990). Biting behavior was observed in fewer trials in our experiment than in studies with adults of *Ambystoma*. When juveniles bit during a trial in our study, however, the number of bites was comparable to those observed during a single trial with adults (Ducey, 1989; Ducey and Heuer, 1991).

While Jaeger et al. (1995) and Mathis et al. (1995) broadly hypothesized juveniles to be the dispersing life stage in salamanders (and therefore juveniles are not territorial), others expressed mixed support for this hypothesis (Walls, 1990; Ousterhout and Liebgold, 2010). We found support for resource defense in juvenile pond-breeding salamanders. Marbled and Spotted Salamander residents displayed aggressive behaviors during interspecific and intraspecific contests when only bites were considered. When all aggressive behaviors were analyzed, Ringed Salamander residents also were aggressive. The agonistic behaviors observed in this study and others (Ducey, 1989; Walls, 1990) support the hypothesis that juvenile salamanders of some species of *Ambystoma* defend resources. Future studies specifically testing whether juveniles display site tenacity, advertise defended areas, and expel intruders are required to fully test for territoriality in juvenile *Ambystoma* (Jaeger and Gergits, 1979).

Walls (1990) suggested that ecologically similar *Ambystoma* may be able to occur in sympatry because of an ontogenetic shift in interference competitive ability. In this model, one species would dominate the larval stage while another would be superior in the terrestrial juvenile stage. Our study did not support this hypothesis. During the aquatic larval stage, competitive interactions among *Ambystoma* are largely size structured (Stenhouse et al., 1983; Urban, 2007). Larvae of the fall-breeding Marbled and Ringed Salamanders are superior competitors or intraguild predators of the spring-breeding Spotted Salamander if not gape limited (Urban, 2007; Anderson and Semlitsch, 2014). If an ontogenetic shift occurred, juveniles of the later breeding Spotted Salamander would be aggressive toward juveniles of the earlier breeding Ringed and Marbled Salamander, and this relationship would be asymmetrical. While we did find evidence of aggression by Spotted Salamanders toward both fall-breeding species, this aggression was reciprocated by Marbled Salamanders: Marbled Salamanders bit Spotted Salamanders in half of all trials whereas most of the aggression exhibited by Spotted Salamanders was directed toward conspecifics. Therefore, our study does not support an ontogenetic shift in competitive advantage amongst this assemblage of juvenile salamanders.

The lack of an ontogenetic shift observed in this study suggests that other factors, in addition to interference competition, may be mediating coexistence. Size, which was controlled for in our experiments, may mediate competitive interactions. Larvae of Spotted Salamanders metamorphose at a greater size when they co-occur with larvae of the fall-breeding Ringed Salamanders than when reared only with conspecifics (Anderson and Semlitsch, 2014). In natural systems, this could result in size asymmetries favoring

juveniles of the spring breeding Spotted Salamanders. Niche partitioning could also mediate coexistence. While all three species utilize burrows, they may partition space vertically by using different burrow depths, or horizontally with juveniles of some species moving farther from their natal ponds than would individuals of other species. Movement studies support this hypothesis. The movement distances of the three species tested in this study differ; however, genetic data and direct movement data show different patterns (Osbourn et al., 2014; Peterman et al., 2015), and future work should attempt to reconcile these differences to determine if space partitioning is mediating coexistence.

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