

Asymmetric effects of intra- and interspecific competition on a pond-breeding salamander

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Abstract. A fundamental goal of evolutionary ecology is to understand how asymmetric competition influences phenotype expression, yet few studies have quantified the relative effects of intra- and interspecific competition on phenotypes. We examined the effects of intra- and interspecific larval competition on both discrete and continuous phenotype expression of the facultatively paedomorphic mole salamander (*Ambystoma talpoideum*). We manipulated the density and frequency of larval *A. talpoideum* and a common competitor, the spotted salamander (*A. maculatum*), in experimental mesocosms within a response surface design. The production of discrete ontogenetic morphs (metamorphs, paedomorphs, and overwintering larvae) was affected more by intraspecific than interspecific competition, but the effect varied between morphs. Paedomorph and metamorph production were more strongly affected by intraspecific than interspecific competition, while the production of overwintering larvae was affected by each type of competition approximately equally. Paedomorphs largely occurred only at low conspecific densities, overwintering larvae primarily occurred at high overall densities, and metamorph production peaked at intermediate densities of con- and heterospecifics. Density-dependent intraspecific competition had stronger effects on body size and growth rates than interspecific competition for both metamorphs and overwintering larvae, whereas interspecific competition more strongly affected paedomorph size. Overall, these results support the hypothesis that intraspecific competition influences both continuous and discrete phenotypic expression more strongly than interspecific competition. Fluctuating strengths of each type of competition can affect variation in life history strategies by influencing discrete ontogenetic pathways via individual body sizes, leading to differential morph production and fitness within and among morphs.

Key words: *Ambystoma maculatum*; *Ambystoma talpoideum*; *asymmetric*; *competition*; *density dependence*; *life history trade-off*; *paedomorphosis*; *phenotype*; *polyphenism*; *resource polymorphism*.

INTRODUCTION

Competition is a fundamental interaction with broad consequences at multiple levels of ecological organization (Connell 1983, Gurevitch et al. 1992, Amarasekare 2003). Intra- and interspecific competition often differ in their relative impacts, such that asymmetric strengths of each type of competition can lead to different outcomes (Connell 1983, Morin 2011). Such asymmetries between each form of competition are pervasive across taxa (Connell 1983, Schoener 1983, Weiner 1990, Gurevitch et al. 1992, Denno et al. 1995), and investigations of these interactions has led to a greater understanding of population dynamics, spatial coexistence theory and the evolutionary consequences of asymmetric competition (Law et al. 1997, Amarasekare 2003, Morin 2011).

A standard outcome for assessing the effects of asymmetric intra- and interspecific competition on individuals is variation in phenotypic expression (i.e., variation in discrete or continuous morphological traits; Skulason and Smith 1995, Smith and Skulason 1996, Schluter 2000). In particular, discrete phenotypic expression can occur in response to absent or reduced interspecific competition coupled with strong intraspecific competition (e.g., Robinson et al. 1993, Bourke et al. 1999), the sole effects of intense interspecific competition (e.g., Schluter and McPhail 1992, Schluter 2000), or the interactive effects of intra- and interspecific competition (e.g., Pfennig 1992, 2002, Pfennig et al. 2007). Intra- and interspecific competition also often differentially affect continuous phenotypic traits such as body size and growth rates, which are important to understand given that variation in these traits often predict future fitness (Kingsolver and Pfennig 2004, Morin 2011). The potentially interactive effects of the two forms of competition that produce discrete phenotypes also likely, and simultaneously, affect variability in continuous traits such as body size and growth rates, with different-sized individuals within each alternative

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phenotype garnering differential fitness (Lively 1986, Denno and Roderick 1992, Whiteman 1994, Pfennig et al. 2007). As competition among individuals form the basis for population level responses, identifying how asymmetric competition affects these responses is critical to understanding its ecological impacts (Weiner 1990). Furthermore, because phenotypic variation is a foundational mechanism in evolutionary ecology, investigations into phenotypic responses to asymmetric competition can lead to predictions for the evolutionary outcomes of such interactions. Yet, simultaneous assessments of intra- and interspecific competition are infrequently performed on these traits.

To better understand asymmetries in competition, we compared the relative magnitude of intra- and interspecific competition on a pond-breeding salamander that produces three discrete ontogenetic morphs (i.e., discrete phenotypes) through a process termed facultative paedomorphosis. Within each discrete morph, we also investigated variation in individual growth rates and body sizes in response to intra- and interspecific competition. As these latter measures provide an indication of fitness in salamanders (Semlitsch et al. 1988, Scott 1994), our study allowed us to assess how competition influences differential fitness among the different morphs.

Facultative paedomorphosis has been a model system for understanding the evolutionary ecology of phenotype expression (Whiteman 1994, Denoel et al. 2005). In this polyphenism, individual salamanders can display three discrete ontogenetic morphs: (1) remain in the aquatic environment and become sexually mature while still in a larval morphology (paedomorph), (2) metamorphose and become a terrestrial adult (metamorph) or (3) delay maturation and remain as overwintering larvae, and become paedomorphic or metamorphic in subsequent years. The expression of each ontogenetic morph is triggered by environmental stimuli experienced during the larval stage, including competition (Whiteman 1994, Doyle and Whiteman 2008, Whiteman et al. 2012), and the resulting adult stages (paedomorphs and metamorphs) exhibit a resource polymorphism, as they are segregated by habitat type (aquatic vs. terrestrial) and utilize different resources (Denoel et al. 2005). Thus, larval competition is a proximate mechanism of ontogenetic morph expression that subsequently influences the resource polymorphism between metamorphs and paedomorphs by altering their relative proportions. Each morph is then maintained within a population through environmental events (e.g., pond drying) and differential fitness payoffs to each life history pathway (Whiteman 1994, 1997).

The mole salamander (*Ambystoma talpoideum*) is the primary species that exhibits facultative paedomorphosis in the southeastern United States, a region with a high diversity of potential interspecific competitors (Petranka 1998). The effects of interspecific interactions among larval stages have been well documented for this

species, particularly with the spotted salamander (*A. maculatum*; e.g., Walls and Jaeger 1987, Semlitsch and Walls 1993, Walls 1996). Larvae of *A. talpoideum* and *A. maculatum* commonly co-occur in ponds, but *A. maculatum* exhibits obligate metamorphosis, and often metamorphoses earlier than *A. talpoideum*, confining the majority of larval interactions between species to approximately the first ten to twelve weeks of the larval period of *A. talpoideum* (Petranka 1998; T. L. Anderson, unpublished data). These two species also show asymmetric competitive abilities, primarily because larval *A. talpoideum* are dominant interference competitors whereas *A. maculatum* are better exploitative competitors (Walls and Jaeger 1987, Semlitsch and Walls 1993, Walls 1996). These differences in larval period and competitive mode suggest the potential for asymmetric effects of intra- and interspecific competition on discrete morph production and growth in *A. talpoideum*. Based on previous studies of competition, including those between the focal species, we expected intraspecific density effects to be stronger than interspecific competition from *A. maculatum* on the production and size of each ontogenetic morph within *A. talpoideum* (Walls and Jaeger 1987, Semlitsch 1988, Semlitsch and Walls 1993, Skulason and Smith 1995). Thus, we predicted that the prevalence of metamorphosis would increase and paedomorphosis would decrease with conspecific density, consistent with the hypothesis that favorable aquatic conditions promote paedomorphosis (Whiteman 1994), and that heterospecific density would have similar but less intense effects on metamorphic and paedomorphic rates than conspecifics. Because overwintering in an immature state delays reproduction and may have other fitness costs for each final adult morph, we predicted that overwintering should primarily occur only under the highest larval densities where larvae cannot complete metamorphosis and/or reach maturity (Whiteman 1994). Within all ontogenetic morphs, we expected negative density-dependent effects on body size and growth rates that would again be influenced more by intra- rather than interspecific competition. Body size at metamorphosis and/or maturity in amphibians strongly correlates with fecundity and adult survival, and thus its response to competition is important to understand (Semlitsch 1985, Semlitsch et al. 1988, Scott 1994, Schmidt et al. 2012).

METHODS

The experiment was conducted in sixty experimental mesocosms (1.52 m diameter, 0.6 m depth) at Murray State University's Hancock Biological Station in January 2010 (see Anderson [2011]) for details. To each mesocosm, we added 1000 L aged well water, 3 kg of dry leaves (*Quercus* spp., *Platanus occidentalis*, and *Liquidambar styraciflua*) and ~2 L of pond water containing concentrated zooplankton from nearby ponds. Tanks were left open to permit deposition by flying insects (e.g., dipterans) to develop a resource base for larval

salamanders, creating a reasonable simulation of natural pond communities (Wilbur 1997). The entire mesocosm array was covered by a shade cloth canopy that permitted 50% light transmission but still allowed natural precipitation to reach the tanks. Additional aged well water was added to tanks as needed to maintain constant water levels.

Salamander eggs came from breeding adults of both *A. talpoideum* and *A. maculatum* from several natural permanent ponds near Murray, Kentucky, USA, in early March 2010, where both focal species are sympatric. Clutches from a minimum of five females of each species were used in the experiment. All eggs were held in environmental chambers until hatching occurred, after which clutches were split apart and hatchlings haphazardly chosen to minimize genetic bias on competitive ability and paedomorphosis. We added hatchlings to tanks during the first week of April. A very slight asynchrony in hatching date resulted in *A. talpoideum* being added 24–48 hours before *A. maculatum*, which is minimal compared to natural hatching variability (Petranka 1998).

We used a response surface experimental design where treatments included 12 different density combinations of the two salamanders spanning three overall densities ($n = 6, 12,$ and 24 larvae) with five replicates of each treatment (Inouye 2001). Six treatments consisted of single-species tanks at each of the three overall densities of each species. The remaining six treatments varied the relative proportions of each species such that conspecific to heterospecific density ratios were 3:1, 1:1, and 1:3 at the medium ($n = 12$ total individuals) and high densities ($n = 24$ total individuals; Appendix: Fig. A1).

We used visible implant elastomer (VIE) tags (Northwest Marine Technology, Tumwater, Washington, USA) to individually mark a subset of larval *A. talpoideum* ($n = 98$) on approximately day 50 of the experiment. We captured larvae by suspending three vinyl-dipped steel minnow traps (42×2 cm, 2.54 cm opening) at night along the walls of each tank that were then checked the following morning. Snout–vent length (SVL, mm), total length (mm), and mass (g) were measured on all larvae prior to marking. Mass and SVL were highly correlated ($r = 0.90$); therefore, only SVL is considered hereafter. A unique VIE color and body position combination was used for each larva that allowed individual growth trajectories to be followed that could then be paired with known phenotypes. Larval SVL was ~ 25 – 30 mm at the time of marking, below the average SVL at maturation (> 32 mm; Petranka 1998). Marked individuals were distributed evenly across all of the density treatments (~ 10 per treatment). Measurements of marked larvae continued every two weeks through September, or until metamorphosis occurred. Once metamorphosis had begun, we checked tanks every other night for metamorphosing individuals from summer 2010 through April 2011 when the experiment ended, aside from periods over the winter

when tanks were frozen. We removed metamorphs from tanks after reabsorbing gills; body size measurements and VIE mark (if present) were recorded. Due to logistical constraints, tanks were drained prior to overwintering individuals becoming paedomorphic or undergoing metamorphosis. The leaf litter of drained tanks was searched for all remaining individuals, and morphological measurements and final phenotype were recorded. Thus, we examined the effects of competition on the three ontogenetic morphs (paedomorphs, metamorphs, and overwintered [OW] larvae). Sexual maturity of paedomorphs was determined upon final capture or at any point during ontogeny by visual inspection of the cloaca, which differentiated them from OW larvae.

Analysis

We used multinomial regression to analyze the number of surviving individuals of each ontogenetic morph of *A. talpoideum* using the mlogit package in the R statistical program (Croissant 2012, Qian et al. 2012, R Development Core Team 2014). Eight candidate models were ranked using AIC to compare the effects of intra- and interspecific competition on the production (i.e., number of individuals) of each phenotype (Appendix; Burnham and Anderson 2002), and included models with intra- and interspecific density separately, both species additively, and their interaction. We also compared models that included survival and the mean date of metamorphosis of *A. maculatum* (Appendix).

To assess the effects of intra- and interspecific competition on size, we analyzed the final SVL for all surviving individuals of each phenotype of *A. talpoideum* using nonlinear mixed effects models, with tank as a random effect (package nlme; Pinheiro et al. 2013). Three competition models were initially compared using the Akaike information criterion adjusted for sample size (AIC_c) to determine the best-fitting model, and included a linear ($y = c + \alpha X_1 - \beta X_2$), Ricker ($y = \alpha X_1 e^{(-\alpha X_1 - \beta X_2)}$), and negative exponential ($y = \alpha e^{(-\alpha X_1 - \beta X_2)}$), where α and β are the intra- and interspecific competition coefficients, and X_1 and X_2 the densities of con- and heterospecifics, respectively. These models have been supported in other competition studies (Wilbur 1982, Van Buskirk 2007).

Individually marked larvae were compared for differences in initial SVL (an estimate of initial growth rate as individuals were added at the same time) using linear mixed effects models, with the eventual phenotype and tank as fixed and random effects, respectively. Growth of marked individuals (i.e., repeated-measures analysis) was analyzed using nonlinear mixed effects models (Pinheiro et al. 2013). We initially compared three different growth models for each phenotype and ranked them using AIC_c . These models included a power law function ($y = aX^b$), the Michaelis-Menten function ($y = ax/[b + X]^{-1}$), and a Gompertz function ($y = ae^{(-be^{-cx})}$) (Bolker 2008). A first-order autoregressive correlation structure was initially included in each

model, but this term did not significantly improve the fit and was subsequently removed. Using the repeated measurements of individuals, we tested whether there were differences in initial growth rates and maximum size between phenotypes. As we saw stronger effects of intraspecific competition (see *Results*), growth rates within each phenotype were also examined as a function of conspecific density using the Michaelis-Menten function using individual growth rate data. One treatment was removed from this analysis for paedomorphs due to only one individual being marked for that density combination. Because not all individuals were marked, smaller sample sizes were present at each level of conspecific density (mean $n = 7$ individuals, range 4–19); however, sparse information exists on individual growth patterns, and these data are important to understand individual variation (Bolnick et al. 2011).

Interpretation of output from nonlinear mixed effects models does not follow standard frequentist statistical measures (i.e., P values are of lesser importance, and standard measures (r^2) of model fit are not equivalent), and thus we report the relative effects of density on differences between phenotypes and individuals. Small increases in size and growth have strong biological meaning for amphibians (Altwegg 2003, Chelgren et al. 2006) and thus this analysis matches with our goals of examining how competition affects phenotype expression.

RESULTS

We recovered 55 paedomorphs, 162 metamorphs, and 164 overwintered (OW) larvae of *A. talpoideum* from the experimental tanks, but the relative proportions of each morph varied by density treatment (Fig. 1A). The vast majority (98%) of individuals that became metamorphs did so prior to the onset of winter. Only three individuals metamorphosed the following spring (~13 months after the experiment started), although many OW larvae had achieved the minimum size to complete metamorphosis (Petranka 1998).

The best-supported model for the production of each morph in *A. talpoideum* included terms for intra- and interspecific density, but not their interaction (Appendix: Tables A1 and A2). The effects of intra- and interspecific density on the predicted likelihood of a larvae becoming a paedomorph, metamorph, or overwintering as a larva also showed asymmetric and nonlinear patterns (Fig. 2A). In general, intraspecific density had a greater effect than interspecific density on the probability of becoming all three potential ontogenetic morphs for *A. talpoideum*. For example, the probability of *A. talpoideum* becoming a paedomorph decreased by 4% with each additional *A. talpoideum* individual, until reaching an upper density threshold of 18 individuals, at which the predicted probability of this fate approached zero. In contrast, each additional *A. maculatum* decreased the probability of *A. talpoideum* becoming a paedomorph by only 1% with no upper threshold within the densities examined. The predicted probability of OW larvae increased by 1%

at low conspecific densities but increased to 5% at higher densities. The density of *A. maculatum* had similar effects as conspecifics, such that the probability of becoming an OW larva increased by 1% and 3% at low and high heterospecific densities, respectively. The predicted probability of becoming a metamorph was highest at intermediate densities of *A. talpoideum* and low *A. maculatum* density, and was predicted to decline by 4% and 1% with each additional conspecific and heterospecific, respectively, above the intermediate peak. At high densities of both species, metamorphosis was unlikely to occur.

The final SVL (mean \pm SE) of each ontogenetic morph was paedomorph, 50.64 ± 0.65 mm; metamorph, 39.27 ± 0.33 mm; and OW larvae, 39.19 ± 0.37 mm (Fig. 1C). The linear competition model for final SVL received substantial support over the negative exponential and Ricker models for all three phenotypes (Appendix: Table A3). The effects of intraspecific competition were three times greater than interspecific competition on metamorph size, and the 95% CI of the interspecific coefficient overlapped zero, indicating nonsignificant effects (Table 1). Each additional conspecific resulted in a 0.3 mm decrease in predicted SVL at metamorphosis (Table 1, Fig. 2B). Similar to metamorphs, the intraspecific coefficient for final SVL of OW larvae was greater than the coefficient for interspecific competition (Table 1). The 95% CI of the latter effect again overlapped zero, indicating the effects of interspecific competition were nonsignificant. Increasing both intra- and interspecific density by one individual resulted in a 0.8 mm and 0.3 mm decrease in SVL of OW larvae, respectively (Fig. 2B). In contrast, interspecific competition negatively affected SVL of paedomorphs, whereas the intraspecific coefficient overlapped zero (Table 1). Each additional con- and heterospecific decreased paedomorph SVL by 0.3 mm and 0.4 mm, respectively (Fig. 2B).

Of the 98 *A. talpoideum* that were individually marked at the first measurement (approximately day 50), 15 became paedomorphic, 61 underwent metamorphosis, and 22 overwintered as immature larvae (Fig. 1B). Of these, individuals that eventually became paedomorphs were significantly larger in SVL at their first measurement (mixed effects ANOVA, $\chi^2 = 19.5$, $df = 2$, $P < 0.001$); larvae and metamorphs were not different (SVL for OW larvae, 28.0 ± 0.48 mm; metamorphs, 28.33 ± 0.34 mm; paedomorphs, 31.33 ± 0.60 mm [mean \pm SE]).

Growth rates of marked individuals were best predicted by the Michaelis-Menten model (Appendix: Table A4). Paedomorphs had higher initial growth rates and reached a larger body size (greater asymptote) than metamorphs and overwintered larvae (Table 2, Fig. 3A). Metamorphs had higher initial growth rates than individuals that overwintered as immature larvae, and also reached larger final sizes (Table 2, Fig. 3A).

An overall pattern of density-dependent growth due to intraspecific competition was observed, where individuals

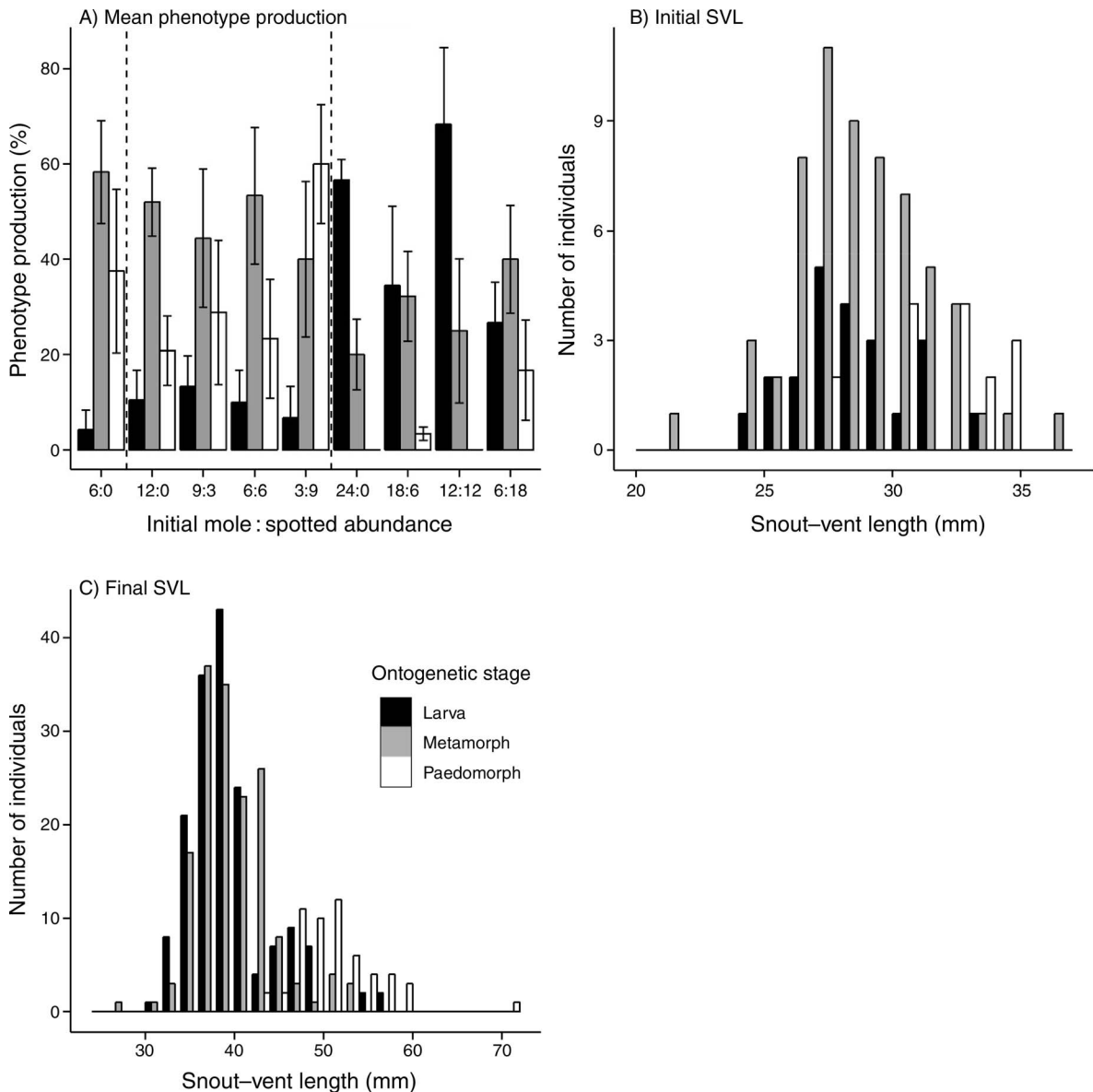


FIG. 1. Raw data on the (A) percent production of overwintering larvae, metamorphs, and paedomorphs of mole salamanders (*Ambystoma talpoideum*; mean \pm SE), (B) distribution of larval snout-vent length (SVL) at the time of individual marking grouped by final ontogenetic morph, and (C) distribution of final SVL of all individuals for the three morphs. The x-axis in panel (A) represents the initial abundance ratio of mole and spotted (*A. maculatum*) salamanders, and the dashed lines separate the low ($n=6$ individuals), medium ($n=12$), and high overall densities ($n=24$).

from the lowest density tanks had higher initial growth rates and reached larger final sizes than individuals from higher densities (Fig. 3B–D). However, consistent changes between each density were not apparent. The growth trajectories of the three morphs also varied among the different conspecific density levels. Predicted maximum SVL of paedomorphs ranged from 69.13 mm at the lowest conspecific density ($n=3$) to 56.58 mm at the highest density where a paedomorph was observed ($n=12$, Fig. 3C; Appendix: Table A5). For metamorphs, the predicted maximum body size asymptote ranged from

57.46 mm SVL at density of three conspecifics per tank to 45.36 mm SVL at 24 individuals per tank (Fig. 3B, Appendix: Table A5). For OW larvae, maximum predicted SVL ranged nearly an equivalent amount, but at lower overall sizes (maximum predicted SVL = 53.11, minimum = 37.26; Fig. 3D, Appendix: Table A5). Overall, increasing conspecific density decreased the initial slope of the growth curve for all phenotypes (Table A5). However, for paedomorphs and metamorphs at higher densities, the initial slope returned to approximately equal values compared with the low densities.

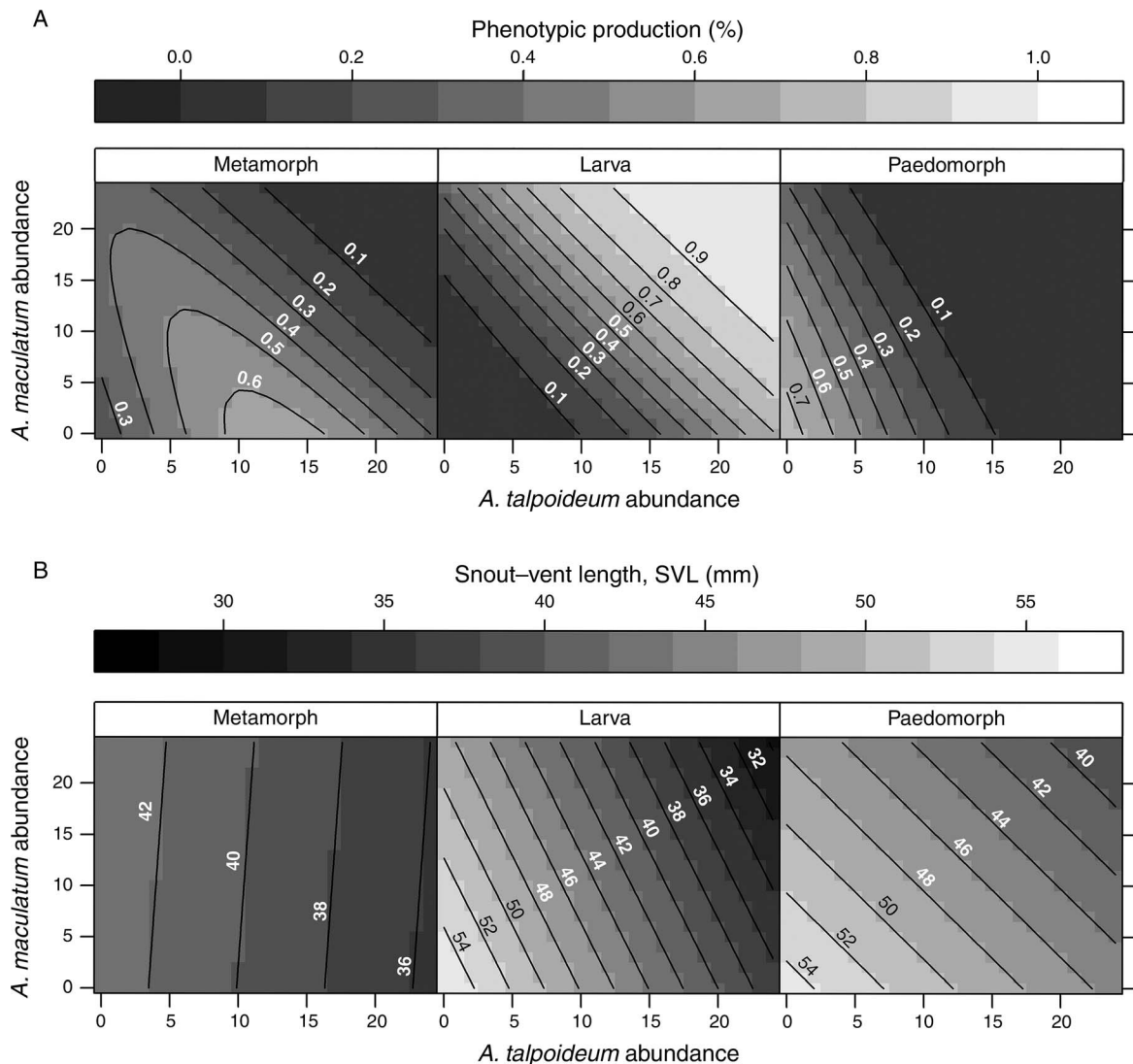


FIG. 2. Model predictions for (A) predicted probabilities of mole salamanders (*Ambystoma talpoideum*) becoming a paedomorph, metamorph, or an overwintering (OW) larva and (B) predicted final SVL of metamorphs, OW larvae, and paedomorphs based on the initial abundance of *A. talpoideum* and spotted salamander (*A. maculatum*) larvae. Values are derived from a multinomial regression model (A), and a linear competition model (B) that included both species' abundances as covariates. In panel (A), the outcomes of the multinomial regression are linked processes, such that percentages sum to one across the three panels at a given density combination and variation in one outcome results in changes to the other outcomes. The grayscale represents the range of (A) ontogenetic morph production (lighter, high probability; darker, lower probability) and (B) sizes (lighter, larger size; darker, smaller size). Vertical isoclines indicate only intraspecific competition is occurring, horizontal isoclines only interspecific competition, and diagonal (45°) isoclines indicate equal intra- and interspecific effects.

TABLE 1. Regression coefficients estimating the effects of intra- and interspecific competition on final body size of each ontogenetic morph of mole salamanders (*Ambystoma talpoideum*) based on a linear regression model ($y = c + \alpha X_1 - \beta X_2$).

Coefficient	Paedomorph			Metamorph			OW Larvae		
	Lower	Estimate	Upper	Lower	Estimate	Upper	Lower	Estimate	Upper
Intraspecific (α)	-1.05	-0.39	0.26	-0.44	-0.31	-0.18	-0.99	-0.79	-0.58
Interspecific (β)	-0.55	-0.30	-0.05	-0.25	0.02	0.29	-0.60	-0.29	0.01
Intercept (c)	47.62	54.80	61.97	40.67	43.08	45.48	51.77	55.74	59.71

Notes: OW stands for overwintering. Upper and lower are 95% confidence intervals. Values in boldface type indicate estimates where the confidence intervals do not overlap zero.

TABLE 2. Parameter estimates from the Michaelis-Menten model for growth rates of individuals within each ontogenetic morph of mole salamanders (*Ambystoma talpoideum*).

Phenotype	<i>a</i>			<i>b</i>			$b \times a^{-1}$
	Lower	Estimate	Upper	Lower	Estimate	Upper	Estimate
Larva	41.27	44.66	48.05	22.06	28.07	34.08	0.63
Metamorph	42.01	49.10	56.18	20.93	33.67	46.41	0.69
Paedomorph	50.58	59.75	68.91	28.27	44.14	60.01	0.74

Notes: The variable *a* is the asymptote, *b* is the half-maximum scale parameter, and $b \times a^{-1}$ is the initial slope. Lower and upper are 95% confidence intervals.

DISCUSSION

Both intra- and interspecific competition can influence several fundamental attributes of individuals, including the expression of both continuous and discrete phenotypic traits (e.g., Bourke et al. 1999, Schluter 2000, Grant and Grant 2006, Pfennig et al. 2007). The

intensity of each type of competition can vary, however, such that differential outcomes would ensue in response to competitive asymmetries. Our results support the hypothesis that intraspecific competition has a stronger effect on the expression of discrete alternative phenotypes than interspecific competition (Skulason and

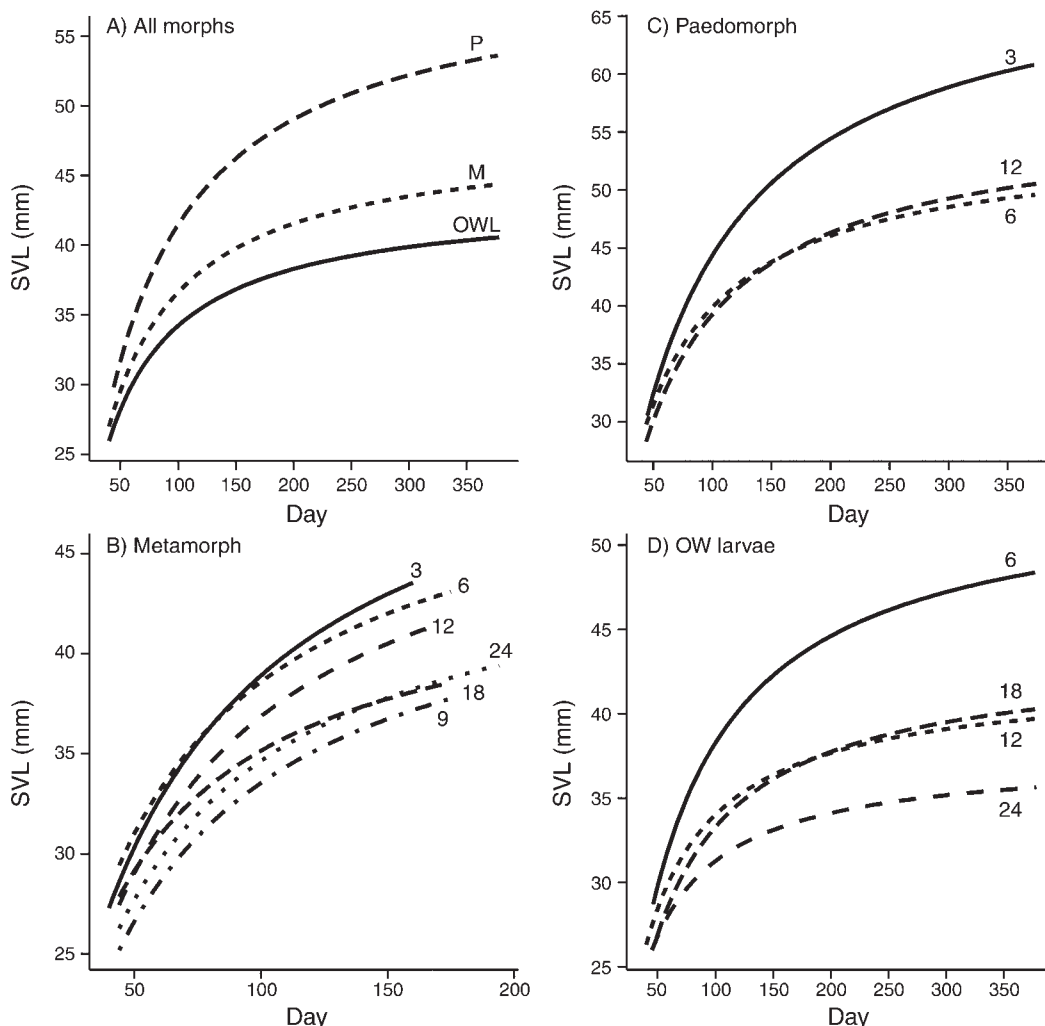


FIG. 3. Predicted growth rates in SVL based on individually marked *Ambystoma talpoideum* using a Michaelis-Menten model. Panel (A) compares growth of each ontogenetic morph (paedomorphs [P], metamorphs [M], and overwintered larvae [L]) based on individual growth rates. Panels (B–D) show the growth of each phenotype as a function of initial conspecific abundance, which is indicated by the number next to each line. “Day” is day of the experiment. See the Appendix for confidence intervals of parameter estimates of panels (B–D).

Smith 1995, Smith and Skulason 1996). The relative change in production of all three ontogenetic morphs of *A. talpoideum* was influenced more by increasing intraspecific rather than interspecific density. The intraspecific coefficients were greater than interspecific coefficients for both OW larvae and metamorphs, indicating continuous trait variation (i.e., in body size and growth rates) within each discrete morph was also affected more by intraspecific competition. Despite these strong asymmetries for most responses, evidence for interspecific competition was also present under certain conditions, suggesting it plays a limited role in morph production. In natural populations, larval densities of both species vary spatially and temporally (T. L. Anderson, *unpublished data*), leading to fluctuating strengths of competition, with subsequent effects on the production and size of each morph of *A. talpoideum*. Such fluctuations may ultimately shift the regulation of phenotype expression based on which form of competition is most prevalent.

Density-dependent competition simultaneously affected morph production and size variation among individuals within each morph of *A. talpoideum*. Paedomorphs were produced primarily at low densities, and their production was affected more by conspecifics. Size variation in paedomorphs was not as affected by initial density, however, likely because so few paedomorphs were produced at densities high enough to elicit a substantial density-dependent response. The relative effects of intra- and interspecific competition on paedomorph size were also more equal than the other two morphs, though only interspecific effects were significant. Overwintering larvae occurred primarily in high density tanks, and their SVL decreased more with increasing intraspecific density compared to interspecific density. The few OW larvae that did occur in low density tanks were much larger than those in high density tanks. Therefore, it appears that overwintering as an immature larva was more related to overall density, and was not as species specific as metamorph or paedomorph production. Metamorphs occurred at all density levels, but their final size and initial growth varied with increasing intraspecific density more than with increasing interspecific density. However, body size variation of metamorphs was lower than the other two phenotypes. It is not entirely clear why intraspecific effects were so much stronger in metamorphs relative to the other two morphs, as a greater proportion of the larval period of metamorphs was affected by *A. maculatum* due to greater temporal overlap. Paedomorphs and OW larvae remained in tanks much longer with only conspecifics and thus the relative effects of intraspecific competition would be expected to be stronger than interspecific effects. Mechanisms that would explain the relatively stronger intraspecific effects cannot be directly evaluated from our study, but previous research suggests that larval *A. talpoideum* show higher levels of aggression than *A. maculatum*, which could intensify intraspecific

interactions (Walls and Jaeger 1987, Walls and Semlitsch 1991).

Interspecific competition was not inconsequential, however, and our study highlights that discrete phenotype expression can be influenced along an interspecific density gradient. For example, high densities of *A. maculatum* still affected paedomorph production, but based on this study, interspecific competitor density would have to be four times higher than intraspecific density to elicit the same production of paedomorphs in *A. talpoideum* as conspecifics. Similar asymmetric thresholds of intra- and interspecific competitor densities influenced phenotype expression and reproductive potential in winged vs. non-winged planthoppers (Denno and Roderick 1992). Ongoing field observations of our two focal species indicate that extremely high densities of interspecific competitors, as well as highly variable density ratios of con- to heterospecifics, represent realistic scenarios in some populations (T. L. Anderson, *unpublished data*). Nonlinear patterns were also apparent in the production of each ontogenetic morph, indicating some potential non-additive effects of intra- and interspecific competition (Anderson and Whiteman, *in press*). In our experiment, the only paedomorphs produced at the highest overall density tanks occurred in the 6:18 conspecific: heterospecific density ratio treatment. The life history strategies that the two species employ explain this result: *A. maculatum* often metamorphose earlier than *A. talpoideum*, do not exhibit paedomorphosis and rarely overwinter as immature larvae. After the majority of *A. maculatum* metamorphosed, the 6:18 density treatment functioned as a low conspecific density tank and thus produced paedomorphs. Ontogenetic niche switches at metamorphosis would relax interspecific competition by lowering larval densities, consistent with the hypothesis that open niche space stimulates alternative phenotype expression (Skulason and Smith 1995), ultimately promoting the paedomorphic pathway. Direct measurements of niche space and availability are needed to verify this hypothesis. Paedomorphs from the 6:18 treatment were the smallest paedomorphs in terms of final size and had lower initial growth rates, indicating carry-over effects of interspecific competition on trait variability. Delayed effects of interspecific interactions of a superior competitor/predator have been found in other studies of amphibians (Segev and Blaustein 2007, Hernandez and Chalcraft 2012), but aside from this one treatment, delayed effects from *A. maculatum* were not observed in our study. This is surprising given the superior foraging abilities of larval *A. maculatum* (Walls 1996), but is consistent with exploitative effects between species not incurring as strong of a cost as interference competition among conspecifics.

Variability in the production of each ontogenetic morph and body size of individuals among each morph suggests that the life history trade-offs inherent in many polymorphic species are affected by both intra- and

interspecific competition (Whiteman 1994, Roff 1996, West-Eberhard 2003). In our system, parental investment (ova size, number, and clutch mass) by *A. talpoideum* varies between paedomorphs and metamorphs of similar ages and sizes (Semlitsch 1985), and time to and size at maturity also vary based on body size in metamorphic adults in this species (Semlitsch et al. 1988). Competition (both intra- and interspecific) can thus strongly influence population demographic rates in *A. talpoideum*. The resulting consequences of variable morph production stemming from larval competition is critical in the maintenance of the adult resource polymorphism, as continued production of one adult phenotype would lead to high densities in either the aquatic or terrestrial habitats, and shift the respective fitness of each pathway (West-Eberhard 2003, Pfennig et al. 2007). The final phenotypic expression of overwintering larvae was not followed in this study, but would be important to understand the implications of delaying maturation on fitness. Information on the fitness consequences of overwintering as larvae in *A. talpoideum* is currently limited (Doyle and Whiteman 2008); this strategy may allow them achieve a larger size at maturity, which may increase their survival probability or enhance reproductive investment (Semlitsch 1985, Semlitsch et al. 1988, Altwegg 2003, Chelgren et al. 2006). Additionally, as the intensity of intraspecific competition leads to variable production of paedomorphs and OW larvae of different size classes (i.e., influencing size structure), the resulting effects could have strong community-level consequences (Wissinger et al. 2010, Miller and Rudolf 2011, Anderson et al. 2013), but further studies are needed to verify this hypothesis.

Our study supports the hypothesis that intraspecific competition is the dominant factor in phenotypic expression, and that variation in conspecific and heterospecific density influence the relative strength of intra- vs. interspecific competition. Thus, there may not be a strong dichotomy for different forms of competition promoting phenotype expression, but rather they may act synergistically, with phenotypic expression determined by varying strengths of intra- and interspecific competition. Overall, the asymmetric nature and strength of intra- and interspecific competition are important factors that affect both discrete and continuous phenotypes, and these processes require further inquiry to understand their ecological and evolutionary consequences.

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SUPPLEMENTAL MATERIAL

Ecological Archives

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