

# Abundance and phenology patterns of two pond-breeding salamanders determine species interactions in natural populations

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**Abstract** Phenology often determines the outcome of interspecific interactions, where early-arriving species often dominate interactions over those arriving later. The effects of phenology on species interactions are especially pronounced in aquatic systems, but the evidence is largely derived from experimental studies. We examined whether differences in breeding phenology between two pond-breeding salamanders (*Ambystoma annulatum* and *A. maculatum*) affected metamorph recruitment and demographic traits within natural populations, with the expectation that the fall-breeding *A. annulatum* would negatively affect the spring-breeding *A. maculatum*. We monitored populations of each species at five ponds over 4 years using drift fences. Metamorph abundance and survival of *A. annulatum* were affected by intra- and interspecific processes, whereas metamorph size and date of emigration were primarily influenced by intraspecific effects. Metamorph abundance, snout–vent length, date of emigration and survival for *A. maculatum* were all predicted by combinations

of intra- and interspecific effects, but often showed negative relationships with *A. annulatum* metamorph traits and abundance. Size and date of metamorphosis were strongly correlated within each species, but in opposite patterns (negative for *A. annulatum* and positive for *A. maculatum*), suggesting that the two species use alternative strategies to enhance terrestrial survival and that these factors may influence their interactions. Our results match predictions from experimental studies that suggest recruitment is influenced by intra- and interspecific processes which are determined by phenological differences between species. Incorporating spatiotemporal variability when modeling population dynamics is necessary to understand the importance of phenology in species interactions, especially as shifts in phenology occur under climate change.

**Keywords** *Ambystoma annulatum* · *Ambystoma maculatum* · Competition · Intraguild predation · Pond · Priority effects

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## Introduction

The order of arrival by different species into a particular habitat has long been recognized as an important factor in ecological interactions (Connell and Slatyer 1977). More recently, increased attention has focused on arrival patterns due to documented shifts in phenology (i.e. the timing of life history events, such as breeding migrations) that have been linked to climate change (Miller-Rushing et al. 2010; Yang and Rudolf 2010). Phenology is important to species interactions because the level of synchrony between species (or temporal overlap) can influence the intensity or outcome of these processes; for example, prey may become more susceptible to predators or competitors may suffer from increased resource overlap (Encinas-Viso et al. 2012; Griffin et al. 2011; Revilla et al. 2013; Yang and Rudolf 2010). Phenology can also influence species interactions when it acts synergistically with other factors, such as the density of competitors, predators or resources, resulting in complex ecological networks (Alford 1989; Hunter and Elkinton 2001; Kardol et al. 2013). Thus, an improved understanding of how shifts in phenology affect species interactions is imperative to predict future population and community level processes under climate change (Blois et al. 2013).

With regards to interactions between antagonistic species, such as competition or predation, species that arrive early into a habitat often dominate the interactions with those that arrive later, ultimately affecting population and community structure of the latter (Almany 2003; Geange and Stier 2009; Shorrocks and Bingley 1994; Stier et al. 2013; Wilbur and Alford 1985). Dominance by early-arriving species in interspecific interactions can occur because of size asymmetries that exist a priori or which develop during ontogeny, which often confer competitive or predatory advantages to the early-arriving species. These size differences can ultimately determine whether phenological patterns result in competition or predator–prey interactions (Geange and Stier 2009; Urban 2007a; Wissinger 1992). Early-arriving species may also modify habitat conditions or preemptively use resources, thereby limiting their availability to species arriving later and thus promoting dominance of the former (Connell and Slatyer 1977; Kardol et al. 2013). While it is often difficult to determine these advantages separately, sufficient evidence exists to support the general pattern of early-arrival dominance in many communities.

The temporal pattern of arrival to ponds for breeding, or breeding phenology, has a strong influence on the outcomes of both competitive and predatory interactions in lentic freshwater habitats (e.g. Alford and Wilbur 1985; Blaustein and Margalit 1996; Orizaola et al. 2013; Padeffke and Suhling 2003; Urban 2007a). For pond-breeding salamanders,

breeding phenology affects larval size-structure, which can lead to larvae of early-breeding species preying upon larvae of those breeding later due to size asymmetries that develop through ontogeny. Nonconsumptive predatory effects and enhanced competitive abilities for prey resources can also exist for larvae of early breeders over subsequent cohorts of those breeding later (e.g. Boone et al. 2002; Eitam et al. 2005; Segev and Blaustein 2007; Urban 2007a). Positive effects of early-arriving species can occur as well if early-arriving species reduce the densities of those arriving later, which reduces competition among the latter group due to thinning effects (Alford 1989; Anderson and Semlitsch 2014; Morin 1983). In predator–prey systems, the presence of species which breed later could also be expected to benefit early-breeding species as a food resource, resulting in enhanced growth rates or decreased times to metamorphosis when there are high densities of late larvae to consume, although to our knowledge this relationship has yet to be shown empirically in natural systems.

The bulk of our understanding of how phenology influences interspecific interactions among amphibians has been established from small-scale experimental investigations. The ability of these experiments to describe natural processes occurring in un-manipulated populations is less well known. The majority of long-term studies that have estimated the population vital rates (e.g. reproduction and survival) necessary to fully understand the impact of species interactions on population dynamics have mostly examined single-species systems (Berven 2009; Schmidt et al. 2012; Wissinger et al. 2010), with few focusing on interspecific effects (Semlitsch et al. 1996). Investigations of interactions between specific ontogenetic stages have found differences in phenology to be strong selective forces (Segev and Blaustein 2007; Stenhouse et al. 1983; Urban 2007a), but the ultimate impacts on recruitment are unknown. Several studies have followed multiple species through metamorphosis (Semlitsch et al. 1996; Stenhouse 1987; Todd et al. 2011; Todd and Winne 2006), but explicit tests of interspecific interactions on population dynamics have been infrequent or at only one study location, providing little information about spatiotemporal variation in the outcome of interactions. This information is important because the persistence or exclusion of those species which arrive later may differ across spatial and temporal scales due to the length of temporal overlap, prior residency and spatial aggregation at each site (Lawler and Morin 1993; Porensky et al. 2012; Shorrocks and Bingley 1994; Urban 2007a). The effects may ultimately influence population spatial structure and contribute to long-term coexistence.

We have examined recruitment and demographic traits (size at and date of metamorphosis) of metamorphs of two pond-breeding salamanders, the ringed (*Ambystoma annulatum*) and spotted salamander (*A. maculatum*), which

differ in breeding phenology. Adults of *A. annulatum* breed in the fall, whereas those of *A. maculatum* breed in the spring, making the larvae of the former an intraguild predator and hatchlings and larvae of the latter an intraguild prey (Anderson and Semlitsch 2014; Hocking et al. 2008; Semlitsch et al. 2014). We monitored populations of these species for 4 consecutive years at five ponds to enumerate both adult and metamorph abundances, as well as the timing of each species' movements into and out of ponds. We compared models representing different biotic processes to gain an understanding of how both abundance and phenology influenced metamorph recruitment and traits. Based on previous research on interactions of fall- and spring-breeding species (Anderson and Semlitsch 2014; Stenhouse 1985, 1987; Stenhouse et al. 1983; Urban 2007a), we expected asymmetric interspecific effects to be present between these two species (*A. annulatum* superior over *A. maculatum*). We also expected positive effects from *A. maculatum* on *A. annulatum* metamorph traits and abundance that would indicate the latter species benefits from the presence of the former as a food resource. Finally, by following several natural populations through multiple years of recruitment, we were able to analyze how stochasticity (i.e. spatiotemporal variation) contributes to metamorph responses.

## Methods

### Study area

Populations of both *A. annulatum* and *A. maculatum* were monitored at five constructed wildlife ponds (surface area 160–330 m<sup>2</sup>) at the Daniel Boone Conservation Area (DBCA; 1,424.5 ha) in Warren County, Missouri, USA from 2004 to 2007 (Semlitsch et al. 2009). DBCA is a secondary growth forest primarily composed of an oak (*Quercus spp.*) and hickory (*Carya spp.*) overstory, with a sugar maple (*Acer saccharum*) and red cedar (*Juniperus virginiana*) understory. Fifty-one constructed ponds exist at DBCA, with a mean interpond distance of 235 m ( $\pm 142$  m) (see map in Semlitsch et al. 2014). The five focal ponds are 27–47 years old, fish-free and permanent in most years, have an interpond distance of 879 m ( $\pm 541$  m) and are used by up to 14 amphibian species (Hocking et al. 2008; Semlitsch et al. 2008, 2009). Both focal salamanders are forest-associated species, occupying ponds with greater canopy closure and with a greater percentage of forest in the surrounding habitat (Peterman et al. 2014). Most breeding adults of *A. annulatum* arrive at ponds from August to October at the DBCA, while *A. maculatum* breeding adults arrive in late February–March (Semlitsch et al. 2014). Eggs of *A. annulatum* hatch in late October and November, and the aquatic larvae overwinter in ponds; emigration of

metamorphs occurs primarily in May and June (Semlitsch et al. 2014). The eggs of *A. maculatum* hatch in March and April, and most larvae complete metamorphosis by the end of the following summer (Hocking et al. 2008). Marbled salamanders (*A. opacum*) also occurred at DBCA, but were present at low frequency (<1 % of total metamorphs and adults) and were excluded from this analysis.

### Sampling

Drift fences that completely encircled each of the five focal ponds were constructed and positioned 1–3 m from the highwater mark, with paired pitfall traps spaced 8 m apart on each side of the fence. A sponge was placed in each trap to prevent desiccation of the captured animals, and a wooden lid was placed 2.5 cm above the lip of the pitfall trap to minimize predation by mammals. All pitfall traps were checked at minimum every 48 h, and every 24 h following rain events, from mid-February to mid-November each year of the study. The sex of each incoming adult was determined by cloacal examination before it was released inside the fence, and all animals received a toe-clip cohort mark as part of an ongoing mark–recapture population study. Snout–vent length (SVL, in mm) was measured on a subset of adults ( $N = 4,536$ ). Body shape, coloration and number of costal grooves were used to identify metamorphosing juvenile salamanders to species (Trauth et al. 2004), which were also measured for SVL ( $n = 4,455$ ). Small individuals caught entering the ponds that could be confused with metamorphs were kept on the outside of the drift fence. Immature individuals and those whose sex was not distinguishable were excluded from analysis in this study (approximately 3 % of captures for each species).

Each female entering the pond during the breeding season was recorded and received a toe-clip cohort mark representative of the first year in which it bred during the study. Some adult *A. annulatum* were caught immigrating/emigrating several times during the breeding season (i.e. daily movement to and from the pond). To account for this movement when estimating reproductive effort, we counted the number of females that were caught incoming at the fence that had already received that year's cohort mark at each pond, which was approximately 10 % for adult females; abundance for all ponds and years was therefore multiplied by 0.9 to make a more conservative estimate of breeding females of *A. annulatum*. We calculated reproductive effort by multiplying the number of breeding females by an average clutch size [ $390 \pm 16$  eggs for *A. annulatum* (Hutcherson et al. 1989) and  $224 \pm 15$  for *A. maculatum* (Shoop 1974)]. This total number was then used as the number of embryos deposited by breeding females at each pond–year combination. Aquatic survival for each species within each year was then calculated by dividing the total

number of metamorphs captured at the pond drift fence by the estimated number of eggs laid at each pond.

### Analysis

We compared a priori mixed models for each species, which represented hypothesized biological processes that would affect each of four response variables: metamorph abundance (the number captured emigrating), metamorph SVL, metamorph date of emigration and survival (number of metamorphs/number of embryos). All models included pond and year as random effects. We modeled survival using a binomial error distribution (Warton and Hui 2011) and abundance with a Poisson distribution. We used the individual data points for metamorph SVL and date of emigration, as the random effects would account for temporal pseudoreplication, and modeled the responses with Gaussian error structures. All models were implemented using the lme4 package in R, and ranked using the corrected Akaike information criterion (AIC<sub>c</sub>) (Bates et al. 2013; R Development Core Team 2013).

The candidate set of models included combinations of adult abundance and timing of breeding and, in some cases, also metamorph abundance and traits (see below; Tables 1, 2). All covariates were centered and scaled to allow for parameter estimates to be directly comparable. We used metamorph abundance and traits as predictor variables within models because this could be a more biologically-relevant estimate of the larval density experienced by *A. maculatum* and *A. annulatum* than initial density (e.g. SVL of metamorphs may have been governed by final density rather than initial density). Similarly, the size of *A. annulatum* metamorphs and their emigration date should influence their predatory potential on *A. annulatum*, as these factors would influence gape limitations and temporal overlap (Anderson and Semlitsch 2014; Urban 2007a), thus justifying their inclusion as predictors in models. Furthermore, in a survey of approximately 100 ponds in similar landscapes in Missouri, larval and metamorph densities were correlated within each species; therefore, our use of metamorph abundance would likely be indicative of the strength of larval interactions (RD Semlitsch, unpublished data). We acknowledge that these relationships only imply correlation, however, and direct causation cannot be determined from our analysis.

### Model formulations

**Intraspecific model** For each species, covariates included the abundance of adult female conspecifics (a proxy for intraspecific larval density-dependence; Scott 1994) and

the mean date of adult female breeding migration, with the expectation that later breeding would reduce survival in each species. For SVL and date of metamorph emigration, metamorph abundance was also included as an estimate of final density in ponds, which often affects these two traits in experimental studies (Anderson and Semlitsch 2014; Scott 1994).

**Interspecific model** For *A. annulatum*, covariates included the abundance of breeding females of *A. maculatum* and the date of their breeding immigration. Negative correlations with the response variables would suggest that *A. maculatum* is having a competitive effect. For *A. maculatum*, the three metamorph traits of *A. annulatum* (metamorph abundance, SVL and date of emigration) were included as covariates, all of which would be proxies for predator abundance, size and phenology (Anderson and Semlitsch 2014; Urban 2007a).

**Joint effects model** For *A. annulatum*, this model examined the hypothesis that facilitation is occurring and included adult abundance and timing of breeding for both species, as well as metamorph abundance of *A. annulatum* in the SVL and emigration models. If *A. maculatum* was acting as a food source, abundance of female *A. maculatum* would be a proxy for hatchling density and therefore should be positively associated with metamorph abundance of *A. annulatum*. The timing of *A. maculatum* breeding should be negatively associated with *A. annulatum* metamorph abundance; as *A. annulatum* breeds later, there would be less opportunity for *A. annulatum* to consume hatchlings and thus survive at higher rates.

For *A. maculatum*, the joint effects model included the abundance, SVL and date of emigration of metamorphs of *A. annulatum*, and the female abundance and date of breeding of *A. maculatum*. These covariates describe how many predators (heterospecific metamorph abundance) and prey existed (conspecific female abundance), predator size (heterospecific metamorph SVL) and how long they overlapped (date of heterospecific emigration, plus date of female breeding in *A. maculatum*).

**Density model** For *A. annulatum*, this model included abundance of con- and heterospecific adult females, as well as metamorph abundance for the response variables SVL and date of emigration. This model tests a general relationship of density-dependence commonly observed in experimental studies of amphibian interactions, where increasing larval density (approximated through the combination of

**Table 1** Model selection results for metamorphs of ringed salamanders (*Ambystoma annulatum*)

Response <sup>a</sup>	Model <sup>b</sup>	Covariates	K	ΔAICc <sup>c</sup>	ω	r <sup>2</sup>
Abundance (N = 20)	<b>Joint effects</b>	<b>Con ♀ Abun + Con ♀ Date + Het ♀ Abun + Het ♀ Date</b>	<b>6</b>	<b>0</b>	<b>1</b>	0.62/0.99
	Phenology	Con ♀ Date + Het ♀ Date	4	121.2	<0.001	
	Inter	Het ♀ Abun + Het ♀ Date	4	147.0	<0.001	
	Intra	Con ♀ Abun + Con ♀ Date	4	399.3	<0.001	
	Density	Con ♀ Abun + Het ♀ Abun	4	400.5	<0.001	
	Null	~1	2	403.4	<0.001	
SVL (N = 2,697)	<b>Phenology</b>	<b>Con ♀ Date + Het ♀ Date + Con Meta Date</b>	<b>5</b>	<b>0</b>	<b>1</b>	0.16/0.65
	Joint effects	Con ♀ Abun + Con ♀ Date + Het ♀ Abun + Het ♀ Date	6	61.2	<0.001	
	Density	Con ♀ Abun + Het ♀ Abun + Con Meta Abun	5	156.0	<0.001	
	Inter	Het ♀ Abun + Het ♀ Date	4	166.4	<0.001	
	Null	~1	2	229.8	<0.001	
	Intra	Con ♀ Abun + Con ♀ Date + Con Meta Abun	5	230.8	<0.001	
Emigration date (N = 2,697)	<b>Density</b>	<b>Con ♀ Abun + Het ♀ Abun + Con Meta Abun</b>	<b>5</b>	<b>0</b>	<b>0.65</b>	0.26/0.55
	Joint effects	Con ♀ Abun + Con ♀ Date + Het ♀ Abun + Het ♀ Date	6	1.2	0.35	
	Intra	Con ♀ Abun + Con ♀ Date + Con Meta Abun	5	23.6	<0.001	
	Inter	Het ♀ Abun + Het ♀ Date	4	29.6	<0.001	
	Phenology	Con ♀ Date + Het ♀ Date	4	42.0	<0.001	
	Null	~1	2	48.4	<0.001	
Survival (N = 20)	<b>Joint effects</b>	<b>Con ♀ Abun + Con ♀ Date + Het ♀ Abun + Het ♀ Date</b>	<b>6</b>	<b>0</b>	<b>1</b>	0.40/0.65
	Phenology	Con ♀ Date + Het ♀ Date	4	50.3	<0.001	
	Inter	Het ♀ Abun + Het ♀ Date	4	85.4	<0.001	
	Density	Con ♀ Abun + Het ♀ Abun	4	323.6	<0.001	
	Intra	Con ♀ Abun + Con ♀ Date	4	342.1	<0.001	
	Null	~1	2	377.2	<0.001	

ω, Akaike information criterion (AIC) weight; K, the number of parameters; AIC<sub>c</sub>, corrected AIC; r<sup>2</sup>, the marginal and conditional values, respectively

<sup>a</sup> N = Sample size

<sup>b</sup> All models included pond and year as random intercept terms. Models presented in bold are the most highly supported models

<sup>c</sup> 1, Intercept only; Con, conspecifics; Het, heterospecific; Meta, metamorph; ♀, adult females; Abun, abundance; Date, Julian date of female breeding migration (Con or Het), or Julian date of metamorph emigration (with Meta); SVL, snout–vent length

female and metamorph abundance) tends to increase the date of metamorphosis and to decrease both size at metamorphosis and the number of metamorphs produced (Scott 1994; Semlitsch et al. 1996). For *A. maculatum*, the abundances of adults of both species and of metamorphs of *A. annulatum* were included in all models, and metamorph abundance of *A. maculatum* was included as a proxy for final intraspecific density for models in which the responses were SVL and date of emigration.

**Phenology model** This model incorporates the date of breeding for conspecific and heterospecific adult females, as well as metamorph emigration date of *A. annulatum* for the response variables of abundance, SVL and survival of *A. maculatum*. This model examines the hypothesis that the timing of ontogenetic events is the only factor that affects

metamorph recruitment and traits by influencing the degree of temporal overlap (Alford 1989; Encinas-Viso et al. 2012; Yang and Rudolf 2010).

The overall fit of the top model was assessed by calculating marginal and conditional r<sup>2</sup> values (Nakagawa et al. 2013). Marginal r<sup>2</sup> incorporates only the fixed effects in a model, and the conditional r<sup>2</sup> includes the contributions of the random effects with the fixed effects, which in our models indicate the contributions of spatiotemporal processes. While the interpretation of these values is not identical to traditional r<sup>2</sup> values, they do provide information on how much variation the fixed effects explain relative to a model that incorporates random effects. We also acknowledge that the high data to covariate ratio for the abundance and survival models (only 20 data points with up to seven predictors) could lead to overparameterization. However, the

**Table 2** Model selection results for metamorphs of spotted salamanders (*Ambystoma maculatum*)

Response <sup>a</sup>	Model <sup>b</sup>	Covariates <sup>c</sup>	<i>K</i>	$\Delta$ AIC	$\omega$	$r^2$
Abundance ( <i>N</i> = 20)	<b>Joint effects</b>	<b>Het Meta Abun + Het Meta SVL + Het Meta Date + Con ♀ Abun + Con ♀ Date</b>	<b>7</b>	<b>0</b>	<b>1</b>	0.27/0.99
	Phenology	Het Meta Date + Con ♀ Date + Het ♀ Date	5	28.5	<0.001	
	Inter	Het Meta Abun + Het Meta SVL + Het Meta Date	5	67.5	<0.001	
	Density	Het Meta Abun + Con ♀ Abun	4	89.6	<0.001	
	Intra	Con ♀ Abun + Con ♀ Date	4	113.5	<0.001	
	Null	~1	2	152.8	<0.001	
SVL ( <i>N</i> = 1,758)	<b>Joint effects</b>	<b>Het Meta Abun + Het Meta SVL + Het Meta Date + Con ♀ Abun + Con ♀ Date</b>	<b>7</b>	<b>0</b>	<b>0.99</b>	0.54/0.62
	Inter	Het Meta Abun + Het Meta SVL + Het Meta Date	5	22.2	0.001	
	Density	Het Meta Abun + Con ♀ Abun	4	147.4	<0.001	
	Phenology	Het Meta Date + Con ♀ Date + Het ♀ Date	5	232.4	<0.001	
	Intra	Con ♀ Abun + Con ♀ Date	4	312.0	<0.001	
	Null	~1	2	370.7	<0.001	
Emigration date ( <i>N</i> = 1,758)	<b>Joint effects</b>	<b>Het Meta Abun + Het Meta SVL + Het Meta Date + Con ♀ Abun + Con ♀ Date</b>	<b>7</b>	<b>0</b>	<b>1</b>	0.16/0.34
	Density	Het Meta Abun + Con ♀ Abun	4	14.0	<0.001	
	Inter	Het Meta Abun + Het Meta SVL + Het Meta Date	5	18.9	<0.001	
	Intra	Con ♀ Abun + Con ♀ Date	4	64.7	<0.001	
	Phenology	Het Meta Date + Con ♀ Date + Het ♀ Date	5	79.9	<0.001	
	Null	~1	2	109.8	<0.001	
Survival ( <i>N</i> = 20)	<b>Joint effects</b>	<b>Het Meta Abun + Het Meta SVL + Het Meta Date + Con ♀ Abun + Con ♀ Date</b>	<b>7</b>	<b>0</b>	<b>1</b>	0.22/0.57
	Phenology	Het Meta Date + Con ♀ Date + Het ♀ Date	5	51.0	<0.001	
	Density	Het Meta Abun + Con ♀ Abun	4	63.0	<0.001	
	Intra	Con ♀ Abun + Con ♀ Date	4	63.1	<0.001	
	Inter	Het Meta Abun + Het Meta SVL + Het Meta Date	5	121.4	<0.001	
	Null	~1	2	149.8	<0.001	

$\omega$ , Akaike information criterion (AIC) weight; *K*, the number of parameters;  $\Delta$ AIC<sub>c</sub>, corrected AIC;  $r^2$  the marginal and conditional values, respectively

<sup>a</sup> *N* = Sample size

<sup>b</sup> All models included pond and year as random intercept terms. Models presented in bold are the most highly supported models

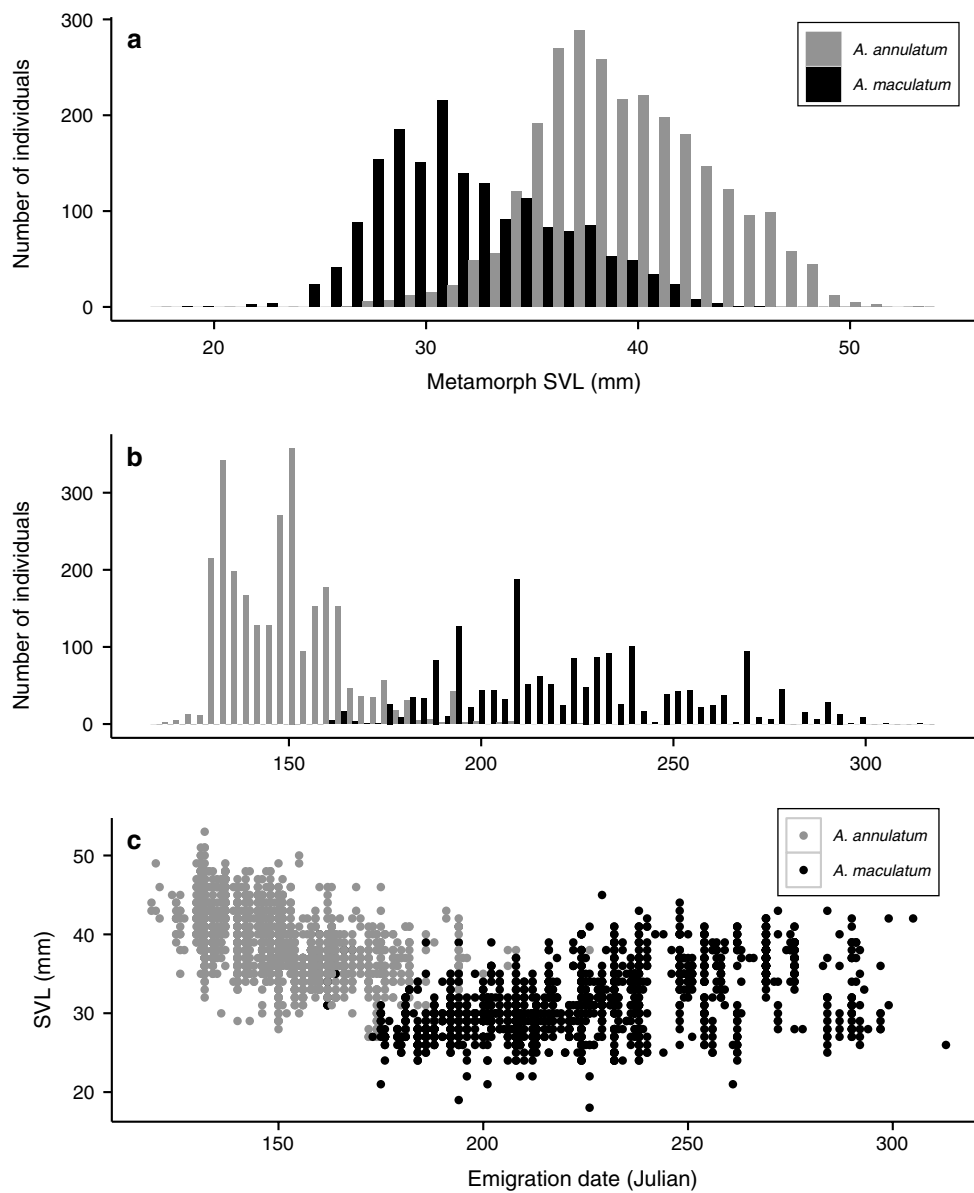
<sup>c</sup> 1, Intercept only; Con, conspecifics; Het, heterospecific; Meta, metamorph; ♀, adult females; Abun, abundance; Date, Julian date of female breeding migration (Con or Het), or Julian date of metamorph emigration (with Meta); SVL, snout–vent length

marginal  $r^2$  values were relatively low, which indicates that adding extra covariates did not result in substantially over-fitted models.

## Results

Across all ponds and years, mean ( $\pm$  standard deviation) abundance of metamorphs of *A. annulatum* and *A. maculatum* was  $139.2 \pm 155.7$  and  $88.6 \pm 87.1$ , respectively. The SVL of metamorphs of *A. annulatum* was greater than that of *A. maculatum* ( $39.16 \pm 3.4$  vs.  $31.39 \pm 4.6$  mm, respectively; Fig. 1a). The mean Julian date of metamorphosis for *A. annulatum* and *A. maculatum* was days  $148 \pm 6.8$  and  $224 \pm 19.0$ , respectively (Fig. 1b). Mean SVL and Julian

date of emigration showed significant and opposite patterns for each species, with SVL and emigration date showing a negative relationship for *A. annulatum* and a positive relationship for *A. maculatum* (Fig. 1c). Abundance of adult females averaged  $229.73 \pm 140.7$  and  $184.9 \pm 120.2$  for *A. annulatum* and *A. maculatum*, respectively. The mean Julian date of adult female immigration was  $254 \pm 8.2$  for *A. annulatum* and  $77 \pm 8.9$  for *A. maculatum*. Survival (abundance of metamorphs/no. of eggs laid) for both species was extremely low and was always  $<1\%$ . The mean temporal overlap of the two species was  $66.1 \pm 9.6$  (range 50–81) days, which was calculated by subtracting the mean emigration date of *A. annulatum* metamorphs from the mean date of *A. maculatum* breeding immigration. This slightly overestimates the overlap of free-swimming larvae



**Fig. 1** Ringed salamander (*Ambystoma annulatum*;  $N = 2,698$ ) and spotted salamander (*A. maculatum*,  $N = 1,758$ ) metamorph snout-vent length (SVL, in mm; **a**), Julian date (day) of metamorph emigra-

tion (**b**) and metamorph SVL–emigration date relationship (**c**). Bars in **b** represent a 3-days totals. For reference, Day 150 is equivalent to 30 May

of both species due to the several weeks it would take for eggs of *A. maculatum* to hatch (Petranka 1998); an overlap of 30–60 days represents a more realistic range of overlap between larvae.

For metamorph abundance of *A. annulatum*, the best supported model was the joint effects model, which contained both intra- and interspecific effects (adult abundance and timing of breeding of both species (Table 1). Conspecific female abundance and date of breeding both showed positive relationships with metamorph abundance, whereas the timing of heterospecific female breeding showed a weaker negative relationship, indicating that as *A. maculatum* bred

later, recruitment in *A. annulatum* was higher (Table 3). For metamorph SVL, the phenology model was the most supported, which included the date of metamorph emigration and the date of breeding for both con- and heterospecific females (Table 1). The date of metamorph emigration and conspecific female breeding date were both negatively correlated with metamorph SVL, but the former was twice as strong as the latter (Table 3). Date of metamorph emigration was best predicted by the density model (Table 1); metamorphs were predicted to emigrate later when more conspecific and heterospecific females bred in each season (Table 3). The joint effects model predicted the survival of

**Table 3** Parameter estimates of the top models for each response of metamorphic ringed salamanders (*A. annulatum*)

Species	Response	Covariates <sup>a</sup>	Estimate	Standard error	Lower CI <sup>b</sup>	Upper CI <sup>b</sup>
<i>A. annulatum</i>	Abundance	(Intercept)	−4.629	0.767	3.126	6.131
		AMMA ♀ Date	0.174	0.095	1.554	1.925
		AMMA ♀ Abun	−0.074	0.053	−0.178	0.031
		AMAN ♀ Abun	0.881	0.084	0.717	1.046
		AMAN ♀ Date	0.603	0.110	0.387	0.819
	SVL	Intercept	40.246	1.993	38.808	43.679
		AMAN ♀ Meta Date	−2.229	0.144	−2.505	−1.943
		AMAN ♀ Date	−1.712	0.368	−2.384	−0.954
		AMMA ♀ Date	0.810	0.286	0.270	1.383
	Emigration date	Intercept	144.275	5.219	134.045	154.504
		AMAN ♀ Abun	−6.356	0.958	−8.235	−4.478
		AMAN Meta Abun	−0.417	0.513	−1.423	0.588
	Survival	(Intercept)	−6.625	0.759	−8.113	−5.317
		AMMA ♀ Date	1.569	0.094	1.385	1.752
		AMMA ♀ Abun	−0.225	0.054	−0.330	−0.119
		AMAN ♀ Abun	0.431	0.084	0.266	0.596
AMAN ♀ Date		0.839	0.110	0.623	1.055	

<sup>a</sup> AMMA, *Ambystoma maculatum*; AMAN, *A. annulatum*; Date, Julian date of female breeding migration or emigration date of metamorphs

<sup>b</sup> Upper and lower CI are the bounds of the 95 % confidence interval

*A. annulatum*, which increased when greater numbers of females of both species bred, increased when *A. annulatum* bred later and decreased when *A. maculatum* bred later (Tables 1, 3).

The joint effects model was the top model for all responses (metamorph abundance, SVL, date of emigration and survival) of *A. maculatum* (Table 2). This model included the metamorph traits and abundance of *A. annulatum* and the abundance of adult females and timing of breeding for *A. maculatum*. The relationships between interspecific effects of *A. annulatum* and metamorph abundance and survival of *A. maculatum* were all negative, whereas a positive relationship existed for the date of breeding of *A. maculatum* and their metamorph abundance (Table 4). Metamorph survival in *A. maculatum* also declined with increasing numbers of conspecific females that bred, but did not vary with *A. annulatum* metamorph abundance (Table 4). Metamorph SVL of *A. maculatum* showed a positive relationship with the abundance and traits of *A. annulatum* metamorphs (Table 4), with the strongest effect on SVL occurring with emigration date of *A. annulatum*; metamorph SVL of *A. maculatum* increased the most when *A. annulatum* metamorphs emigrated later. Date of emigration for *A. maculatum* showed a negative relationship with the abundance of *A. annulatum* metamorphs, whereas all other variables in the joint effects model showed a positive relationship (Table 4). The two strongest positive relationships with the date of emigration in this species were conspecific female breeding date and *A. annulatum* metamorph emigration date (Table 4).

## Discussion

Overwhelming experimental evidence in aquatic communities suggests that the order of arrival of organisms into an environment substantially affects the outcome of species interactions and community assembly (Geange and Stier 2009; Hernandez and Chalcraft 2012; Stier et al. 2013; Wissinger 1992). For pond-breeding salamanders, results from several experimental and short-term field studies suggest breeding phenology differences should result in significant negative effects from fall-breeding species on spring-breeding species due to size asymmetries that exist between larvae (Segev and Blaustein 2007; Urban 2007a). We found that combinations of intra- and interspecific effects best explained metamorph abundance and survival in natural populations of each species. The relationships between each effect and the response variables also supports the hypothesis that fall-breeding *A. annulatum* negatively affects recruitment of the spring-breeding *A. maculatum*, matching the results of experimental studies (Anderson and Semlitsch 2014). Our results also indicate metamorph size and date of emigration within each species were affected by different processes (largely intraspecific effects for *A. annulatum* and combinations of intra- and interspecific interactions for *A. maculatum*), which contribute to different size–date relationships that have implications on terrestrial survival and adult fitness.

Greater numbers of conspecific females of *A. annulatum* resulted in increased survival and abundance of metamorphs, similar to data reported in other studies (Semlitsch et al. 1996). Later breeding also increased metamorph



**Table 4** Parameter estimates of top models for each response of metamorphic spotted salamanders (*A. maculatum*)

Response	Covariates	Estimate	SE	Lower CI <sup>a</sup>	Upper CI <sup>a</sup>
Abundance	(Intercept)	4.100	0.837	2.460	5.740
	AMAN Meta Abun	−0.539	0.062	−0.661	−0.417
	AMAN Meta SVL	−0.146	0.062	−0.269	−0.024
	AMMA ♀ Date	1.289	0.147	1.001	1.576
	AMAN Meta Date	−0.337	0.051	−0.437	−0.237
	AMMA ♀ Abun	−0.019	0.057	−0.131	0.094
SVL	(Intercept)	31.226	0.769	29.719	32.733
	AMAN Meta Abun	0.496	0.171	0.161	0.831
	AMAN Meta SVL	2.163	0.181	1.808	2.519
	AMAN Meta Date	3.621	0.188	3.252	3.990
	AMMA ♀ Date	0.535	0.346	−0.143	1.213
	AMMA ♀ Abun	0.933	0.184	0.572	1.293
Emigration date	(Intercept)	221.464	7.052	207.641	235.285
	AMAN Meta Abun	−7.520	1.465	−10.391	−4.649
	AMAN Meta SVL	5.689	1.556	2.640	8.738
	AMAN Meta Date	9.488	1.629	6.295	12.682
	AMMA ♀ Date	9.885	2.771	4.454	15.316
	AMMA ♀ Abun	5.982	1.602	2.842	9.123
Survival	(Intercept)	−6.222	0.800	−7.789	−4.654
	AMAN Meta Abun	−0.439	0.061	−0.559	−0.320
	AMAN Meta SVL	−0.144	0.062	−0.267	−0.022
	AMAN Meta Date	−0.250	0.054	−0.355	−0.144
	AMMA ♀ Date	1.217	0.145	0.933	1.501
	AMMA ♀ Abun	−0.505	0.057	−0.618	−0.393

<sup>a</sup> Upper and lower CI are the bounds of the 95 % confidence interval

abundance and survival of *A. annulatum*, potentially due to reduced predation by ectothermic predators in colder water temperatures in the fall. A positive relationship between the reproductive effort of *A. maculatum* and *A. annulatum* recruitment was also observed, supporting the hypothesis that *A. maculatum* is a food source for *A. annulatum* that increases their survival (Anderson and Semlitsch 2014). The timing of *A. maculatum* breeding may also be important for *A. annulatum*, as later *A. maculatum* breeding migrations resulted in increased *A. annulatum* metamorph abundance, suggesting that a separation of the larval period may potentially reduce negative interspecific interactions on early breeding species. Other studies have also suggested that a decreasing overlap may release species from negative interactions (Encinas-Viso et al. 2012; Revilla et al. 2013; Yang and Rudolf 2010). Overall, the combination of these two interspecific effects suggest that there may be a complex relationship between phenology and abundance, where metamorph production of *A. annulatum* increases when there are more prey (*A. maculatum* hatchlings), as long as they do not overlap for long periods of time that would increase competition with the *A.*

*maculatum* that escape via a size refugia (Urban 2007b). The date of emigration for *A. annulatum* also increased when more females bred the previous fall, which matches data reported from experimental studies showing density-dependent metamorphic rates (Anderson and Semlitsch 2014). The density model had relatively low explanatory power, even when accounting for the random effects, suggesting factors other than biotic interactions are also important for emigration. In particular, metamorph emigration date is likely influenced more by rainfall patterns than by biotic interactions, as individuals can undergo metamorphosis but not emigrate until favorable terrestrial conditions exist (Semlitsch et al. 1996; Todd and Winne 2006).

Metamorph abundance and survival of *A. maculatum* were negatively correlated with the metamorph traits and abundance of *A. annulatum* at our study site. Based on this model, greater abundance, later emigration dates (i.e. greater temporal overlap) and larger sizes of *A. annulatum* metamorphs all were negatively associated with *A. maculatum* metamorph abundance/survival. Abundance and survival of metamorphs increased when *A. maculatum* bred later, however. The direction of these effects supports

results from previous studies which suggest that the density and size of predators, as well as the synchrony of temporal overlap of predators and prey, are important to the outcome of interspecific interactions (Anderson and Semlitsch 2014; Griffin et al. 2011; Stier et al. 2013; Urban 2007a). Metamorph SVL for *A. maculatum* showed positive relationships with the size of *A. annulatum* metamorphs and the date of their emigration—but not with their abundance. This indicates that when *A. annulatum* were bigger and remained aquatic for longer, *A. maculatum* had reduced survival and metamorphosed at a larger size, which could be evidence for thinning effects (Van Buskirk and Yurewicz 1998). Furthermore, *A. maculatum* metamorphosed earlier at higher abundances of *A. annulatum* metamorphs, but did so at smaller sizes, indicating a potential cost on future fitness (Semlitsch et al. 1988). One potential factor that may confound our results is that the abundance of larval *A. annulatum* when *A. maculatum* bred may be different than metamorph abundance of *A. annulatum*. Larval abundance is the more biologically relevant predator density at the time of *A. maculatum* egg hatching, but was not measured in our study. Our use of metamorph abundance as an indication of predation level within the pond is likely an underestimation of the predatory effects of *A. annulatum*, which would only strengthen the argument of their negative effects.

External factors, such as predation by other species (i.e. aquatic invertebrates), hydroperiod and habitat quality, may determine the strength of interspecific interactions in more heterogeneous landscapes/ponds than those studied at DBCA (Amarasekare 2003). The hydroperiod of a pond is often considered to be the most important influence on larval abundance/survival and the amount of forested habitat as the most important influence on juvenile/adult survival (Rittenhouse et al. 2009; Rothermel and Semlitsch 2006; Wellborn et al. 1996). The five ponds within our study site all had nearly permanent hydroperiod regimes, which can lead to a build-up of invertebrate predators (Wellborn et al. 1996). Larval interactions may be more important in ephemeral ponds, as density-dependent processes would potentially be greater due to reduced densities of invertebrate predators and higher larval densities in these habitats. Intraguild predation would then be the dominant interspecific effect in these ponds where larval *A. annulatum* are the top predators, which ultimately could have significant top-down impacts on population dynamics and traits of spring-breeding species (Urban 2007a, 2010). The terrestrial habitat was also relatively homogenous in terms of forest cover, although management activities did occur at DBCA (see Semlitsch et al. 2009), indicating that accounting for spatial patterns alone may be uninformative if spatial variation in habitat factors is low. In other locations, predicted larval abundance of *A. maculatum* was twofold that of *A.*

*annulatum* in ponds surrounded by increasing amounts of forested habitat (Peterman et al. 2014). Thus, we predict that in a landscape of heterogeneous habitats (i.e. a gradient of hydroperiod cycles and varying terrestrial habitat types), concomitant variation in the strength of species interactions would occur due to varying densities (Amarasekare 2003).

The relationship of size and date of metamorphosis for metamorphs of the fall-breeding *A. annulatum* was negative, whereas metamorphs of *A. maculatum*, the spring-breeder, showed a positive relationship between the two responses. Size at and timing of metamorphosis are critical components to amphibian fitness (Scott 1994; Semlitsch et al. 1988), and our data show that differences in breeding phenology may result in differential patterns of selection on characters necessary for survival in a terrestrial environment. For *A. annulatum*, strong intraspecific competitors may dominate larval resource competition and/or prey upon conspecifics (Nyman et al. 1993), resulting in individuals that metamorphose early and at a large size. Individuals that cannot acquire sufficient resources as rapidly (i.e. poorer competitors) emigrate smaller and later with a reduced long-term fitness. Emerging early and large as a metamorph may reduce the risk of desiccation in the terrestrial environment as they would have a smaller body surface area:volume ratio, and spring temperatures would be lower than those of early summer (Peterman et al. 2013b; Semlitsch et al. 1988). Selection appears to operate in the opposite direction for *A. maculatum*. Early in ontogeny, individuals experience competition from conspecifics simultaneous to intraguild predation from resident species such as *A. annulatum*; the latter species can also deplete resource levels that would negatively affect *A. maculatum* (Anderson and Semlitsch 2014; Hernandez and Chalcraft 2012; Urban 2007a). *A. maculatum* individuals thus experience a trade-off, where those which undergo early metamorphosis escape negative aquatic conditions but do so at a cost of small juvenile size, which in turn is linked to reduced terrestrial survival (Rothermel and Semlitsch 2006). Individuals of *A. maculatum* that remain aquatic experience reduced larval competition as other conspecifics undergo metamorphosis (Semlitsch and Caldwell 1982), and they have access to greater food resources as invertebrate and vertebrate prey levels increase throughout the summer. In ephemeral habitats, this risky strategy increases the potential for mortality due to pond drying, however. Interestingly, individuals that metamorphosed at the same time for each species (late *A. annulatum* and early *A. maculatum*) were approximately the same size, indicating that life history differences of the two species may intensify their interactions as late-stage larvae and as metamorphs at the margins of their respective emigration distributional patterns. While little is known about juvenile terrestrial competition, equal-sized individuals may experience

greater interspecific competition as they would potentially be selecting similar-size burrows, unless there are other site-selection and/or behavioral differences between the two species (e.g. increased aggressiveness), which are currently unknown.

Understanding spatiotemporal variation in population dynamics is critical to accurately predict fluctuations in abundance that occur across space and time. In our study, accounting for spatiotemporal patterns (i.e. differences in marginal and conditional  $r^2$  values) varied from no improvement to explaining up to an additional 70 % of the variance, further highlighting the need to account for many factors when examining natural populations. Examinations of spatial and temporal patterns in amphibian assemblages often rely on presence/absence data or abundance of aquatic stages, with primary foci on population turnover and little emphasis on actual recruitment out of the aquatic habitat (Hecnar and M'Closkey 1996; Van Buskirk 2005; Werner et al. 2007). Juvenile salamanders are considered the important life history stage for population growth rates (Biek et al. 2002; Harper et al. 2008; Vonesh and De la Cruz 2002); therefore, understanding the parameters that affect spatiotemporal variation in recruitment and size is critical. As many species occur within spatially structured populations (i.e. metapopulations), understanding the factors (biotic and abiotic) that lead to spatial variability in recruitment is important for identifying mechanisms that differentiate high- and low-quality populations (i.e. sources and sinks). The designation of these categories may change between years based on the temporal variation we observed, necessitating multi-year monitoring of populations (Peterman et al. 2013a). Additionally, long-term monitoring of multiple populations would yield greater insight into natural fluctuations of abundance and may be necessary to understand variability in recruitment and long-term persistence (Semlitsch et al. 1996; Whiteman and Wissinger 2005).

Shifts in phenology due to climate change have been documented in many species (Miller-Rushing et al. 2010; Yang and Rudolf 2010), especially in amphibian breeding cycles (Todd et al. 2011). Therefore, an increased understanding of how phenology affects species interactions is critical to predict changes in community assembly patterns. Changes in temporal overlap or synchrony can result in novel interactions or decouple necessary interactions, such as plant-pollinators or pulses in food resources essential to consumers (Yang and Rudolf 2010). The translation of pairwise or guild interactions into community-level effects in which they are embedded are often difficult to determine, but could have important ecological and evolutionary consequences (Gilman et al. 2010). This study also provides baseline information on the phenology and abundance patterns of two interacting species that can provide a yardstick

for understanding future variation in phenology, as well as act as a framework for future investigations (Rafferty et al. 2013; Visser and Both 2005). Incorporating spatiotemporal variability would also facilitate more developed and broad conclusions regarding which processes influence variation in population dynamics, especially as climate shifts occur. Although it is often difficult to monitor and/or tease apart the multitude of factors affecting natural populations, concurrent experimental studies with observations of natural populations are necessary to understand when and where species interactions become relevant in their effects on population and community dynamics.

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## References

- Alford RA (1989) Variation in predator phenology affects predator performance and prey community composition. *Ecology* 70:206–219
- Alford RA, Wilbur HM (1985) Priority effects in experimental pond communities: competition between *Bufo* and *Rana*. *Ecology* 66:1097–1105
- Almany GR (2003) Priority effects in coral reef fish communities. *Ecology* 84:1920–1935
- Amarasekare P (2003) Competitive coexistence in spatially structured environments: a synthesis. *Ecol Lett* 6:1109–1122. doi:10.1046/j.1461-0248.2003.00530.x
- Anderson TL, Semlitsch RD (2014) High intraguild predator density induces thinning effects on and increases temporal overlap with prey populations. *Popul Ecol* 56:265–273. doi:10.1007/s10144-013-0419-9
- Bates D, Maechler M, Bolker BM (2013) lme4: Linear mixed-effects models using Eigen and Eigen. R package version 1.0-5. Available at: <http://CRAN.R-project.org/package=lme4>
- Berven KA (2009) Density dependence in the terrestrial stage of wood frogs: evidence from a 21-year population study. *Copeia* 2009:328–338
- Biek R, Funk WC, Maxell BA, Mills LS (2002) What is missing in amphibian decline research: insights from ecological sensitivity analysis. *Conserv Biol* 16:728–734
- Blaustein L, Margalit J (1996) Priority effects in temporary pools: nature and outcome of mosquito larva-toad tadpole interactions depend on order of entrance. *J Anim Ecol* 65:77–84
- Blois JL, Zarnetske PL, Fitzpatrick MC, Finnegan S (2013) Climate change and the past, present, and future of biotic interactions. *Science* 341:499–504. doi:10.1126/science.1237184
- Boone MD, Scott DE, Niewiarowski PH (2002) Effects of hatching time for larval ambystomatid salamanders. *Copeia* 2002:511–517
- Connell JH, Slatyer RO (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *Am Nat* 111:1119–1144
- Eitam A, Blaustein L, Mangel M (2005) Density and intercohort priority effects on larval *Salamandra salamandra* in temporary pools. *Oecologia* 146:36–42. doi:10.1007/s00442-005-0185-2

- Encinas-Viso F, Revilla TA, Etienne RS (2012) Phenology drives mutualistic network structure and diversity. *Ecol Lett* 15:198–208. doi:10.1111/j.1461-0248.2011.01726.x
- Geange SW, Stier AC (2009) Order of arrival affects competition in two reef fishes. *Ecology* 90:2868–2878
- Gilman SE, Urban MC, Tewksbury J, Gilchrist GW, Holt RD (2010) A framework for community interactions under climate change. *Trends Ecol Evol* 25:325–331. doi:10.1016/j.tree.2010.03.002
- Griffin KA, Hebblewhite M, Robinson HS, Zager P, Barber-Meyer SM, Christianson D et al (2011) Neonatal mortality of elk driven by climate, predator phenology and predator community composition. *J Anim Ecol* 80:1246–1257
- Harper EB, Rittenhouse TA, Semlitsch RD (2008) Demographic consequences of terrestrial habitat loss for pool-breeding amphibians: predicting extinction risks associated with inadequate size of buffer zones. *Conserv Biol* 22:1205–1215. doi:10.1111/j.1523-1739.2008.01015.x
- Hecnar SJ, M'Closkey RT (1996) Regional dynamics and the status of amphibians. *Ecology* 77:2091–2097
- Hernandez JP, Chalcraft DR (2012) Synergistic effects of multiple mechanisms drive priority effects within a tadpole assemblage. *Oikos* 121:259–267. doi:10.1111/j.1600-0706.2011.19221.x
- Hocking DJ, Rittenhouse TAG, Rothermel BB, Johnson JR, Conner CA, Harper EB et al (2008) Breeding and recruitment phenology of amphibians in Missouri oak-hickory forests. *Am Midl Nat* 160:41–60
- Hunter AF, Elkinton JS (2001) Interaction between phenology and density effects on mortality from natural enemies. *J Anim Ecol* 68:1093–1100
- Hutcherson JE, Peterson CL, Wilkinson RF (1989) Reproductive and larval biology of *Ambystoma annulatum*. *J Herpetol* 23:181–183
- Kardol P, Souza L, Classen AT (2013) Resource availability mediates the importance of priority effects in plant community assembly and ecosystem function. *Oikos* 122:84–94. doi:10.1111/j.1600-0706.2012.20546.x
- Lawler SP, Morin PJ (1993) Temporal overlap, competition, and priority effects in larval anurans. *Ecology* 74:174–182
- Miller-Rushing AJ, Hoyer TT, Inouye DW, Post E (2010) The effects of phenological mismatches on demography. *Philos Trans R Soc Lond Ser B Biol Sci* 365:3177–3186. doi:10.1098/rstb.2010.0148
- Morin PJ (1983) Predation, competition, and the composition of larval anuran guilds. *Ecol Monogr* 53:120–138
- Nakagawa S, Schielzeth H, O'Hara RB (2013) A general and simple method for obtaining  $R^2$  from generalized linear mixed-effects models. *Methods Ecol Evol* 4:133–142. doi:10.1111/j.2041-210x.2012.00261.x
- Nyman S, Wilkinson RF, Hutcherson JE (1993) Cannibalism and size relations in a cohort of larval ringed salamanders (*Ambystoma annulatum*). *J Herpetol* 27:78–84
- Orizaola G, Dahl E, Nicleza AG, Laurila A (2013) Larval life history and anti-predator strategies are affected by breeding phenology in an amphibian. *Oecologia* 171:873–881. doi:10.1007/s00442-012-2456-z
- Padeffke T, Suhling F (2003) Temporal priority and intra-guild predation in temporary waters: an experimental study using Namibian desert dragonflies. *Ecol Entomol* 28:340–347
- Peterman WE, Earl JE, Rittenhouse TAG, Semlitsch RD (2013a) Demographic network and multi-season occupancy modeling of *Rana sylvatica* reveal spatial and temporal patterns of population connectivity and persistence. *Landsc Ecol* 28:1601–1613. doi:10.1007/s10980-013-9906-9
- Peterman WE, Locke JL, Semlitsch RD (2013b) Spatial and temporal patterns of water loss in heterogeneous landscapes: using plaster models as amphibian analogues. *Can J Zool* 91:135–140
- Peterman WE, Anderson TL, Drake DL, Ousterhout BH, Semlitsch RD (2014) Maximizing pond biodiversity across the landscape: a case study of larval ambystomatid salamanders. *Anim Conserv* 17:275–285. doi:10.1111/acv.12090
- Petranka JW (1998) Salamanders of the US and Canada. Smithsonian Institution Press, Washington, DC
- Porensky LM, Vaughn KJ, Young TP (2012) Can initial intraspecific spatial aggregation increase multi-year coexistence by creating temporal priority? *Ecol Appl* 22:927–936
- R Development Core Team (2013) R: a language and environment for statistical computing, 3.0.2 edn. R Foundation for Statistical Computing, Vienna
- Rafferty NE, Caradonna PJ, Burkle LA, Iler AM, Bronstein JL (2013) Phenological overlap of interacting species in a changing climate: an assessment of available approaches. *Ecol Evol* 3:3183–3193. doi:10.1002/ece3.668
- Revilla T, Encinas-Viso F, Loreau M (2013) (A bit) Earlier or later is always better: phenological shifts in consumer–resource interactions. *Theor Ecol* 7:149–162. doi:10.1007/s12080-013-0207-3
- Rittenhouse TA, Semlitsch RD, Thompson FR III (2009) Survival costs associated with wood frog breeding migrations: effects of timber harvest and drought. *Ecology* 90:1620–1630
- Rothermel B, Semlitsch R (2006) Consequences of forest fragmentation for juvenile survival in spotted (*Ambystoma maculatum*) and marbled (*Ambystoma opacum*) salamanders. *Can J Zool* 84:797–807
- Schmidt BR, Hodl W, Schaub M (2012) From metamorphosis to maturity in complex life cycles: equal performance of different juvenile life history pathways. *Ecology* 93:657–667
- Scott DE (1994) The effect of larval density on adult demographic traits in *Ambystoma opacum*. *Ecology* 75:1383–1396
- Segev O, Blaustein L (2007) Priority effects of the early breeding fire salamander on the late breeding banded newt. *Hydrobiologia* 583:275–283. doi:10.1007/s10750-006-0565-6
- Semlitsch RD, Caldwell JP (1982) Effects of density of growth, metamorphosis, and survivorship in tadpoles of *Scaphiopus holbrookii*. *Ecology* 63:905–911
- Semlitsch RD, Scott DE, Pechmann JH (1988) Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum*. *Ecology* 69:184–192
- Semlitsch R, Scott D, Pechmann J, Gibbons J (1996) Structure and dynamics of an amphibian community: evidence from a 16-year study of a natural pond. In: Cody ML, Smallwood JA (eds) Long-term studies of vertebrate communities. Academic Press, San Diego, pp 217–248
- Semlitsch RD, Conner CA, Hocking DJ, Rittenhouse TA, Harper EB (2008) Effects of timber harvesting on pond-breeding amphibian persistence: testing the evacuation hypothesis. *Ecol Appl* 18:283–289
- Semlitsch RD, Todd BD, Blomquist SM, Calhoun AJK, Whitfield Gibbons J, Gibbs JP et al (2009) Effects of timber harvest on amphibian populations: understanding mechanisms from forest experiments. *Bioscience* 59:853–862. doi:10.1525/bio.2009.59.10.7
- Semlitsch RD, Anderson TL, Ousterhout BH, Osbourn MS (2014) Structure and dynamics of ringed salamander (*Ambystoma annulatum*) populations in Missouri. *Herpetologica* 70:14–22
- Shoop CR (1974) Yearly variation in larval survival of *Ambystoma maculatum*. *Ecology* 55:440–444
- Shorrocks B, Bingley M (1994) Priority effects and species coexistence: experiments with fungal-breeding *Drosophila*. *J Anim Ecol* 63:799–806
- Stenhouse SL (1985) Interdemic variation in predation on salamander larvae. *Ecology* 66:1706–1717
- Stenhouse SL (1987) Embryo mortality and recruitment of juveniles of *Ambystoma maculatum* and *Ambystoma opacum* in North Carolina. *Herpetologica* 43:496–501
- Stenhouse SL, Hairston NG, Cobey AE (1983) Predation and competition in *Ambystoma* larvae: field and laboratory experiments. *J Herpetol* 17:210–220

- Stier A, Geange SW, Hanson KM, Bolker B (2013) Predator density and timing of arrival affect reef fish community assembly. *Ecology* 94:1057–1068
- Todd BD, Winne CT (2006) Ontogenetic and interspecific variation in timing of movement and responses to climatic factors during migrations by pond-breeding amphibians. *Can J Zool* 84:715–722. doi:10.1139/z06-054
- Todd BD, Scott DE, Pechmann JH, Gibbons JW (2011) Climate change correlates with rapid delays and advancements in reproductive timing in an amphibian community. *Proc R Soc B Biol Sci* 278:2191–2197. doi:10.1098/rspb.2010.1768
- Trauth SE, Robison HW, Plummer MV (2004) The amphibians and reptiles of Arkansas. University of Arkansas Press, Fayetteville
- Urban MC (2007a) Predator size and phenology shape prey survival in temporary ponds. *Oecologia* 154:571–580. doi:10.1007/s00442-007-0856-2
- Urban MC (2007b) Risky prey behavior evolves in risky habitats. *Proc Natl Acad Sci USA* 104:14377–14382. doi:10.1073/pnas.0704645104
- Urban MC (2010) Microgeographic adaptations of spotted salamander morphological defenses in response to a predaceous salamander and beetle. *Oikos* 119:646–658
- Van Buskirk J (2005) Local and landscape influence on amphibian occurrence and abundance. *Ecology* 86:1936–1947
- Van Buskirk J, Yurewicz KL (1998) Effects of predators on prey growth rate: relative contributions of thinning and reduced activity. *Oikos* 82:20–28
- Visser ME, Both C (2005) Shifts in phenology due to climate change: the need for a yardstick. *Proc R Soc Lond Ser B Biol Sci* 272:2561–2569. doi:10.1098/rspb.2005.3356
- Vonesh J, De la Cruz O (2002) Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines. *Oecologia* 133:325–333. doi:10.1007/s00442-002-1039-9
- Warton DI, Hui FK (2011) The arcsine is asinine: the analysis of proportions in ecology. *Ecology* 92:3–10
- Wellborn GA, Skelly DK, Werner EE (1996) Mechanisms creating community structure across a freshwater habitat gradient. *Annu Rev Ecol Syst* 27:337–363
- Werner EE, Yurewicz KL, Skelly DK, Relyea RA (2007) Turnover in an amphibian metacommunity: the role of local and regional factors. *Oikos* 116:1713–1725. doi:10.1111/j.2007.0030-1299.16039.x
- Whiteman HH, Wissinger SA (2005) Amphibian population cycles and long-term data sets. In: Lannoo MJ (ed) *Amphibian declines: conservation status of US species*. California University Press, Los Angeles, pp 177–184
- Wilbur HM, Alford RA (1985) Priority effects in experimental pond communities: responses of *Hyla* to *Bufo* and *Rana*. *Ecology* 66:1106–1114
- Wissinger SA (1992) Niche overlap and the potential for competition and intraguild predation between size-structured populations. *Ecology* 73:1431–1444
- Wissinger S, Whiteman HH, Denoel M, Mumford ML, Aubee CB (2010) Consumptive and nonconsumptive effects of cannibalism in fluctuating age-structured populations. *Ecology* 91:549–559
- Yang LH, Rudolf VH (2010) Phenology, ontogeny and the effects of climate change on the timing of species interactions. *Ecol Lett* 13:1–10. doi:10.1111/j.1461-0248.2009.01402.x