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Biotic and Abiotic Predictors of Larval Salamander Size and Density

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Both abiotic and biotic factors influence population and community structure. However, the simultaneous assessment of the relative importance of both types of factors is rarely performed for multiple traits of a population, such as body size and abundance. Comparisons among different demographic rates are necessary for teasing apart the importance of species interactions and/or environmental conditions on both population and community structure. We tested whether biotic (e.g., larval competition) or abiotic factors influenced larval salamander density and body size in natural populations of two known salamander competitors, *Ambystoma talpoideum* and *A. maculatum*. Over six years, we surveyed 33 ponds where these species co-occur in western Kentucky, USA. We found that larval densities between species were positively correlated, and that habitat features had contrasting, species-specific effects. Larval sizes for each species showed negative intra- and interspecific relationships with larval densities of each species, but larval *A. maculatum* generally exerted the stronger relative interspecific effect. Overall, our study highlights that different characteristics of a population (i.e., body size or abundance) may be differentially affected by abiotic and biotic factors, even for ecologically similar, sympatric species. Understanding which traits are regulated by each component will advance our knowledge on how populations and communities are structured.

THE relative importance of abiotic and biotic factors as limiting constraints for an organism commonly varies among species, such that when individuals interact (e.g., interspecific competitors, predator-prey), species-specific responses to a shared environment can dictate the outcomes (Menge and Sutherland, 1987; Chesson, 2000). Variability among these responses can occur even for seemingly similar species (either ecologically or taxonomically), which may be important in explaining the outcome of their interactions and resulting patterns of coexistence (Amarasekare, 2003; Resetarits and Chalcraft, 2007). Asymmetric responses to abiotic and biotic constraints among species also results in the potential for apparent effects to emerge, where the effects of one limiting factor mimics those of others, resulting in erroneous conclusions about the true mechanism of variable demographic rates (e.g., apparent competition; Holt, 1977). Identifying how interacting species respond to limiting biotic and abiotic factors in a shared environment is therefore necessary to understand the underlying mechanisms that influence each species' population dynamics, as well as community structure.

Larval amphibian communities in pond ecosystems are constrained by both biotic and abiotic factors (Wilbur, 1997). Hydroperiod is arguably the dominant abiotic constraint, as it can limit recruitment when ponds dry prior to the completion of metamorphosis (Semlitsch et al., 1996; Anderson et al., 2015a). Hydroperiod also dictates the predator communities co-occurring with larval amphibians (Wellborn et al., 1996; Semlitsch et al., 2015), which can have strong consumptive and non-consumptive effects on amphibians (Relyea, 2007; Wissinger et al., 2010; Davenport et al., 2014). Canopy cover (Earl et al., 2011), water chemistry (Sadinski and Dunson, 1992), and the amount of suitable terrestrial habitat surrounding ponds (Peterman et al., 2014) also all affect the abundance of different amphibian species. Among biotic factors, density-dependent competition (intra- and interspecific) is particularly influential for larval amphibians, affecting both individual traits such as growth rates, size at metamorphosis, time to metamorphosis, and survival (Semlitsch and Caldwell, 1982; Anderson and Whiteman, 2015a), as well as population growth rates (Gazzola and Van Buskirk, 2015; Băncilă et al., 2016).

Many recent studies of natural populations of amphibians that have investigated population dynamics have consistently found that abiotic factors, such as canopy cover and hydroperiod, are more important in determining a species' occupancy and larval density than biotic factors, such as competition (Van Buskirk, 2005; Werner et al., 2007; Peterman et al., 2014; Ousterhout et al., 2015). However, other traits of populations have infrequently been investigated *in situ*. For example, few *in situ* studies have examined variation in body size as a result of density-dependent competition (Van Buskirk and Smith, 1991; Werner et al., 2009; Indermaur et al., 2010; Grözinger et al., 2014; Anderson et al., 2015b), which is often a focus of mesocosm or laboratory studies. Furthermore, Ousterhout et al. (2015) found that habitat factors determined intraspecific variation in larval salamander density in natural populations, but intra- and interspecific competitor density determined larval size, suggesting different factors may regulate these two responses. Few studies have investigated this hypothesis, however, and because body size is often correlated with adult fitness (Semlitsch et al., 1988; Earl and Whiteman, 2015), understanding which factors regulate different aspects of larval ecology (abundance versus body size) is critical in understanding population structure and dynamics. Alternatively, processes occurring at the individual level may have negligible impacts on overall population dynamics (Vonesh and De la Cruz, 2002).

The primary objective of this study was to quantify the relative contributions of biotic and abiotic factors on larval body size and abundance in natural populations of two pond

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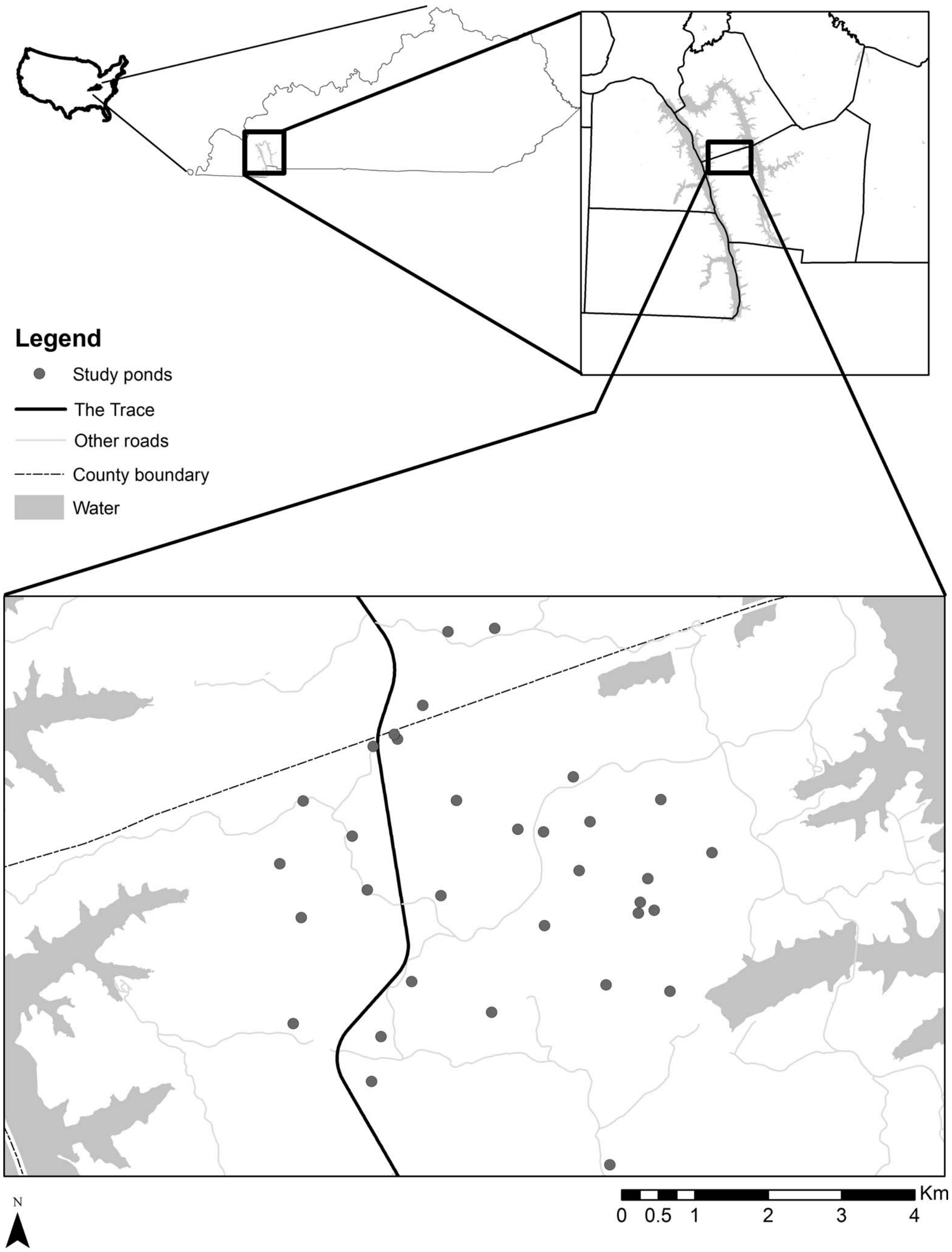

Fig. 1. Study area in Land Between the Lakes National Recreation Area (LBL), Kentucky, USA. The Trace is the primary paved road through LBL. Water to the west of the study area is Kentucky Lake and water to the east is Lake Barkley. The county boundary line separates Trigg (south) and Lyon (north) counties.

breeding salamanders, the spotted salamander (*Ambystoma maculatum*), and the mole salamander (*Ambystoma talpoideum*). We report the results of monitoring efforts at 33 populations in western Kentucky, USA, where abundance and larval body size were tracked over six years. We predicted that each species would exhibit negative density-dependent size variation, but that intraspecific competition would influence this relationship more than interspecific competition (Semlitsch and Walls, 1993; Anderson and Whiteman, 2015a). We also expected that, similar to Ousterhout et al. (2015), habitat variables would be a better predictor of a focal species' density when compared to interspecific competitor density.

MATERIALS AND METHODS

Study species.—*Ambystoma talpoideum* and *A. maculatum* are both common pond-breeding amphibians throughout much of the southeastern USA (Petranka, 1998) that utilize similar breeding ponds (but see Semlitsch, 1988) and show dietary overlap (Branch and Altig, 1981; Freda, 1983; Taylor et al., 1988). Walls and Jaeger (1987) documented alternative competitive strategies between individuals of these species, wherein larvae of *A. maculatum* are superior exploitative competitors and larvae of *A. talpoideum* are dominant interference competitors. Experimental studies have shown strong intraspecific competition occurs among individuals of both species with weaker interspecific effects by *A. talpoideum* on *A. maculatum*, but without strong reciprocal effects of *A. maculatum* on *A. talpoideum* (Semlitsch and Walls, 1993; Anderson and Whiteman, 2015a, 2015b).

Study location.—We monitored natural populations of larval *A. talpoideum* and *A. maculatum* over six years in a 65 km^2 section of the Land Between the Lakes National Recreation Area (LBL) in Trigg and Lyon counties, Kentucky (Fig. 1). We determined pond locations using aerial photographs (e.g., Google Earth©), LBL trail maps, and known breeding sites of *A. talpoideum* (A. F. Scott, pers. comm.). Ponds were primarily constructed for wildlife by the Tennessee Valley Authority beginning in 1966 (Jacobs, 2004), though the ages of the ponds we surveyed are unknown. Most ponds are surrounded by mixed hardwood forest and within 50 m of current or abandoned agricultural fields, while a few ponds are located within open grasslands. Pond area varied from 25 m^2 to 4500 m^2, resulting in differential canopy closure over ponds. Hydroperiod was nearly permanent for all ponds; subsequent visits to ponds in late summer and fall determined the majority of the ponds maintained relatively constant water levels and very few dried every year. Pond benthos were composed largely of leaf litter dominated by oak (*Quercus* spp.), hickory (*Carya* spp.), sweetgum (*Liquidamber styraciflua*), American beech (*Fagus grandifolia*), and sycamore (*Platanus occidentalis*). Several ponds had emergent grasses, rushes, and cattails along the margins, but few ponds were dominated by emergent or floating vegetation.

Several other salamanders co-occur with the focal species at our study site. Red-spotted newts (*Notophthalmus viridescens*) were observed in nearly all ponds each year, whereas marbled salamanders (*Ambystoma opacum*) and eastern tiger salamanders (*A. tigrinum*) were observed infrequently in a low number of ponds (12 and 1 total ponds over six years, respectively) and usually at low densities (TLA, unpubl. data). Most ponds are also inhabited by several ranids, with most observations being *Rana clamitans* and *R. sphenocephala/ palustris* (indistinguishable as tadpoles) and only a few *R. catesbeiana*. We also have observed paedomorphic and overwintering larval stages of *A. talpoideum* in all but one pond where this species occurred, which potentially have predatory effects on population dynamics of these species (Anderson et al., 2013), though we typically observe low densities of each of the larger stages (TLA, unpubl. data). For this study, we did not analyze *A. talpoideum* from older cohorts, or include them in counts of individuals contributing to competitive effects, focusing only on competition within a given cohort. The results of the analyses were qualitatively similar regardless of their inclusion.

Sampling procedure.—We surveyed a variable number of ponds within each year of the study and used different survey techniques split across two distinct time periods (2009–2011 and 2013–2015; hereafter, Period 1 and Period 2). The switch in sampling protocols occurred due to a change in research focus, as Period 1 was developed for Anderson (2011), whereas Period 2 corresponds to ongoing projects on population ecology of *A. talpoideum*. The switch also occurred due a better understanding of and wanting to account for imperfect detection in sampling and analyses (MacKenzie et al., 2002; Royle, 2004). The number of ponds surveyed varied due to differing time constraints and availability of personnel in each year.

For Period 1, we surveyed 30 ponds in 2009, 32 ponds in 2010, and 24 ponds in 2011. All ponds in this period were visited once between 27 May and 25 July, and surveyed using a modified form of quantitative enclosure sampling (i.e., Shaffer et al., 1994). We determined survey points within a pond by placing two tape measures along pond margins to form a 90-degree angle and choosing two random distances; their point of intersection from the tape measures was the sample point. At each sample point, we placed a plastic cylindrical drop sampler (i.e., pipe sampler; volume = 0.1462 m^3, circumference = 152.5 cm, height = 79 cm) firmly into the pond bottom to ensure no salamanders could escape horizontally. Points deeper than 0.8 m were not sampled as that depth exceeded the sampler height, though the range of depths where salamanders were captured only spanned 3–52 cm. If underwater structures (i.e., downed trees) blocked a seal from occurring, the sample point was abandoned. We recorded the water depth of the survey point and used a dip net to remove all salamanders within the sampler; three consecutive scoops yielding no salamanders determined the end of each sample point. Sampling occurred until 30 total larval salamanders (both *A. talpoideum* and *A. maculatum* combined) were captured in each pond, or until ten sample points were conducted at each pond. In ponds where we caught 30 salamanders in fewer than ten sample points, we conducted a minimum of at least three samples. We calculated naïve larval density as the number of individuals divided by the total volume of water sampled, as we did not have repeat visits to calculate densities adjusted for detection (see below).

In Period 2, we sampled 13 ponds in 2013, 33 ponds in 2014, and 33 ponds in 2015 between 9 May and 3 July using a combination of dip net sweeps and collapsible mesh minnow traps (38 × 28 × 28 cm, 6 mm opening; Memphis Net and Twine, Memphis, TN). The number of traps and dip net sweeps were scaled to pond area, where we performed one dip net or set one trap per 25 m^2 of surface area and added one dip/trap as surface area doubled (Shulse et al., 2010; Peterman et al., 2014). We set traps and dip netted within 2 m of the shoreline at each pond. In each year, we primarily conducted 5–6 surveys at most ponds (3 dip net samples and 2–3 trap nights per pond); two ponds had one trap night and two dip net sweeps in 2014, and three ponds in 2015 received only one dip net survey as they were newly discovered at the end of sampling. We identified all amphibians to species and life stage, and released them back to the pond. We calculated a naïve density estimate during this period by dividing the number of larvae captured for each species by sampling effort (total number of dipnets and traps performed, or capture per unit effort, CPUE).

For both survey periods, we placed up to 30 captured salamanders in plastic containers to measure body size. In 2009 and 2010, we measured salamander snout–vent length (SVL) and total length (TL) using a wooden measuring board. In 2011–2015, we photographed larvae in a pan of water over a ruler and measured SVL, TL, and head width (HW) from photographs using ImageJ (Rasband, 1997; Abràmoff et al., 2004).

For abiotic variables, we recorded a combination of local and landscape level features. Pond area was determined by pacing or using a tape measure along the maximum length and width. We determined canopy closure using a spherical densiometer during full leaf-out in the summer of 2014 and assumed this number would provide a similar estimate for all years. We calculated the amount of deciduous forested habitat within a 500 m (in km^2) circular buffer around each pond (National Land Cover Database; http://kygeonet.ky.gov/), which encompasses where most adults and juveniles live (Semlitsch, 1998; Scott et al., 2013). We also determined the number of ponds within 1000 m (pond clustering), which is the maximum dispersal distance for most ambystomatids (Smith and Green, 2005). Both of these metrics were calculated using Arc GIS 10.3 (ESRI, Redlands, CA).

Statistical analysis.—Due to the differing methodologies used, we conducted separate analyses for each sampling period. We acknowledge this limits direct quantitative comparisons

Table 1. Capture summaries by year for *Ambystoma talpoideum* and *A. maculatum* in ponds at Land Between the Lakes National Recreation Area from 2009–2014.

Year	Total ponds surveyed	Ponds with only *A. maculatum*	Ponds with only *A. talpoideum*	Ponds with both species	Ponds with no detections
2009	30	17	1	12	0
2010	32	21	1	8	2
2011	24	10	0	7	7
2013	13	2	0	10	0
2014	33	11	2	17	2
2015	33	17	0	17	0

among the two study periods but at least provides qualitative comparisons of the same study sites across different years and methods. Such qualitative comparisons among study periods would be analogous to comparing our study with other published studies that used similar methods.

For Period 1, we analyzed two different response variables: larval abundance (raw total number of larvae captured) and larval size. Each response was modeled using a single mixed effects model. We modeled abundance using both a Poisson (log link) and a zero-inflated Poisson distribution for both species, but they provided equivalent fits and thus we report only the Poisson model. Abundance models for each species included covariates of naïve heterospecific density, percent canopy cover, pond surface area, pond clustering, mean sampling date and mean sampling depth. Hereafter, we distinguish the terminology larval abundance and larval density (as calculated above) as our response variable and a predictive covariate, respectively. Abundance models contained pond, year, and an individual level random effects to account for repeated sampling of ponds across years and to correct for overdispersion. Abundance models also included the total volume of water sampled as an offset term. An offset term adjusts responses that are measured at different rates (Kéry, 2010); in our case, the offset adjusts our counts by sampling effort (e.g., volume of water sampled), making our response variable comparable to an estimate of density (number/m^3). Larval size (SVL) was analyzed with linear mixed models using a normal distribution and the same covariates as above, with the addition of the naïve density of conspecifics, and pond and year as random effects. All covariates were centered and scaled prior to analysis; this procedure subtracts the variable mean and divides by the variable standard deviation for each value, which puts covariates that were measured on different scales in equivalent units. Importantly, it allows for a direct assessment of the relative strength of each covariate and improves convergence in JAGS models (Kéry, 2010). We initially tested for, but did not find, evidence of strong collinearity among any covariates ($r < 0.4$ for all pairwise combinations).

In Period 2, we again fit a single model for each of the two responses for each species. Because we conducted repeat visits in Period 2, we were able to analyze abundance while accounting for imperfect detection. Our analysis followed Kéry (2010), where we used binomial mixture models to estimate abundance (Royle, 2004). We used a Poisson distribution with a log link for abundance models, and abundance covariates (centered and scaled) included the naïve heterospecific density estimate, pond area, percent canopy cover, mean Julian date of sampling, pond clustering, and the amount of forest habitat within 500 m. We used sampling method (dip or trap) as a survey-specific detection covariate. We included the total number of traps and dip nets performed as an offset term to account for uneven sampling effort at ponds. We fit all three years of data together, with pond and year as random effects to account for the repeated sampling of ponds across years (Kéry, 2010). For size in Period 2, we again analyzed SVL but had to impute several (209 of 1992 measurements, or ~10%) of the values due to missingness. This procedure was conducted so that we could assess how covariates affected the same body size metric (SVL) between sampling periods. We imputed values based off of a linear mixed model of body size relationships, log(HW)~log(SVL)*Species, with pond and year as random effects. Using this imputation equation accounts for differences in body size allometries among species, a common trait among larval salamanders (Schmidt et al., 2006; Anderson et al., 2016). We modeled SVL using linear mixed models following a normal distribution, with canopy cover, pond area, naïve density estimates of each species, Julian date of sampling, the amount of forest within 500 m, and pond clustering as covariates, and pond and year as random effects.

We fit all mixed models within a Bayesian framework using Markov chain Monte Carlo simulation in JAGS via the jagsUI function in R (Plummer, 2003; Kellner, 2015; R Core Team, 2016). We used all uninformative normal or uniform priors. We ran all simulations in Period 1 and size models (including the allometry model) in Period 2 for 75,000 iterations with three chains, an adaptation and burn-in period of 10,000 iterations, and a thinning rate of 1:50. For Period 2, we had to run abundance models for considerably longer chains (750,000 iterations) with greater burn-in periods (250,000 iterations) and thinning rates (1:250). We considered models to have converged once all parameters obtained an Rhat of < 1.1, as well as visually inspected chains to ensure thorough mixing occurred. We also assessed model fit using Bayesian p-values (Gelman et al., 2014). These p-values range from 0–1, with values approaching 0.5 indicating a good fit. Our observed range of Bayesian p-values for all models fell within a reasonable range of this criterion ($P = 0.46$–0.56). We considered covariates to be significantly supported if more than 95% of their posterior distributions shared the same directionality of the posterior mean (*f*). We also report marginal effects, which we define as posterior distributions sharing 90% the same directionality as the mean. For the allometry model, we calculated the difference in intercepts and slopes between species, and classified parameters as different if the posterior difference did not include zero. Written formulation of models and example code can be found in the supplementary material (see Data Accessibility).

RESULTS

We captured at least one species of salamander in nearly all ponds in all years (Table 1), but *A. maculatum* was captured at

Table 2. Parameter estimates, 95% credible intervals (lower and upper), and the percent of the distribution that shared the same sign as the mean (*f*) for larval abundance of *Ambystoma maculatum* and *A. talpoideum*. Bold values indicate posterior distributions that are >95% the same sign as the mean, and italic values indicate posterior distributions that are >90% the same sign as the mean estimate.

Period	Species	Covariate	Estimate	Lower	Upper	*f*
Period 1	*A. maculatum*	Density of *A. talpoideum*	0.055	−0.299	0.411	0.623
		Canopy cover	*0.260*	*−0.121*	*0.640*	*0.911*
		Depth	**−0.462**	**−0.849**	**−0.060**	**0.988**
		Forest cover	0.058	−0.344	0.459	0.623
		Pond area	**−0.531**	**−0.943**	**−0.134**	**0.993**
		Pond clustering	0.019	−0.368	0.409	0.360
		Sampling date	**−0.889**	**−1.289**	**−0.495**	**1.000**
	A. talpoideum	Density of *A. maculatum*	0.048	−0.104	1.071	0.550
		Canopy cover	0.382	−0.702	1.611	0.749
		Depth	0.008	−0.094	0.115	0.550
		Forest cover	−0.436	−1.710	0.707	0.778
		Pond area	0.262	−0.755	1.476	0.687
		Pond clustering	0.539	−0.531	1.829	0.830
		Sampling date	−0.162	−1.141	0.769	0.635
Period 2	*A. maculatum*	Density of *A. talpoideum*	**0.162**	**−0.026**	**0.437**	**0.951**
		Canopy cover	−0.039	−0.565	0.496	0.566
		Forest cover	0.116	−0.399	0.664	0.662
		Pond area	0.118	−0.283	0.570	0.700
		Pond clustering	*−0.382*	*−0.968*	*0.186*	*0.919*
		Sampling date	**−0.429**	**−0.737**	**−0.123**	**0.997**
	A. talpoideum	Density of *A. maculatum*	**0.556**	**0.320**	**0.881**	**1.000**
		Canopy cover	0.338	−0.448	1.181	0.800
		Forest cover	−0.335	−1.170	0.553	0.794
		Pond area	−0.044	−0.589	0.470	0.553
		Pond clustering	0.459	−0.401	1.348	0.856
		Sampling date	−0.248	−0.665	0.162	0.885

more ponds and at higher densities than *A. talpoideum*. On average, the two species co-occurred in 43% of ponds surveyed. The average number of larvae caught per pond using the drop sampler in Period 1 was 18 *A. maculatum* (range: 0–77) and 2 *A. talpoideum* (range: 0–23). These values equate to average densities of 9.6 larvae/m^3 and 0.58 larvae/m^3, respectively. In Period 2, the average number of larvae caught was 21.6 *A. maculatum* (range: 0–217 for 3 day totals) and 1.9 *A. talpoideum* (range: 0–35 for 3 day totals) using dip nets and 11.9 *A. maculatum* (range: 0–97 for 3 day totals) and 1.8 *A. talpoideum* (range: 0–58 for 3 day totals) using minnow traps. CPUE estimates (larvae per total number of dip nets or traps) for *A. maculatum* were 5.6 (dips) and 3.1 (traps) and 0.50 (dips) and 0.38 (traps) for *A. talpoideum*.

Larval abundance.—In Period 1, larval abundance of *A. maculatum* was negatively related to pond area, mean sampling depth, and mean sampling date (Table 2, Fig. 2). There was also a marginal positive relationship of canopy cover with abundance of *A. maculatum* (91% probability that the effect was positive; Table 2, Fig. 2). For *A. talpoideum*, no covariates significantly predicted abundance.

In Period 2, larval abundance of *A. maculatum* showed a positive relationship with density of larval *A. talpoideum* and a negative relationship with sampling date (Table 1, Fig. 2). Pond clustering also showed a marginally negative relationship with abundance (Table 1, Fig. 2). Detection probability was significantly higher using dip nets compared with traps (mean detection [95% CI] probability in dip nets = 0.58 [0.13, 0.80], traps = 0.25 [0.16, 0.36]). Larval abundance of *A. talpoideum* in Period 2 was positively associated with density of *A. maculatum* (Table 2, Fig. 2), and no other factors were strong predictors. Similar to *A. maculatum*, detection probability was significantly higher with dip nets compared with traps for *A. talpoideum* (mean detection [95% CI] probability in dip nets = 0.78 [0.47, 0.93], traps = 0.26 [0.15, 0.39]).

Larval size.—In Period 1, larval SVL of *A. maculatum* showed negative relationships with conspecific density, density of *A. talpoideum*, canopy cover, and water depth, and positive relationships with pond area and sampling date (Table 3, Fig. 3). The effect of conspecific density on size of *A. maculatum* was twice as large as the effect of density of *A. talpoideum* (Table 3). For *A. talpoideum*, SVL showed negative relationships with density of *A. maculatum* and mean sampling depth (Table 3, Fig. 4). All other habitat covariates had posterior distributions that substantially overlapped zero.

For larval size in Period 2, there were significant differences in HW-SVL relationships between *A. maculatum* and *A. talpoideum* (Fig. 5). The scaling equations for each species were as follows: *A. maculatum* = $\log(\text{HW}) \sim -0.699 + 0.827 * \log(\text{SVL})$; *A. talpoideum* = $\log(\text{HW}) \sim -0.817 + 0.880 * \log(\text{SVL})$. Both intercept and slope values were significantly different between species, where *A. maculatum* showed greater allometry and *A. talpoideum* was more isometric. Larval SVL of *A. maculatum* was negatively associated with canopy cover and density of *A. talpoideum* and positively associated with sampling date and pond area (Table 3, Fig. 3). Larval SVL of *A. talpoideum* was positively related to sampling date (Table 3, Fig. 4), but no other covariates had strong support.

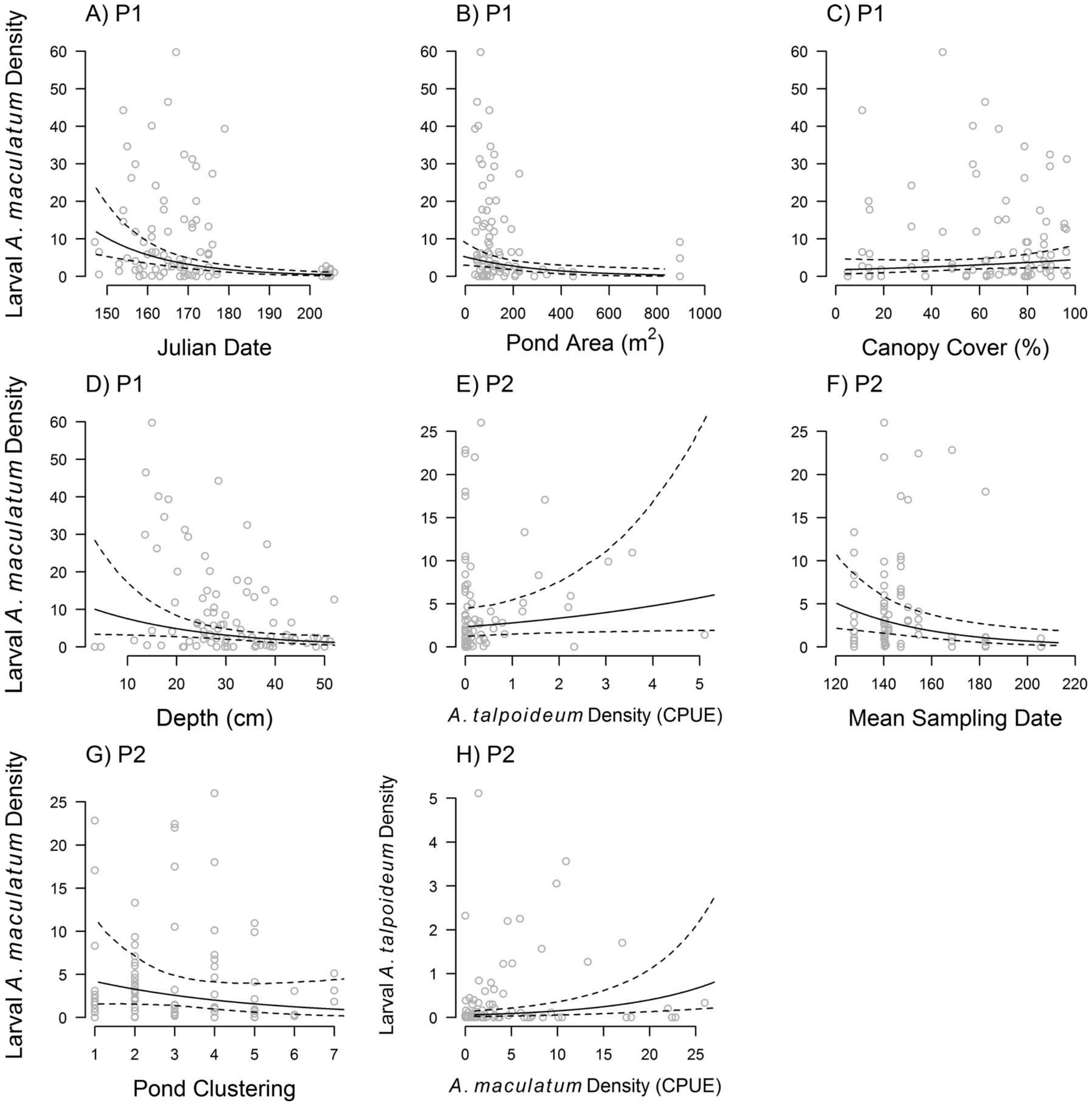

Fig. 2. Predicted relationships for significant covariates of larval abundance of *A. maculatum* and *A. talpoideum* (panel H) in Period 1 (P1) and Period 2 (P2). Gray circles are naïve estimates of larval abundance. Solid lines are predicted estimates of abundance and dashed lines are 95% credible intervals. Note the difference in scales in y-axes between P1 and P2.

DISCUSSION

Both abiotic and biotic factors contribute to structuring populations, yet the relative impacts of each potential mechanism on different population traits are infrequently assessed. The goal of this study was to determine the relative effects of biotic and abiotic factors on larval abundance and body size of two known competitors, *Ambystoma talpoideum* and *A. maculatum*. We found that larval abundances and sizes were indeed predicted by different factors, but the manner of this result varied between species. Only a few habitat and methodological variables predicted larval abundance of *A. maculatum*, whereas heterospecific density was the only predictor for *A. talpoideum* across the two study periods. For larval size, the predominant effects were from *A. maculatum*. In Period 1, the density of each species was supported for *A. maculatum* (e.g., both intra- and interspecific competitor density predicted larval size), but they were highly asymmetric in strengths (*A. maculatum* having generally stronger effects). Furthermore, canopy cover was the only habitat feature that predicted larval size. Overall, our findings support the hypothesis that abiotic factors are stronger predictors of abundance and biotic factors were more predictive of body size, similar to a previous study of larval ambystomatids (Ousterhout et al., 2015). Our study bolsters this hypothesis because we span a six-year temporal gradient in addition to spatial variation. As demographic rates were species-specific across these seasonal (e.g., the effects of sampling date) and yearly effects (e.g., variable density dependence among sampling periods), our study shows that understanding population dynamics may require monitoring a complex suite of drivers coupled with multiple population traits to encompass enough spatiotemporal variability.

The factors predicting larval abundance varied between species and sampling periods. For *A. maculatum*, sampling date had a negative effect on abundance in both years and may reflect that the later a sample was taken within a season, the more individuals would have metamorphosed or died, leading to lower density estimates. This was not apparent in *A. talpoideum*, likely because they have a longer larval period (Anderson and Whiteman, 2015a) and were still present later

Table 3. Parameter estimates, 95% credible intervals (lower and upper), and the percent of the distribution that shared the same sign as the mean (*f*) for larval snout–vent length (SVL) of *Ambystoma maculatum* and *A. talpoideum*. Bold values indicate posterior distributions that are >95% the same sign as the mean, and italic values indicate posterior distributions that are >90% the same sign as the mean estimate.

Period	Species	Covariate	Estimate	Lower	Upper	*f*
Period 1	*A. maculatum*	Density of *A. maculatum*	**−0.151**	**−0.175**	**−0.126**	**1.000**
		Density of *A. talpoideum*	**−0.059**	**−0.084**	**−0.034**	**1.000**
		Canopy cover	*−0.080*	*−0.168*	*0.021*	*0.947*
		Depth	**−0.103**	**−0.143**	**−0.064**	**1.000**
		Forest cover	0.017	−0.093	0.119	0.641
		Pond area	**0.093**	**0.078**	**0.332**	**1.000**
		Pond clustering	0.029	−0.061	0.120	0.741
		Sampling date	**0.206**	**0.165**	**0.246**	**1.000**
	A. talpoideum	Density of *A. maculatum*	**−0.631**	**−0.773**	**−0.481**	**1.000**
		Density of *A. talpoideum*	−0.030	−0.145	−0.093	0.688
		Canopy cover	−0.219	−0.726	0.203	0.851
		Depth	**−0.600**	**−0.941**	**−0.280**	**1.000**
		Forest cover	−0.032	−0.342	0.396	0.595
		Pond area	0.103	−0.207	0.464	0.741
		Pond clustering	−0.180	−0.603	0.239	0.826
		Sampling date	−0.111	−0.316	−0.155	0.688
Period 2	*A. maculatum*	Density of *A. maculatum*	−0.020	−0.068	0.027	0.803
		Density of *A. talpoideum*	**−0.316**	**−0.544**	**−0.087**	**0.998**
		Canopy cover	**−0.730**	**−1.538**	**0.050**	**0.964**
		Forest cover	0.266	−0.514	1.078	0.749
		Pond area	**0.746**	**0.288**	**1.206**	**1.000**
		Pond clustering	0.191	−0.711	1.067	0.664
		Sampling date	**2.694**	**2.382**	**3.007**	**1.000**
	A. talpoideum	Density of *A. maculatum*	0.497	−0.286	1.303	0.891
		Density of *A. talpoideum*	0.268	−0.647	1.176	0.721
		Canopy cover	−1.253	−3.886	1.357	0.841
		Forest cover	−0.016	−2.203	2.093	0.505
		Pond area	−0.369	−2.179	1.367	0.652
		Pond clustering	−0.484	−3.215	2.321	0.646
		Sampling date	**2.621**	**1.610**	**3.628**	**1.000**

in the summer. Based on this result, sampling multiple populations over a short time span (e.g., less than three weeks) may be necessary to eliminate this confounding effect and to make ponds more comparable for species with shorter larval periods.

We also observed a decline in abundance of *A. maculatum* with increasing pond area in Period 1. This result could occur from two potential processes. First, ponds with greater area were often deeper and thus harder to sample with pipe samplers, leading to areas of the pond being inaccessible using our methodology in Period 1 and thus underestimating larval density. This is supported by the fact that abundance declined as mean sampling depth increased, though this could also be due to habitat partitioning (Brodman and Krause, 2007). Alternatively, lower densities in larger ponds could result from biotic processes, namely that larger ponds contain more larval predators: Semlitsch et al. (2015) found that both amphibian and invertebrate predator abundance and diversity peaked in ponds with intermediate pond areas (<1000 m^2) and increasingly permanent hydroperiods, which generally matches the characteristics of the ponds we surveyed. Therefore, predators could have reduced density of larval *A. maculatum* in the larger ponds. Our study sites did not vary as much in forested habitat around ponds or canopy cover as other studies, which may explain why these factors were less important in predicting density when compared with other studies of amphibians (Van Buskirk, 2005; Peterman et al., 2014).

Only abundance of *A. maculatum* predicted the abundance of *A. talpoideum*, and the two were positively correlated, which likely resulted from these species having similar life histories and habitat requirements (Petranka, 1998). Positive covariance in abundance has been observed in other studies on pond-breeding amphibians (Pechmann et al., 1991; Ousterhout et al., 2015), supporting the hypothesis that certain ponds are high quality habitat for numerous species. While these species are known competitors, resulting in the expectation of a negative species covariance, most experiments using *A. talpoideum* and *A. maculatum* show negative interspecific effects occur only on growth and development, not survival (Semlitsch and Walls, 1993; Anderson and Whiteman, 2015a, 2015b). While behavioral responses to predators vary between these two species (Walls, 1995), other factors (e.g., spatial or temporal niche partitioning) that would promote their coexistence are currently unknown. More generally, larval abundance may also be a highly stochastic process that operates independently from site-level regulatory factors, such as shared regional climate factors that synchronize breeding and life histories for both species within years, leading to positive covariance of abundances (Trenham et al., 2003; Houlahan et al., 2007). However, larval abundances observed at one point in time may not adequately capture the effect of interactions on population abundance, as larval input (i.e., breeding effort) is not accounted for directly. Multiple estimates of abundance

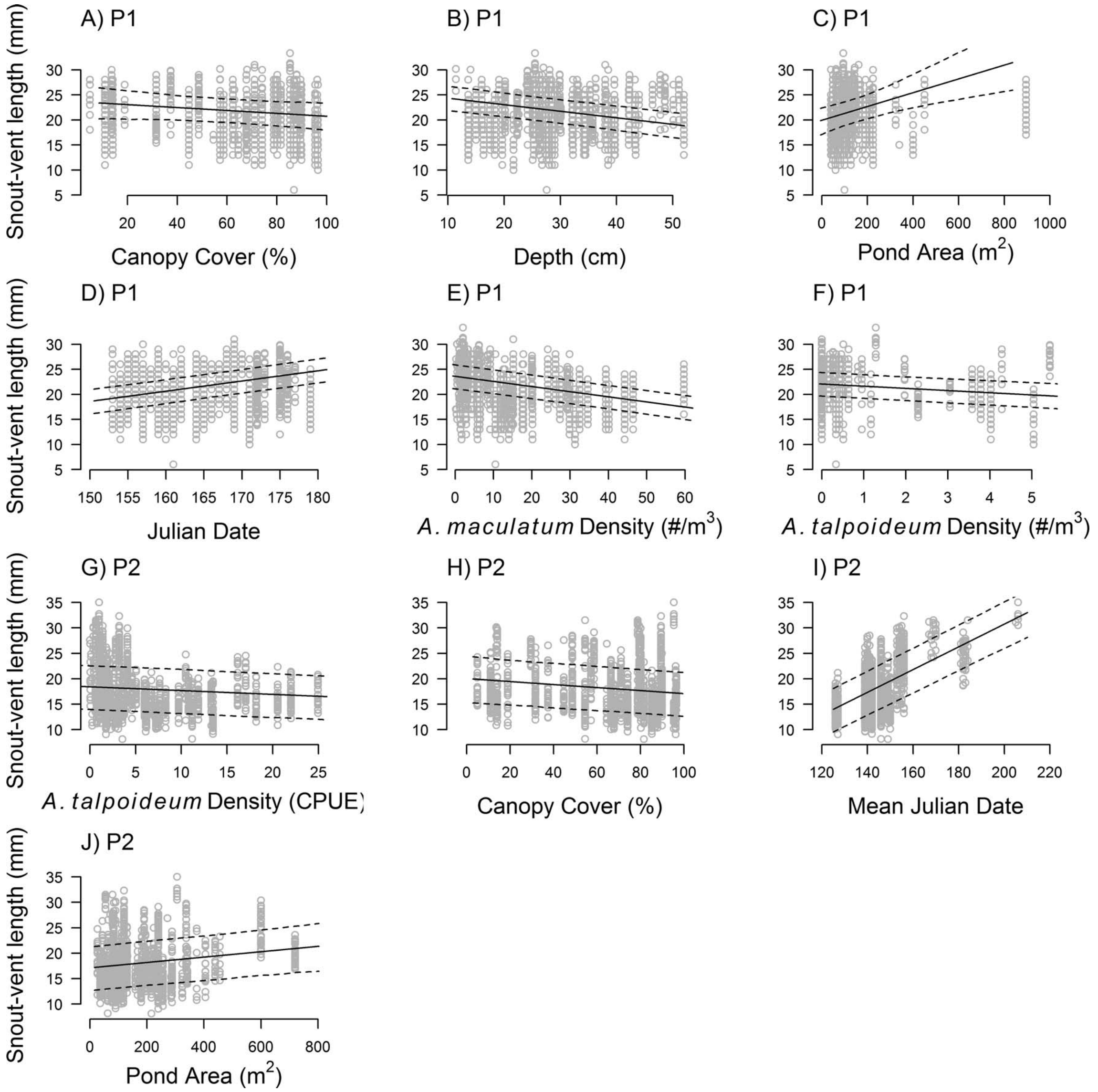

Fig. 3. Predicted relationships for significant covariates of larval size of *A. maculatum* in Period 1 (P1) and Period 2 (P2). Solid lines are predicted relationships of abundance and dashed lines are 95% credible intervals. Gray circles are raw values of SVL. Note the difference in scales in y-axes between P1 and P2. See Figure 4 for *A. talpoideum*.

through time may better elucidate how competitor densities change population trajectories for each species.

Asymmetric effects of competition are a common phenomenon across many taxa (Morin and Johnson, 1988; Freckleton and Watkinson, 2001; Young, 2004). In our study, larval size in both species was more strongly predicted by *A. maculatum* than *A. talpoideum*, which received little support. Additionally, the effect of density of *A. maculatum* was stronger than that of *A. talpoideum* on size of *A. talpoideum* in Period 1, indicating highly asymmetric effects. These results stem from the higher observed densities of *A. maculatum*, which could exert a larger effect on body size. High densities often lead to reduced body sizes due to interference or exploitative processes, both of which limit individual growth rates (Van Buskirk and Smith, 1991; Scott, 1994), though previous experiments would support the latter mechanism as *A. maculatum* are superior exploitative competitors (Walls, 1996). We did observe significant interspecific effects from *A. talpoideum* on *A. maculatum* in Period 1, but the effect size was still only half that of *A. maculatum*, indicating the competitive effects of *A. talpoideum* were weaker. Yet, the only competitive effect on *A. maculatum* in Period 2 was from density of *A. talpoideum*, indicating interspecific competition is potentially still important for this species. Consistent with these results, experimental studies of these species have found that intraspecific competition was the dominant limiting influence, and that *A. talpoideum* had weak interspecific effects on *A. maculatum* (Semlitsch and Walls, 1993; Anderson and Whiteman, 2015a, 2015b). Because *A. talpoideum* is a more dominant interference competitor and *A. maculatum* a better exploitative competitor (Walls and Jaeger, 1987), we also would have predicted that *A. talpoideum* is a stronger interspecific competitor. This discrepancy between observational and experimental venues could arise from *A. maculatum* exhibiting substantially higher average larval densities than *A. talpoideum* in the populations we surveyed, suggesting that: 1) local population density may override intrinsic competitive abilities; 2) exploitative competition exerts a stronger effect than interference competition in this interaction; or 3) an interaction of these two factors. Further research is necessary to test these hypotheses.

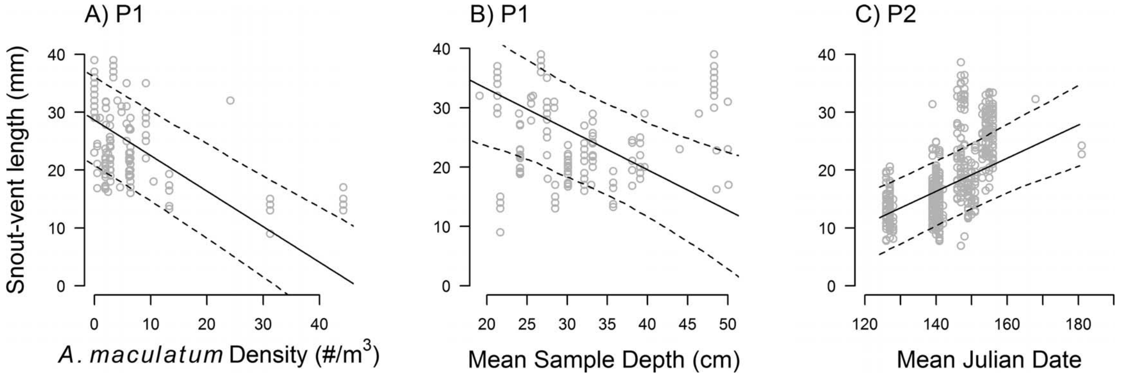

Fig. 4. Predicted relationships for significant covariates of larval size of *A. talpoideum* in Period 1 (P1) and Period 2 (P2). Solid lines are predicted relationships of abundance and dashed lines are 95% credible intervals. Gray circles are raw values of SVL.

We assessed larval interactions within and between species for a given year's cohort of salamanders. However, the dominant interaction type is likely to change when the life history of *A. talpoideum* is considered (Whiteman, 1994): larvae in this species can either undergo typical metamorphosis or retain larval features (e.g., gills) and become a sexually mature, aquatic adult (paedomorph). The presence of paedomorphs in *A. talpoideum*, which do not occur in *A. maculatum*, could switch their interaction from competition to predation, as large stage classes of *A. talpoideum* are effective predators of smaller age classes, assuming gape limitations are not exceeded (Anderson et al., 2013). When high densities of either paedomorphic or large overwintering larvae occur, these older stages would potentially influence population dynamics of both *A. talpoideum* and *A. maculatum* more than within-cohort competition, either through predation or asymmetric competition resulting from greater size disparities, as has been observed in other paedomorphic species (Wissinger et al., 2010). Typically, we observed low densities of these large stage classes at our study site, though high densities of older cohorts were observed at a single pond in two different years during this study (TLA, unpubl. data); future work will focus on how life history of *A. talpoideum* influences population dynamics of these species.

While we cannot discount how changing methodologies may have influenced our results, the inconsistency we observed in density-dependent competition among sampling periods matches the conclusions drawn from the known *in situ* studies, which show substantial variability in these patterns. Both Grözinger et al. (2014) and Anderson et al. (2015b) saw negligible effects of larval density on size at metamorphosis in anurans and salamanders, respectively, and Werner et al. (2009) found positive relationships of competitor biomass on anuran size. Van Buskirk and Smith (1991) found strong negative density-dependent patterns in larval salamanders, whereas Indermaur et al. (2010) only saw density-dependent size variation in toad tadpoles in open canopy ponds. Based on the findings of this latter study, density dependence may not be common at our study site, as most of our ponds were fairly closed canopy (mean canopy closure = 62%). We also observed a negative effect of canopy cover on size of *A. maculatum*, which contrasts with patterns observed under controlled conditions (Earl et al., 2011). Such discrepancies could arise from temperature differences among ponds that slowed growth rates or the marginally positive relationship of larval abundance and canopy cover, i.e., individuals were smaller in higher canopy sites because densities were also higher. Overall, the fact that such caveats must be presented to explain density-dependent size variation both in this study and when comparing other studies suggests that these relationships are highly mutable, and that finding patterns in one year or population may not be translatable across taxa or study areas.

In conclusion, we found evidence for asymmetric density-dependent competition between species that influenced body size of both species; fewer factors explained patterns of abundance, and primarily were habitat or methodological covariates (e.g., sampling date) that had weak effects on abundance. This result further highlights the need to collect landscape-scale data on multiple populations to tease apart temporal and spatial variation in parameters that contribute to population growth and demographic vital rates. As these sources of variation are often substantial, sufficient replication across different habitat types is needed to disentangle the importance of local conditions and to identify characteristics that distinguish high vs. low quality sites, which will ultimately advance our understanding of spatiotemporal dynamics. Such findings also have conservation implications, as ponds with differing demographic rates may differentially contribute to regional population structure

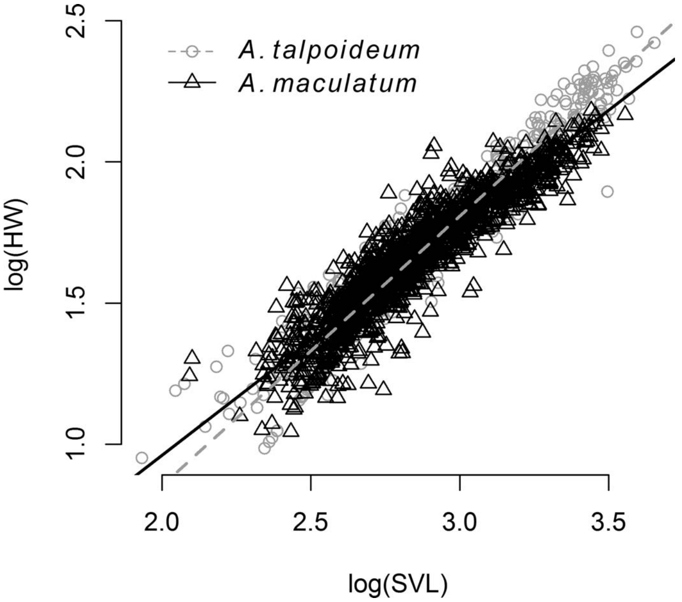

Fig. 5. Relationship of head width (HW) to snout–vent length (SVL) for larval *A. maculatum* (black triangles and line) and *A. talpoideum* (gray circles and line). Symbols show raw data values, and lines show predicted relationships.

(Marsh and Trenham, 2000; Peterman et al., 2013, 2016). Our results also highlight that using one species as a surrogate for another, even if they are highly similar in life history and ecological role, may not fully capture important local- or landscape-scale factors important to the conservation of each species (Ficetola et al., 2007; Peterman et al., 2014). Maximizing monitoring efforts on other relevant factors not studied here, such as prey densities or water quality, would result in a more holistic view of the relative importance of biotic and abiotic influences on larval amphibian community structure.

DATA ACCESSIBILITY

Supplemental material is available at http://www.copeiajournal.org/ce-16-515.

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LITERATURE CITED

Abràmoff, M. D., P. J. Magalhães, and S. J. Ram. 2004. Image processing with ImageJ. Biophotonics International 11:36–42.

Amarasekare, P. 2003. Competitive coexistence in spatially structured environments: a synthesis. Ecology Letters 6: 1109–1122.

Anderson, T. L. 2011. Experimental and observational approaches to assess competition between larval salamanders. Unpubl. Master's thesis, Murray State University, Murray, Kentucky.

Anderson, T. L., D. J. Hocking, C. A. Connor, J. E. Earl, E. B. Harper, M. S. Osbourn, W. E. Peterman, T. A. Rittenhouse, and R. D. Semlitsch. 2015b. Abundance and phenology patterns of two pond-breeding salamanders determine species interactions in natural populations. Oecologia 177:761–773.

Anderson, T. L., C. L. Mott, T. D. Levine, and H. H. Whiteman. 2013. Life cycle complexity influences intraguild predation and cannibalism in pond communities. Copeia 2013:284–291.

Anderson, T. L., B. H. Ousterhout, D. L. Drake, J. J. Burkhart, F. E. Rowland, W. E. Peterman, and R. D. Semlitsch. 2016. Differences in larval allometry among three ambystomatid salamanders. Journal of Herpetology 50:464–470.

Anderson, T. L., B. H. Ousterhout, D. L. Drake, W. E. Peterman, and R. D. Semlitsch. 2015a. Life history differences influence the impacts of drought on two pond-breeding salamanders. Ecological Applications 25: 1896–1910.

Anderson, T. L., and H. H. Whiteman. 2015a. Non-additive effects of intra- and interspecific competition between two larval salamanders. Journal of Animal Ecology 84:765–772.

Anderson, T. L., and H. H. Whiteman. 2015b. Asymmetric effects of intra- and interspecific competition on a pond-breeding salamander. Ecology 96:1681–1690.

Băncilă, R. I., A. Ozgul, T. Hartel, T. Sos, and B. R. Schmidt. 2016. Direct negative density-dependence in a pond-breeding frog population. Ecography 39:449–455.

Branch, L. C., and R. Altig. 1981. Nocturnal stratification of three species of *Ambystoma* larvae. Copeia 1981:870–873.

Brodman, R., and H. D. Krause. 2007. How blue-spotted and small-mouthed salamander larvae coexist with their unisexual counterparts. Herpetologica 63:135–143.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31: 343–366.

Davenport, J. M., B. R. Hossack, and W. H. Lowe. 2014. Partitioning the non-consumptive effects of predators on prey with complex life histories. Oecologia 176:149–155.

Earl, J. E., T. M. Luhring, B. K. Williams, and R. D. Semlitsch. 2011. Biomass export of salamanders and anurans from ponds is affected differentially by changes in canopy cover. Freshwater Biology 56:2473–2482.

Earl, J. E., and H. H. Whiteman. 2015. Are commonly used fitness predictors accurate? A meta-analysis of amphibian size and age at metamorphosis. Copeia 103:297–309.

Ficetola, G. F., R. Sacchi, S. Scali, A. Gentilli, F. De Bernardi, and P. Galeotti. 2007. Vertebrates respond differently to human disturbance: implications for the use of a focal species approach. Acta Oecologica 31:109–118.

Freckleton, R. P., and A. R. Watkinson. 2001. Asymmetric competition between plant species. Functional Ecology 15: 615–623.

Freda, J. 1983. Diet of larval *Ambystoma maculatum* in New Jersey. Journal of Herpetology 17:177–179.

Gazzola, A., and J. Van Buskirk. 2015. Isocline analysis of competition predicts stable coexistence of two amphibians. Oecologia 178:153–159.

Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 2014. Bayesian Data Analysis. Chapman and Hall/CRC, Boca Raton, Florida.

Grözinger, F., J. Thein, H. Feldhaar, and M.-O. Rödel. 2014. Giants, dwarfs and the environment—metamorphic trait plasticity in the Common Frog. PLOS ONE 9:e89982.

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology 12:197–229.

Houlahan, J. E., D. J. Currie, K. Cottenie, G. S. Cumming, S. K. Ernest, C. S. Findlay, S. D. Fuhlendorf, U. Gaedke, P. Legendre, J. J. Magnuson, B. H. McArdle, E. H. Muldavin, D. Noble, R. Russell, R. D. Stevens, T. J. Willis, I. P. Woiwod, and S. M. Wondzell. 2007. Compensatory dynamics are rare in natural ecological communities. Proceedings of the National Academy of Sciences of the United States of America 104:3273–3277.

Indermaur, L., B. R. Schmidt, K. Tockner, and M. Schaub. 2010. Spatial variation in abiotic and biotic factors in a floodplain determine anuran body size and growth rate at metamorphosis. Oecologia 163:637–649.

Jacobs, R. 2004. Final Environmental Impact Statement for the Land and Resource Management Plan: Land Between the Lakes National Recreation Area. Vol. 1. U. S. F. Service (ed.). U.S. Department of Agriculture.

Kellner, K. 2015. jagsUI: Run JAGS from R (an alternative user interface for rjags). 1.3.1. http://cran.r-project.org/package=jagsUI

Kéry, M. 2010. Introduction to WinBUGS for Ecologists: Bayesian Approach to Regression, ANOVA, Mixed Models and Related Analyses. Academic Press, Burlington, Massachusetts.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. Andrew Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.

Marsh, D. M., and P. C. Trenham. 2000. Metapopulations dynamics and amphibian conservation. Conservation Biology 15:40–49.

Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. American Naturalist 130:730–757.

Morin, P. J., and E. A. Johnson. 1988. Experimental studies of asymmetric competition among anurans. Oikos 53:398–407.

Ousterhout, B. H., T. L. Anderson, D. L. Drake, W. E. Peterman, and R. D. Semlitsch. 2015. Habitat traits and species interactions differentially affect abundance and body size in pond-breeding amphibians. Journal of Animal Ecology 84:914–924.

Pechmann, J. H. K., D. E. Scott, R. D. Semlitsch, J. P. Caldwell, L. J. Vitt, and J. W. Gibbons. 1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. Science 253:892–895.

Peterman, W. E., J. E. Earl, T. A. G. Rittenhouse, and R. D. Semlitsch. 2013. Demographic network and multi-season occupancy modeling of *Rana sylvatica* reveal spatial and temporal patterns of population connectivity and persistence. Landscape Ecology 28:1601–1613.

Peterman, W. E., T. L. Anderson, D. L. Drake, B. H. Ousterhout, and R. D. Semlitsch. 2014. Maximizing pond biodiversity across the landscape: a case study of larval ambystomatid salamanders. Animal Conservation 17:275–285.

Peterman, W. E., B. H. Ousterhout, T. L. Anderson, D. L. Drake, R. D. Semlitsch, and L. S. Eggert. 2016. Assessing modularity in genetic networks to manage spatially structured metapopulations. Ecosphere 7:e01231.

Petranka, J. W. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, D.C.

Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling, p. 125. *In:* Proceedings of the 3rd International Workshop on Distributed Statistical Computing. Vol. 124. Technische Universit at Wien.

R Core Team. 2016. R: a language and environment for statistical computing. Version 3.3.0. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Rasband, W. S. 1997. ImageJ. US National Institutes of Health, Bethesda, Maryland.

Relyea, R. A. 2007. Getting out alive: how predators affect the decision to metamorphose. Oecologia 152:389–400.

Resetarits, W. J., Jr., and D. R. Chalcraft. 2007. Functional diversity within a morphologically conservative genus of predators: implications for functional equivalence and redundancy in ecological communities. Functional Ecology 21:793–804.

Royle, J. A. 2004. N-Mixture models for estimating population size from spatially replicated counts. Biometrics 60: 108–115.

Sadinski, W. J., and W. A. Dunson. 1992. A multilevel study of effects of low pH on amphibians of temporary ponds. Journal of Herpetology 26:413–422.

Schmidt, B., N. Ramer, and J. Van Buskirk. 2006. A trophic polymorphism induced by both predators and prey. Evolutionary Ecology Research 8:1301–1309.

Scott, D. E. 1994. The effect of larval density on adult demographic traits in *Ambystoma opacum*. Ecology 75: 1383–1396.

Scott, D. E., M. J. Komoroski, D. A. Croshaw, and P. M. Dixon. 2013. Terrestrial distribution of pond-breeding salamanders around an isolated wetland. Ecology 94: 2537–2546.

Semlitsch, R. D. 1988. Allotopic distribution of two salamanders: effects of fish predation and competitive interactions. Copeia 1988:290–298.

Semlitsch, R. D. 1998. Biological delineation of terrestrial buffer zones for pond-breeding salamanders. Conservation Biology 12:1113–1119.

Semlitsch, R. D., and J. P. Caldwell. 1982. Effects of density of growth, metamorphosis, and survivorship in tadpoles of *Scaphiopus holbrooki*. Ecology 63:905–911.

Semlitsch, R. D., W. E. Peterman, T. L. Anderson, D. L. Drake, and B. H. Ousterhout. 2015. Intermediate pond sizes contain the highest density, richness, and diversity ofpond-breeding amphibians. PLOS ONE 10:e0123055.

Semlitsch, R. D., D. E. Scott, and J. H. K. Pechmann. 1988. Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum*. Ecology 69:184–192.

Semlitsch, R. D., D. E. Scott, J. H. K. Pechmann, and J. W. Gibbons. 1996. Structure and dynamics of an amphibian community: evidence from a 16-year study of a natural pond, p. 217–248. *In:* Long-Term Studies of Vertebrate Communities. M. L. Cody and J. A. Smallwood (eds.). Academic Press, San Diego, California.

Semlitsch, R. D., and S. C. Walls. 1993. Competition in two species of larval salamanders: a test of geographic variation in competitive ability. Copeia 1993:587–595.

Shaffer, H., R. Alford, B. Woodward, S. Richards, R. Altig, and C. Gascon. 1994. Quantitative sampling of amphibian larvae, p. 130–141. *In:* Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster (eds.). Smithsonian Institution Press, Washington, D.C.

Shulse, C. D., R. D. Semlitsch, K. M. Trauth, and A. D. Williams. 2010. Influences of design and landscape placement parameters on amphibian abundance in constructed wetlands. Wetlands 30:915–928.

Smith, M. A., and D. M. Green. 2005. Dispersal and the metapopulation paradigm in amphibian ecology and conservation: Are all amphibian populations metapopulations? Ecography 28:110–128.

Taylor, B. E., R. A. Estes, J. H. K. Pechmann, and R. D. Semlitsch. 1988. Trophic relations in a temporary pond:

larval salamanders and their microinvertebrate prey. Canadian Journal of Zoology 66:2191–2198.

Trenham, P. C., W. D. Koenig, M. J. Mossman, S. L. Stark, and L. A. Jagger. 2003. Regional dynamics of wetland-breeding frogs and toads: turnover and synchrony. Ecological Applications 13:1522–1532.

Van Buskirk, J. 2005. Local and landscape influence on amphibian occurrence and abundance. Ecology 86:1936–1947.

Van Buskirk, J., and D. C. Smith. 1991. Density-dependent population regulation in a salamander. Ecology 72:1747–1756.

Vonesh, J., and O. De la Cruz. 2002. Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines. Oecologia 133:325–333.

Walls, S. C. 1995. Differential vulnerability to predation and refuge use in competing larval salamanders. Oecologia 101: 86–93.

Walls, S. C. 1996. Differences in foraging behaviour explain interspecific growth inhibition in competing salamanders. Animal Behaviour 52:1157–1162.

Walls, S. C., and R. G. Jaeger. 1987. Aggression and exploitation as mechanisms of competition in larval salamanders. Canadian Journal of Zoology 65:2938–2944.

Wellborn, G. A., D. K. Skelly, and E. E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. Annual Review of Ecology and Systematics 27:337–363.

Werner, E. E., R. A. Relyea, K. L. Yurewicz, D. K. Skelly, and C. J. Davis. 2009. Comparative landscape dynamics of two anuran species: climate-driven interaction of local and regional processes. Ecological Monographs 79:503–521.

Werner, E. E., K. L. Yurewicz, D. K. Skelly, and R. A. Relyea. 2007. Turnover in an amphibian metacommunity: the role of local and regional factors. Oikos 116:1713–1725.

Whiteman, H. H. 1994. Evolution of facultative paedomorphosis in salamanders. The Quarterly Review of Biology 69: 205–221.

Wilbur, H. M. 1997. Experimental ecology of food webs: complex systems in temporary ponds. Ecology 78:2279–2302.

Wissinger, S., H. H. Whiteman, M. Denoel, M. L. Mumford, and C. B. Aubee. 2010. Consumptive and nonconsumptive effects of cannibalism in fluctuating age-structured populations. Ecology 91:549–559.

Young, K. A. 2004. Asymmetric competition, habitat selection, and niche overlap in juvenile salmonids. Ecology 85:134–149.