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Effects of Relative Size on Growth Rate and Time to Metamorphosis in Mole Salamanders (*Ambystoma talpoideum*)

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ABSTRACT.—**Phenotypic variation in a population is a key requirement for natural selection. Body size variation, in particular, can affect the dynamics, life history, and ecological relationships in a population. Past work suggests that variation in body size within a population reflects a competitive gradient in which larger individuals negatively affect smaller individuals because of the superior ability to obtain limited resources, a result of exploitative or interference competition. We hypothesized that, if larger individuals outcompete smaller individuals through aggressive interactions (interference competition), the individual's position in the size distribution of their population (relative size) would be a better predictor of growth rate and time to metamorphosis than would their absolute size. We tested for the effect of body size on future larval growth rates, time to metamorphosis, and aggressive behaviors in individual *Ambystoma talpoideum* using experimental microcosms. Larvae were reared in small groups, producing variation in growth and development within each group. Using mixed-model analyses, we found that relative size was the best predictor of time to metamorphosis and aggressive behaviors and that growth rate of individuals within these populations was best explained by absolute or relative size depending on life stage. The largest individuals within a tank made the most aggressive attacks, had faster growth rates when young, and the quickest time to metamorphosis, regardless of their absolute size. This study found evidence for a complex relationship between population size structure, growth rate, and time to metamorphosis by tracking the effects of relative size on individuals within a population.**

Variation in size among individuals within a population can occur because of differences in stage of development, age, or other factors (Wilbur and Collins, 1973; Smith, 1990; Hopper and Crowley, 1996). Differences in individual size within a population distribution have been found to affect body morphology in phenotypically plastic animals (Maret and Collins, 1994; Frankino and Pfennig, 2001; Doyle and Whiteman, 2008), mating and predator avoidance strategies (Gross, 1996; Mathis et al., 2003), as well as life-history characteristics such as time to metamorphosis and future growth rate (Semlitsch, 1987; Chazal et al., 1996; Kohmatsu et al., 2001).

Past studies of amphibians have found that variation in body size within a population can reflect a competitive gradient in which larger individuals negatively affect smaller individuals because of a superior ability in obtaining limited resources (Wilson, 1975; Ziemba and Collins, 1999). This can be caused by more efficient handling time of prey items resulting from reduced gape limitation or increased energetic reserves in larger individuals (exploitative competition; Wilbur and Collins, 1973; Brodman, 1999; Van Buskirk and Schmidt, 2000) or from superior abilities in aggressive interactions over resources (interference competition; Smith, 1990; Brodman, 1999; Johnson et al., 2003; Mott and Sparling 2009). If exploitative competition is in effect, Ziemba and Collins (1999) predicted that there will be a linear relationship between body size and the individual's share of the resources, whereas with interference competition, resources would primarily be garnered by the largest individuals. Smith (1990) found size-dependent effects on growth when Marbled Salamander (*Ambystoma opacum*) larvae could interact freely but not in a purely exploitative system, thus supporting the interference competition hypothesis. Additional evidence suggests that interference competition may occur when large individuals monopolize the majority of resources through greater numbers of aggressive attacks on smaller individuals (Smith, 1990; Ziemba and Collins, 1999). Past studies have found that larger

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salamander larvae are more aggressive than smaller individuals (Brunkow and Collins, 1998; Johnson et al., 2003), and those smaller salamander larvae have decreased feeding rates when grouped with larger individuals (Ziemba and Collins, 1999). The above studies provide evidence that patterns of aggression by differently sized individuals serve as indicators of interference competition among salamander larvae, as has been found in other taxa (Faragher and Jaeger, 1998; Tsuruta and Goto, 2007).

Another indicator of competition is the strength of the relationship between growth parameters and absolute size (mass or length of an individual) or relative size (a ratio that represents how large or small an individual is relative to the rest of the population; Ziemba and Collins, 1999). Past studies have shown that body size differences within a population determine the outcome of competition by affecting larval growth rates, timing to metamorphosis, and survivorship of individuals (Smith, 1990; Brunkow and Collins, 1996, 1998). If the method through which larger individuals affect smaller, potentially gape-limited individuals is via exploitative competition, we hypothesize that absolute size will be a better predictor of future growth rate and time to metamorphosis than relative size and that aggressive attacks made and received will not be related to size. If larger individuals outcompete smaller individuals primarily through aggressive interactions (interference competition), we hypothesize that relative size will be a better predictor than absolute size: the largest individuals in a population will perform the most aggressive attacks and subsequently have the fastest growth rate and time to metamorphosis, regardless of their absolute size.

In this study, we investigated whether absolute or relative size of individuals within a population explained the most variation in aggression, future growth rate, and time to metamorphosis in the Mole Salamander, *Ambystoma talpoideum*. This study improves on past work in several key ways. First, this study followed individuals to determine the relationship between individual body size, aggression, future growth rate, and time to metamorphosis, in contrast to past studies that used average body size within each tank (Smith, 1990; Brunkow and Collins, 1996; Ziemba and Collins, 1999; Wildy et al., 2001) or did not consider behavioral characteristics in connection with life-history characteristics (Maret and Collins, 1994; Brunkow and Collins, 1998). Second, although many studies have considered the effects of relative or absolute size (Maret and Collins, 1994; Brunkow and Collins, 1996, 1998; Frankino and Pfennig, 2001), none have considered whether absolute or relative size is the best predictor of future growth and time to metamorphosis. Because *A. talpoideum* is a facultatively paedomorphic species, the effect of size variation on morphotype was also considered, although it was not the primary goal of this study.

MATERIALS AND METHODS

Study Organism.—*Ambystoma talpoideum* is widespread across the southeastern United States and is facultatively paedomorphic throughout its range (reviewed in Petranka, 1998). Variation in larval body size is common in nature, in part because paedomorphs typically breed and produce offspring earlier than metamorphic adults (Scott, 1993; Whiteman and Semlitsch, 2005). The initial growth advantage of these larvae may result in larger body size and increased likelihood of survival (Ryan and Plague, 2004). Larvae can mature and begin metamorphosing by the following summer, and those that do not metamorphose may mature as paedomorphs (Semlitsch, 1987; Gibbons and Semlitsch, 1991).

Experimental Design.—Embryos of *A. talpoideum* were collected on 20 February 2004 from Ridley Pond in Murray, Kentucky, an ephemeral pond surrounded by forest and agricultural fields. Sampling was conducted around the entire perimeter of the pond to ensure that the embryos came from clutches of multiple females. Our initial experimental design sought to create independent variation in both absolute size (through temperature treatments) and relative size (as a result of variation in growth and mortality within a population). Therefore, embryos in groups of 97 eggs, 144 eggs, and 112 eggs were raised in separate incubators at temperatures of 6°, 9.5°, and 13°C, respectively. Some of the collected embryos were more developmentally advanced than others and were preferentially selected for the 13°C treatment. All other embryos were randomly dispersed among treatments. On 5 March 2004, embryos were removed and randomly dispersed into replicates consisting of eight individuals raised at room temperature within a 5.7-L plastic storage container (dimensions: 34.3 L × 21 W × 12.1 cm H, hereafter ''tank''). Larvae hatched and developed in these containers until ultimately being moved to larger mesocosms (see below). We used 12 replicates of 6°C individuals (96 total individuals), 18 replicates of 9.5°C individuals (144 total individuals), and 12 replicates of 13°C individuals (96 total individuals) for a total of 42 tanks. This experimental design had an unequal number of replicates because it was originally designed for another experiment.

When incubation ended on 5 March 2004, embryos that developed at warmer temperatures were in later Harrison stages of development than those raised at cooler temperatures. Specifically, embryos raised at 6°, 9.5°, and 13°C were at approximate Harrison stages 18–19, 29–30, and 41–43 (Harrison, 1969). As a result, individuals raised at higher temperatures hatched earlier than those raised at lower temperatures. Larva raised at 6°, 9.5°, and 13°C hatched within 13–18, 4–14, 0–6 days, respectively, of being introduced into tanks. The position of an individual larva within the size distribution of individuals raised at the same temperature was, thus, the result of intrinsic variation within the tank. Likewise, differences in density among tanks resulted from natural mortality and cannibalism.

We placed paper partitions between containers such that visual cues from individuals in the surrounding treatments would not affect individuals within a container (Collins and Cheek, 1983). Larvae were fed brine shrimp (0.015 g of eggs per larvae; Collins and Cheek, 1983) on a daily basis for six weeks and then switched to a diet of California blackworms (0.02 g per larvae initially, increasing as the larvae grew to 0.20 g per larvae). In both cases, food was distributed evenly across the tank. We siphoned wastes from the plastic containers twice per week and replaced 2–6 liters of water weekly to keep the water level constant. After roughly four months, salamanders had grown large enough that they required larger plastic containers (18.9 L; dimensions: 42.2 cm L × 29.9 cm W × 17.8 cm H), and wastes were siphoned and replaced (as above) once per week.

On 8 June 2004, fungal contamination caused mortality in animals from six tanks; thus, treatments with larvae raised at 6°, 9.5°, and 13°C now contained 10, 15, and 11 replicates, respectively. By July 2004, larvae were large enough to measure and mark individually ($>$17 mm, Doyle and Whiteman, 2008) using visible implant elastomers (Northwest Marine Technologies, Tumwater, WA). Individuals also began to mature sexually at this time. On a bimonthly basis, we measured individuals for snout–vent length (SVL) and total length with a metric ruler (nearest millimeter) and mass with a balance (nearest 0.1 g). Tanks were checked daily for metamorphosing individuals once larvae had reached a minimum size of 35 mm (Semlitsch, 1987). We immediately measured metamorphosed individuals for SVL, total length, and mass. Sexual maturity was determined by inspection. Then we sacrificed metamorphs in 0.04% benzocaine solution before being fixed in 10% formalin for 24 h and preserved in 70% EtOH. In March 2005, all animals that had not metamorphosed were sacrificed, fixed, and preserved.

Preserved animals were dissected in July 2005 to confirm sex and reproductive status. Females had oviducts and egg clutches, whereas males had convoluted vas deferens. When none of the above characteristics were visible, the animal was considered immature. We scored males and females as mature or immature. Males scored as mature had black, translucent, and extremely convoluted vas deferens, whereas immature males had translucent, slightly wavy vas deferens. Mature females had fully developed egg sacs with differentiated eggs as well as thick, white, and extremely convoluted oviducts. Immature females had slightly wavy, white oviducts, and white egg sacs with undifferentiated eggs (HHW, unpubl. data).

Behavioral Observations.—We conducted behavioral observations between July and September 2004. Larvae remained in their containers during trials, and each had been individually marked as described above. On a biweekly basis, frequency of aggressive behaviors was quantified for 10 min for each replicate of each treatment (a 3-min acclimation period to human presence was maintained prior to each observation period). Food was placed in each container at the beginning of the 3-min acclimation period. Encounters were defined as occurring when two larvae approached within 1 cm of each other (Brunkow and Collins, 1998). We recorded which individual displayed the aggressive behavior (attacks made) and which individual received it (attacks received). Aggressive behaviors were classified as ''move toward'' (aggressor larva moves toward second larva, which moves away immediately), ''snaps'' (aggressor larva rapidly opens and closes mouth toward a second larva, which moves away) and ''lunges'' (aggressor larva moves rapidly and abruptly toward a second larva) (Brunkow and Collins, 1998). All aggressive behaviors were summed for analyses of the relationship between aggressive behavior and body size (relative and absolute). Nonaggressive behaviors, or ''close proximities,'' were said to occur when two larvae encountered and remained near each other without displaying aggression (Brunkow and Collins, 1998).

Analyses.—Preliminary analyses using stepwise regression found that, for a given time point, mass was a better predictor of time to metamorphosis than SVL or total length ($r^2 = 0.5$, $P < 0.0001$). The three body size variables were correlated (all $r > 0.94$, all P-values < 0.0001), and as a result, subsequent analyses

TABLE 1. Mean, standard error, and range for absolute and relative mass across five time points. Absolute mass is in grams. Relative mass was calculated by averaging mass for the entire tank and then dividing an individual's mass by the mean.

Independent variables	Time	Mean	SE	Range
Absolute mass	1	1.44	0.08	0.32–3.64
	2	4.92	0.21	0.89–8.71
	3	7.84	0.41	2.08–14.28
	4	11.04	0.58	3.3–18.12
	5	14.19	0.72	4.67–22.23
Relative mass	1	0.63	0.03	0.08–1.56
	2	1.05	0.05	0.26–2.63
	3	1.02	0.06	0.19–1.75
	4	1.04	0.05	0.28–1.69
	5	1.08	0.05	0.36–1.78

used only mass for calculations of absolute and relative body size. We also determined that, as of July 2004 (the point at which larvae were large enough to mark individually), there were no significant differences in mean mass between individuals from the three temperature treatments (repeated-measures ANOVA; $F_{2,83} = 1.1$, $P = 0.34$). As a result, the temperature treatment was excluded from further analysis.

All statistical analyses were conducted using StatView 5.0.1 (vers.; SAS Institute, Cary, NC, 1998) or SAS 9.3.1 (SAS Institute, Cary, NC, 1999). For each sampling period, absolute mass, relative mass, density within the tank, and resulting future growth rate were calculated for each individual. Relative mass of individuals was determined by dividing the mass of the individual by the mean mass of all individuals within the same tank (N ranged between 2 and 8 individuals depending on time during the experiment, as individuals were removed from tanks when they metamorphosed). Future growth rate was calculated from the difference in mass between two time points, divided by the number of days between those time points. To determine whether variability in size between individuals within a tank changed over time, the coefficient of variation of mass for each tank was calculated for each repeated measure. With the exception of behavioral analyses, log- or arcsine-square root transformations were used to help satisfy normality and/or homogeneity assumptions.

The available data were analyzed on several different levels. As predictor variables, we considered relative body size, absolute body size, and density in analyzing each of the following responses: (1) future growth rate, mixed-model repeated-measures analysis; (2) time to metamorphosis, mixed-model repeated-measures analysis; and (3) behavior, mixed-model repeated-measures analysis with a Poisson distribution (separate analyses were conducted for both attacks made and attacks received).

The SAS MIXED procedure was used to obtain responses 1 and 2. The GLIMMIX procedure was used to accomplish response 3. The GLIMMIX procedure was additionally used to analyze the effects of time and density on type of aggressive attack (Poisson mixed-model repeated-measures). First-order autoregressive (appropriate for repeated-measures analysis) was used to model the covariance structure in the above analyses. Sample sizes and degrees of freedom differed between data analyses and sampling dates, as the time at which an individual metamorphosed chiefly determined how many data points were relevant to a particular time point or analysis. The MIXED and GLIMMIX procedures in SAS are both appropriate for analyzing missing and unbalanced data (SAS System for Mixed Models, R. C. Little, G. A. Milliken, W. W. Stroup, and R. D. Wolfinger, SAS Institute, Cary, NC, 1996).

Explanatory variables and their higher order interactions were included in an initial model. If the highest-order interactions (third or fourth order) were nonsignificant (P-values > 0.05), they were dropped from the model. This process was repeated with the next highest-order interactions, until only main effects and significant interactions remained in the model.

RESULTS

Absolute mass, relative mass, and future growth rate varied across time points (Tables 1, 2). Factors associated with growth rate are presented in Table 3 (mixed-model analysis), and the final model is growth rate $= 0.05011 + 0.000869_{\text{absolute mass}} + 0.03_{\text{relative mass}} - 0.00344_{\text{density}} + 0.000952_{\text{absolute mass} \times \text{density}} - 0.00302_{\text{absolute mass} \times \text{relative mass}}$. There were significant main effects of relative size and

TABLE 2. Mean, standard error, and range for future growth rate, attacks made, attacks received, and time to metamorphosis across relevant time points. Growth rate was calculated as the difference in mass between two time points, divided by the number of days between time points (g/day). Time to metamorphosis is measured in days from July 2004, when animals were large enough to be marked.

Dependent variables	Time	Mean	SE	Range
Growth rate	1	0.048	0.002	0.007–0.089
	2	0.059	0.003	0.0120–0.14
	3	0.058	0.003	0.010–0.103
	4	0.066	0.003	0.017–0.110
	5	0.069	0.004	0.026–0.115
Attacks made	1	1.95	0.20	0–13
	2	1.99	0.19	0–13
	3	1.58	0.20	0–11
Attacks received	1	1.98	0.15	0–9
	2	1.93	0.16	0–7
	3	1.57	0.18	0–8
Time to metamorphosis	n/a	74.49	4.49	2–225

density, but interpretations must be made carefully in light of the interactions of both density and relative mass with absolute mass. The main effects apply when the absolute mass is small and contributions from the interactions are minimized. When the animals are of small mass, the coefficients indicate that growth rate increased with relative size and decreased with increasing density. The coefficients on the interactions for density × absolute size and relative × absolute size are of the opposite sign as the respective main effects, meaning that the main effects of relative size and density were diminished as animals aged and grew larger. For these larger animals, absolute mass was the determining factor in their growth rate.

To visualize how absolute and relative size affect growth rate, we identified individuals of small absolute mass (25th percentile and below; Fig. 1A) and large mass (75th percentile and above; Fig. 1B) across all time points in the data set. For each group, we plotted growth rate by relative mass, demonstrating that this relationship is most informative when individuals of small absolute mass are considered (Fig. 1A).

Of the 192 animals dissected for maturity, 161 metamorphosed during the experiment, 29 became paedomorphic, and 2 remained larval. There was a negative relationship between time to metamorphosis and relative mass (mixed-model analysis, Table 3). To visualize these data, we graphed the relationship between time to metamorphosis and relative size in July only (Fig. 2). Time to metamorphosis was not significantly affected by density, absolute mass, or any of the higher order interactions (all $F < 2.95$, all P-values > 0.05). Therefore, the final model was time to metamorphosis $= 0.1070 - 0.5479_{\text{relative mass}}$.

Mixed-model analysis with a Poisson distribution revealed that number of attacks made on other individuals was best explained by relative size (Table 3). The best model is attacks made $= -0.4738 + 0.4334_{\text{relative mass}}$. The number of attacks made by individuals increased with the relative mass of the individual within the tank ($F_{1,77} = 5.97$, $P = 0.02$) but was unaffected by absolute mass, density, or any of the higher order interactions (all $F < 0.25$, all P-values $>$ 0.05). Number of attacks received by individu-

TABLE 3. Relationships between individual life-history parameters and aggressive behaviors and relative size, absolute size, and density. Mixed-model analysis was used to assess the significance of each effect.

Dependent variable	Independent variable	Parameter estimate	SE	df	P-value
Growth rate (per day)	Absolute mass	0.000869	0.0014	170	0.54
	Relative mass	0.03092	0.0060	234	<0.0001
	Density	−0.00344	0.0013	248	0.013
	Absolute mass × density	0.000952	0.0002	206	0.0001
	Absolute × relative mass	−0.00302	0.0009	204	0.002
Time to metamorphosis	Absolute mass	−0.03832	0.05602	149	0.4950
	Relative mass	−0.5479	0.1266	149	<0.0001
	density	0.01567	0.01552	149	0.3144
Attacks made	Absolute mass	0.04332	0.05925	77	0.4669
	Relative mass	0.4334	0.1774	77	0.0168
	density	0.1081	0.06175	77	0.0840

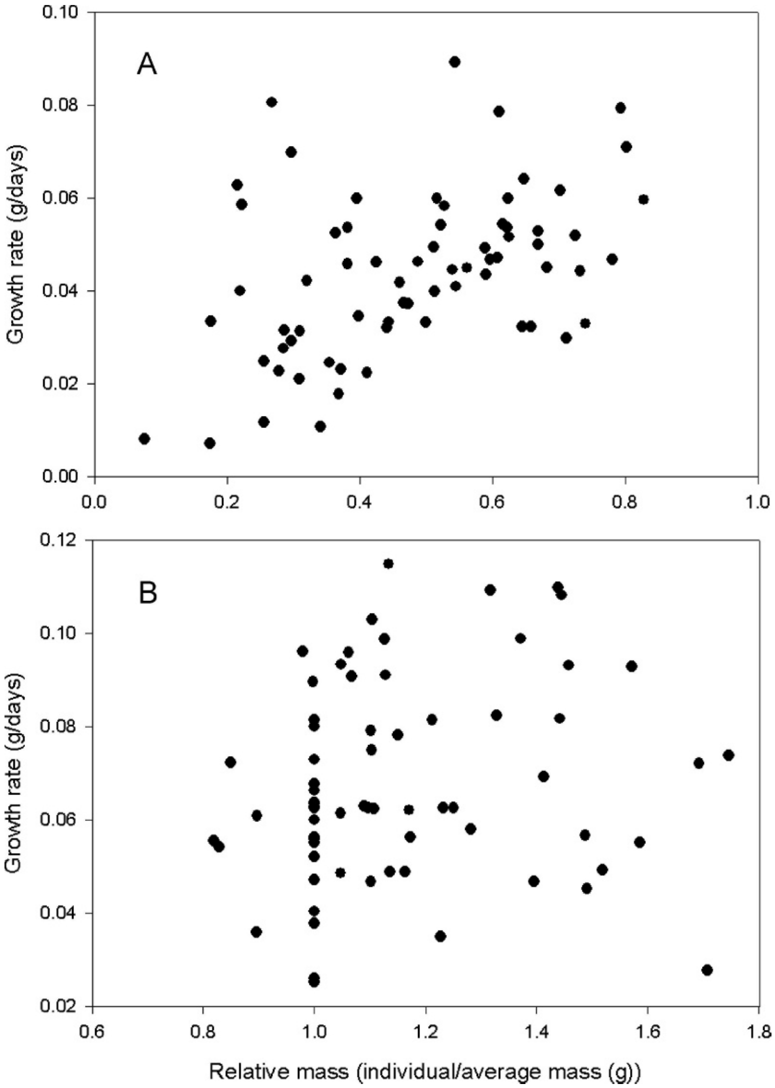

FIG. 1. The relationship between relative size and growth rate in small (25th percentile or below; panel A) and large (75th percentile or above; panel B) individuals. The full model found that relative size was positively related to growth rate (mixed-model analysis, $F = 26.63$, $P < 0.0001$; Table 3) but that the relationship was most important when animals were small.

als were unaffected by any of the variables considered in this study (Table 2; all $F < 2.53$, all P-values > 0.05).

Across tanks, each type of aggressive behavior increased significantly with increasing density within tanks (mixed-model analysis, Table 4). Lunges also increased significantly with time ($F_{2,60} = 4.35$, $P = 0.02$), but neither move toward nor snaps were significantly affected (all $F < 1.43$, all P-values > 0.05). Number of nonaggressive behaviors (close-proximities) was significantly related to time ($F_{2,60} = 3.83$, $P = 0.03$) and density ($F_{1,60} = 7.37$, $P = 0.009$).

DISCUSSION

Future Growth Rate and Time to Metamorphosis.—In this study, we hypothesized that if larger individuals out-compete smaller individuals through interference competition then larger individuals will perform the most aggressive attacks and relative size will be a better predictor than absolute size of life-history parameters such as growth rate and time to metamorphosis. The interaction between relative and absolute mass indicates that future growth rate of individuals within these populations can be a function of both interference

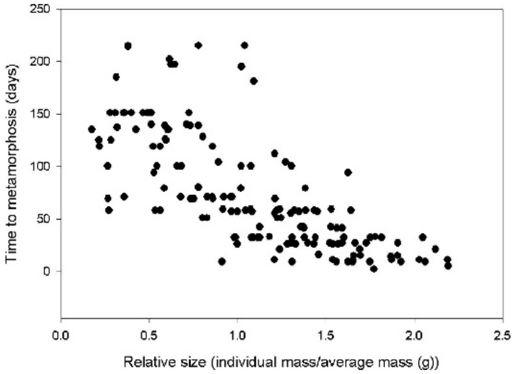

FIG. 2. The relationship between time to metamorphosis and relative size in July 2004. The full model found that time to metamorphosis was negatively related to relative size (mixed-model analysis, $F = 18.72$, $P < 0.0001$; Table 3).

and exploitative competition in proportions that depend on life stage. Relative size (associated with interference competition) explained more variation in growth rate for smaller animals, but absolute size (associated with exploitative competition) had more influence on growth rate as individuals grew. The relative importance of the two types of competition was difficult to unravel because of the complexity of the relationships (but see below).

The interaction between density and absolute mass had a positive effect on future growth rate; thus, the greatest positive contributions to growth rate occurred at both high densities and high absolute mass. At small absolute sizes, however, density had a negative effect on growth rate. Absolute size may reflect the extent of energetic reserves better than relative size, which can affect the duration of aggressive encounters (Englund and Olsson, 1990; Mathis and Simons, 1994). Aggressive behaviors increase with increasing density, making absolute mass increasingly important for successfully obtaining resources. Alternatively, the effects of the interaction primarily may be caused by absolute size, because density and absolute size were negatively correlated ($r = -0.62$, $P < 0.0001$).

A disproportionate number of metamorphs, as opposed to paedomorphs, were produced from this experiment. Metamorphosis is favored in drying ponds (Semlitsch, 1987), and the relatively low water level in tanks and high density of individuals/L may have prompted the majority of larvae to metamorphose. Time to metamorphosis was best explained by relative mass, with the largest individuals in a tank metamorphosing, whereas smaller larvae delayed transformation. Wilbur and Collins (1973) argued that, if growth rate is rapid but body size is small, larvae will delay metamorphosis to take advantage of growth opportunities in the aquatic habitat. If the body size is small and growth rate is slow, natural selection favors metamorphosis rather than remaining in the pond and risking predation within the aquatic community (Wilbur and Collins, 1973). The cues that an individual receives about their growth rate and ability to metamorphose and compete in a terrestrial environment may be based on the size of surrounding individuals, not just absolute size. For example, Maret and Collins (1994) found that the development of a cannibalistic phenotype was influenced by the relative size of a larva within the size distribution of their population, not their absolute size.

Aggressive Behavior and Size.—In this study, larger larvae had a size advantage in physical interactions and aggressive behavior toward other individuals was best predicted by an individual's relative position within a size distribution, not their absolute size. These results support the hypothesis that larger individuals secure more resources through interference competition than smaller individuals, as predicted by this study. Like Brunkow and Collin's (1998) study, aggressive attacks were not made differentially on smaller versus medium-sized larvae, as the model explaining attacks received was not significantly related to size or density. Brunkow and Collins (1998) explained the lack of discrimination between small- and medium-sized larvae with the hypothesis that the aggressive behaviors of large larvae may serve different purposes. Attacks on smaller larvae may be attempted cannibalism, whereas attacks on medium-sized larvae may be to displace them from food.

Across tanks, total number of behaviors and number of each type of aggressive behavior did

TABLE 4. Relationships between aggressive behaviors within populations and density and time. Mixed-model analysis was used to assess the significance of each effect.

Dependent variable	Independent variable	Parameter estimate	SE	df	*P*-value
Snaps	Density	0.3962	0.09895	60	0.0002
Move toward	Density	0.3070	0.08172	60	0.0004
Lunges	Density	0.2713	0.1003	60	0.0089

not change significantly with time (with the exception of lunges increasing with time) but were positively related to density. No overt trade-offs appear to occur between more aggressive behaviors (i.e., lunges) and less aggressive behaviors (i.e., move toward). Size variation is known to influence patterns of aggression (Brunkow and Collins, 1998), and we hypothesized that density might have been correlated with differences in size variation within tanks (i.e., size variation decreasing within tanks as large individuals metamorphosed and were removed). A positive relationship did exist between density and size variation within tanks, because tanks with decreased density housed more similarly sized individuals. However, past research has found that populations of similarly sized individuals are typically more aggressive (Brunkow and Collins, 1998); thus, it is odd that in this case, populations with decreased size variation enjoyed less antagonistic environments. In our study, aggression may have been related to over-crowding within tanks, which decreased as density decreased, rather than body size.

In sum, this study found evidence for a complex relationship between population size structure, future growth rate, and time to metamorphosis by tracking the effects of relative size on individuals within a population, something that has not been attempted in earlier work. When we consider all of the above analyses, they indicate that relative size is the best predictor of life-history parameters in larval Mole Salamanders. The increase in aggressive behaviors displayed by relatively larger individuals provides particularly strong evidence for the role of interference competition in regulating populations. However, future studies should contain populations with greater overall size differences; hence, that absolute size and relative size can be independently compared. Studies such as these legitimize the importance population ecologists place on individual phenotypic variability with populations (Hassel and May, 1985; Sutherland, 1996), whereas the effects of size structure found on time to metamorphosis and growth rate exemplify how populations are affected by phenotype-specific fitness characteristics.

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