



Demographic effects of phenological variation in natural populations of two pond-breeding salamanders

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Abstract

Phenology is a key driver of population and community dynamics. Phenological metrics (e.g., first date that an event occurred) often simplify information from the full phenological distribution, which may undermine efforts to determine the importance of life history events. Data regarding full phenological distributions are especially needed as many species are shifting phenology with climatic change which can alter life-history patterns and species dynamics. We tested whether skewness, kurtosis or maximum duration of breeding phenology affected juvenile emigration phenology and survival in natural populations of ringed (*Ambystoma annulatum*) and spotted salamanders (*A. maculatum*) spanning a 7-year period at two study locations. We evaluated the relative importance of different phenological metrics in breeding phenology and larval density dependence on emigration phenology and survival. We found that variability in emigration phenology differed by species, with ringed salamanders having a shorter duration and distributions that were more often right-skewed and leptokurtic compared to spotted salamanders. Emigration phenology was not linked to any measure of variability in breeding phenology, indicating phenological variability operates independently across life stages and may be subject to stage-specific influences. Emigration duration and skewness were partially explained by larval density, which demonstrates how phenological distributions may change with species interactions. Further tests that use the full phenological distribution to link variability in timing of life history events to demographic traits such as survival are needed to determine if and how phenological shifts will impact species persistence.

Keywords *Ambystoma* · Amphibian · Ontogeny · Phenology · Synchrony

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Introduction

Phenology, or the timing of seasonal life history events, influences numerous important ecological processes, including population demography and trophic dynamics (Miller-Rushing et al. 2010; Nakazawa and Doi 2012; Yang and Rudolf 2010). The importance of phenology is determined in part by how relative differences in the timing of individuals affects intra- and interspecific interactions. In recent years, investigations have documented shifts in the phenology of numerous taxa, including birds, amphibians, plants, and insects (Parmesan 2006). However, the degree to which such shifts will reshape population and community dynamics is largely unknown (Miller-Rushing et al. 2010; Yang and Rudolf 2010; Nakazawa and Doi 2012), especially when considering the multitude of ways that phenological change may manifest. Furthermore, there is substantial variability in the degree of phenological shifts among species

(CaraDonna et al. 2014; Diez et al. 2012; Parmesan 2007), which could have large implications for species interactions and ultimately communities as a whole.

Typically, measures of phenology include a single event for a population, such as the first or median date of some important life-history characteristic (Inouye et al. 2019; Miller-Rushing et al. 2010). However, phenology is better represented as a distribution of events carried out by many individuals in a population cumulatively over a season or life-history stage (CaraDonna et al. 2014; Carter et al. 2018; Inouye et al. 2019; Miller-Rushing et al. 2010). Therefore, single event metrics provide only a portion of the available information about phenology, especially in regards to describing all individuals within a distribution. In particular, the degree of variability among individuals making up the phenological distribution within a population can strongly affect demography. For example, the degree of synchrony in breeding can influence susceptibility to predators (Ims 1990) or the strength of intra- and interspecific interactions (Carter and Rudolf 2019; Rasmussen and Rudolf 2015, 2016). The consequences of phenological variability on population and community dynamics, as opposed to other shifts (e.g., mean or median of the distribution), are poorly understood for many species, especially from natural populations.

Many organisms have ontogenies characterized by discrete stages that occupy distinct habitats (i.e., complex life cycles; Wilbur 1980). Such organisms could therefore have multiple important phenological events across their lifetime as they transition between habitats. Understanding whether variability in phenology differs across ontogenetic stages is important for connecting phenological shifts due to climate change to impacts on life history and population dynamics. Understanding differences in phenology across ontogeny may be especially important if certain life stages disproportionately affect a population. Furthermore, observing whether shifts at one ontogenetic stage can affect the phenology of a subsequent stage can help show whether carry over effects may occur. For example, using an experimental system, Rasmussen and Rudolf (2015) found that decreasing phenological synchrony (i.e., an increase in variation) of the hatching stage of an amphibian resulted in decreased synchrony (increased variability) of metamorphosis, depending on the strength of density dependence. However, the degree to which phenology is coupled across ontogeny is still largely unexplored (Augspurger 1981; Augspurger and Zaya 2020; Carter and Rudolf 2019; Rasmussen and Rudolf 2015), especially in natural systems, and would be a critical next step in identifying whether and how phenological shifts will ultimately affect population and community dynamics.

The goal of this study was to assess the importance of phenological variability to the demography of natural populations of two pond-breeding amphibians, the ringed salamander (*Ambystoma annulatum*) and spotted salamander

(*A. maculatum*). We leveraged data from two intensive population monitoring studies that spanned 2001–2007 to examine three metrics (phenological duration, skewness, and kurtosis) of two phenological processes: adult breeding and juvenile emigration. Our specific study aims were to test whether: (1) species and life stages differed in their degree of phenological variability; (2) variability in juvenile emigration was associated with variability in the timing of adult breeding migrations; and (3) phenological variability in breeding impacted survival of eggs and larvae.

Methods

Study system

Pond-breeding amphibians are a model system for examining phenological shifts across ontogeny, because many species have discrete life stages that occupy specific habitats, each separated by distinct phenological events. For instance, many anurans and caudates have terrestrial adults that undergo mass migrations to breeding ponds in response to suitable temperature and rainfall conditions (Todd and Winne 2006). Some amphibian species have shown shifts in the average or median breeding date in response to changing climates (Ficetola and Maiorano 2016). A second major phenological process of many amphibians is metamorphosis, where aquatic larvae transition to terrestrial juveniles and emigrate from the natal site. However, whether changes to juvenile emigration patterns have occurred and/or whether this process is influenced by adult breeding phenology is unknown for most taxa (but see Benard 2015). Furthermore, experimental evidence suggests that phenological variability can impact survival of aquatic stages by altering body size variability and subsequent interaction strengths (Murillo-Rincón et al. 2017; Petranka and Thomas 1995; Rasmussen and Rudolf 2015). In particular, greater size variability among individuals increases cannibalism rates during the aquatic stages of ambystomatid salamanders (Anderson et al. 2013; Nyman et al. 1993; Wissinger et al. 2010). The degree of metamorph emigration synchrony has also been suspected as a mechanism to increase survival via predator confusion and satiation (DeVito 2003). However, the effects of phenology on demographic traits (e.g., survival) in natural populations have rarely been tested (Benard 2015).

Ringed and spotted salamanders co-occur throughout the Central Interior Highlands of Missouri, Arkansas and Oklahoma (Petranka 1998). Adults are fossorial and live primarily in forested areas surrounding fishless wetlands. The main life history difference between species is that ringed salamanders undergo breeding migrations in the fall, whereas spotted salamanders migrate to breeding ponds in the spring (Hocking et al. 2008; Petranka 1998). This difference in

breeding phenology results in larval ringed salamanders overwintering in ponds and metamorphosing in late spring to early summer (6–9 month larval period). Body size variability in ringed salamanders, which would be expected with greater variability in phenology, has also been hypothesized to play a role in cannibalism among larvae (Nyman et al. 1993). In contrast, the spotted salamander larval period typically lasts 2–6 months, with individuals typically undergoing metamorphosis in mid-summer through the fall. Cannibalism has rarely been reported in spotted salamanders (Mott and Sparling 2016), though presumably would occur if sufficient size differences existed among individuals. Rainfall patterns are the primary environmental driver initiating breeding and emigration movements for spotted salamanders (Semlitsch and Anderson 2016), whereas temperature and rainfall influences ringed salamanders (Online Resource S1).

Field methods

We used data from two long-term population monitoring studies in Missouri, USA. First, we used data from the Land-Use Effects on Amphibian Populations (LEAP) study, a project that investigated the effects of different forestry practices on amphibian populations (Semlitsch et al. 2009). The methods have been described in detail previously, so we do not repeat them in full here and instead relay the pertinent methodological information: (1) five constructed ponds at Daniel Boone Conservation Area (38.772, -91.400) near Hermann, Missouri were monitored from 2004–2007, (2) monitoring consisted of encircling each pond with complete drift fences and pitfall traps to capture breeding adults and metamorphosing juveniles as they moved between the ponds and the terrestrial landscape, and (3) pitfall traps were monitored at least every other day during the months in which amphibian movements occur (February–October), thus ensuring a thorough record of amphibian phenological patterns for both adult breeding and juvenile emigration. We used data for both focal salamanders at the LEAP sites (Online Resource S3, Table S1).

The second data set came from two ponds at the Baskett Wildlife Research Area and one pond in the adjacent Mark Twain National Forest near Ashland, Missouri (38.748, -92.193), collected from 2001–2003 (hereafter, Baskett sites; Hocking et al. 2008; Rittenhouse and Semlitsch 2006). Sampling methods were similar to the LEAP sites with ponds encircled with drift fences and pitfall traps that were checked during the active season. Only spotted salamanders are present at Baskett, and thus was the only species included from that site (Online Resource S3, Table S1). We limited our analysis to events when > 10 juveniles emerged from a pond in a given year to maintain more robust assessments of emigration phenology; this eliminated two data points for ringed salamanders where only seven individuals

were caught emigrating. Thus, across both sites, the total sample size used for each species was: $N = 13$ for ringed salamanders (5 ponds over 3 years at one location, minus 2 for insufficient data); $N = 28$ for spotted salamanders (8 ponds over 7 years at 2 locations).

Analyses

First, we visually inspected histograms of day of the year of movement events of each ontogenetic stage and species (Online Resource S2, Figs. S1–S4) and removed outlier individuals based on typical ontogenetic periods for that species (Petranka 1998). This primarily excluded 13 adult spotted salamanders that were caught in the fall between 6 Aug and 31 Oct at the LEAP ponds. Our exact cut-offs were after July 19 (DOY = 200) for adult ringed salamanders, before June 29 (DOY = 180) for adult spotted salamanders (Online Resource S2, Fig. S1–S4).

We calculated three metrics to assess phenological variability: the duration of the phenological event (i.e., the number of days between the first individual and the last individual), the skewness of a population's distribution, and the kurtosis of the distribution. We calculated each metric for both adult breeding females and emigrating juveniles. A longer duration would indicate less synchrony among individuals, while a shorter duration would be indicative of higher synchrony. Positive skewness values would indicate a right-tailed distribution, whereas negative values would indicate a left-tailed distribution. A normal distribution has a kurtosis value of 3, with higher values indicating a shift towards the center and the tails of the distribution (high synchrony) and lower values indicate a shift towards a more uniform distribution (low synchrony). Together, we used these three metrics to determine the effects of phenological variability on demographic patterns.

We first tested for species differences in each metric (phenological duration, skewness and kurtosis), which would indicate whether species varied in the degree of phenological variability. We attempted to use linear mixed effects models, with species as a fixed effect, and pond and year as random effects on the intercept to account for repeated sampling of ponds. We implemented the analysis using the 'lme4' package (version 1.1-23; Bates et al. 2015) in the R statistical program (version 4.0; R Core Team 2020). However, in some models, the variance of these effects was 0, suggesting either the random effects were unimportant, or the models had poor fits, likely due to small sample sizes (Bolker et al. 2009). When this happened, we tried switching pond and/or year to a fixed effect, or omitted their inclusion entirely and used general linear models (GLMs), though we acknowledge this creates the potential for pseudoreplication; other studies have similarly treated repeated sampling

of ponds as independent data points (Van Buskirk 2005; Werner et al. 2009).

Within each species, we analyzed phenological relationships using a combination of GLMs and linear mixed effects models (for the same reasons as above; Online Resource, Table S1) to test whether breeding variability or the number of breeding females (N_f) predicted variability in juvenile emigration and an index of survival, calculated as the number juveniles per female ($N_j \times N_f^{-1}$). Multiplying N_f by average clutch size ($N = 224$ eggs for spotted salamanders; 390 eggs for ringed salamanders) in this equation would make our estimates comparable to survival values calculated in other studies (Peterson et al. 1991; Shoop 1974). We again used our three measures of variability for each life stage (duration, skewness and kurtosis) as response variables, but only used the same measure of breeding variability to predict emigration variability, i.e., we tested only for effects of breeding duration on emigration duration, breeding skewness on emigration skewness, and breeding kurtosis on emigration kurtosis. We had no a priori reason that one measure of variability would predict a different measure (i.e., breeding duration would predict emigration skewness). In all models, we included N_f at a given pond in a given year to approximate the initial larval density, based on previous analyses showing density dependence can influence phenological patterns (Anderson et al. 2017; Rasmussen and Rudolf 2015). We log-transformed the survival index due to model residuals indicating non-normality. For all models of spotted salamanders, we also included location (Baskett or LEAP) as an additional predictor. Based on graphical assessments of the data (Figs. 2, 3), we performed a post-hoc test for spotted salamanders that included two-way interactions between location and N_f and our measures of breeding variability, though this analysis was exploratory rather than expected a priori.

We examined significance of individual covariates in mixed models based on chi-square test statistics using the *Anova* function in the ‘car’ package (Fox and Weisberg 2011). For all mixed models, we also calculated the marginal (R_m^2) and conditional (R_c^2) R^2 values to assess the relative contributions of the fixed and the fixed + random effects to explaining variation in the responses using the *r.squaredGLMM* function in the ‘MuMIn’ package (Barton 2018; Nakagawa et al. 2013). For GLMs, we evaluated covariate significance using standard F-tests and calculated the coefficient of variation (R^2). Because of the number of statistical tests we conducted ($N = 28$), we examined whether correcting for multiple tests using false discovery rate methods influenced our results (Verhoeven et al. 2005). All statistically significant results remained so after correction, except for two, which we highlight below. All model structures and parameter estimates are reported in Online Resource S3, Tables S1 and S2.

Results

Models comparing species for breeding duration, skewness, and kurtosis converged using only year as a random effect. Comparisons of emigration duration, skewness and kurtosis across species would not converge with random effects and therefore we used GLMs (Online Resource S3, Table S1).

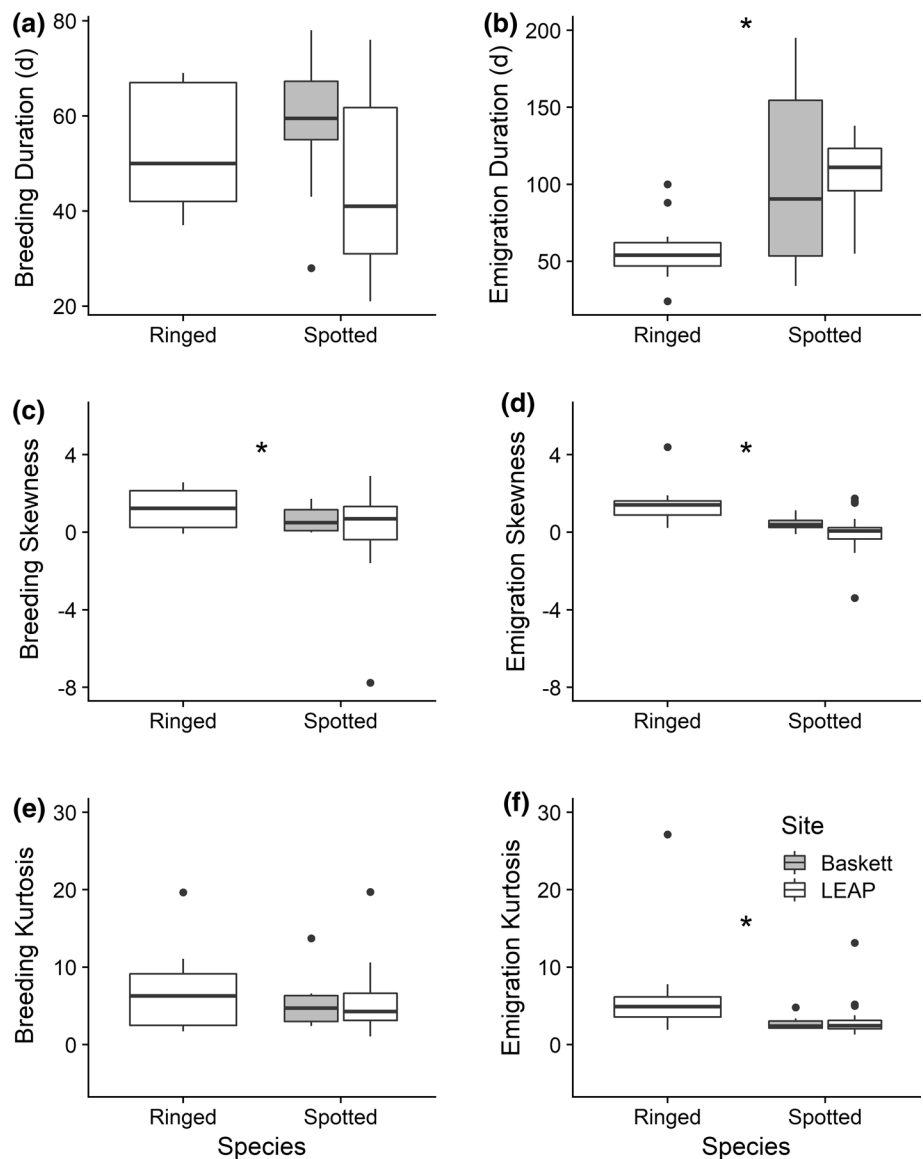
Species comparison

Breeding durations spanned lengths of 20–80 days across both species, whereas emigration durations spanned 24–295 days (Fig. 1A, B). Only for emigration duration was there a significant difference between species, with spotted salamanders having a longer duration of emigration (breeding: $\chi^2 = 1.07$, $df = 1$, $P = 0.30$; $R_m^2 = 0.02$; $R_c^2 = 0.32$; emigration: $F_{1,39} = 17.86$, $P = 0.0001$; $R^2 = 0.30$). The mean value for spotted salamander breeding duration was nearly identical to the value of ringed salamanders (Fig. 1A), while they had nearly double the duration value for emigration (Online Resource S3, Table S1; Fig. 1B).

The skewness in female breeding duration significantly varied by species ($\chi^2 = 24.92$, $df = 1$, $P < 0.001$; $R_m^2 = 0.23$; $R_c^2 = 0.73$). Female ringed salamander skewness values were more than double that of spotted salamanders (Online Resource 3, Table S1) and were higher, positive numbers, meaning they had a right-tailed distribution (Fig. 1C). Emigration skewness was also significantly higher for ringed salamanders (Online Resource S3, Table S1; $F_{1,39} = 18.90$, $df = 1$, $P < 0.001$; $R^2 = 0.31$); across both sites, there was a 136% difference in skewness. Similar to breeding in ringed salamanders, emigration skewness was more often positive-valued, meaning a right-tailed distribution (Fig. 1D).

Across both species, 70% of the kurtosis values for breeding were greater than 3 (kurtosis of a normal distribution = 3), indicating species tended to have leptokurtic distributions, with more values in the tails and center of the distribution (Fig. 1E). After omitting an outlier data point for spotted salamanders (kurtosis = 64), breeding kurtosis was slightly higher for ringed salamanders than spotted salamanders, though this difference was not significant at our a priori alpha level of 0.05 (Online Resource S3, Table S1; $\chi^2 = 3.12$, $df = 1$, $P = 0.08$; $R_m^2 = 0.11$; $R_c^2 = 0.37$; Fig. 1E). Emigration kurtosis was two times higher for ringed salamanders (Online Resource S3, Table S1; $F_{1,38} = 29.41$, $P < 0.001$; $R^2 = 0.13$), again indicating leptokurtosis (Fig. 1F). In contrast, the average kurtosis for spotted salamanders was less than 3, indicating that the data frequently were more uniformly distributed.

Fig. 1 Species differences in the maximum duration (in days) (a, b), skewness (c, d), and kurtosis (e, f) for female breeding (a, c, e) and juvenile emigration (b, d, e) phenology ($N=13$ for ringed salamanders; $N=28$ for spotted salamanders). Asterisk indicates a significant difference between species. Significant relationships remain even if values at ~ -8 in c and ~ 28 in f are removed. One value is omitted in e for spotted salamanders at ~ 64 . The black solid line indicates the median value, the edges of the boxes reach the first and third quartiles, and the whiskers extend to 1.5 times the interquartile range



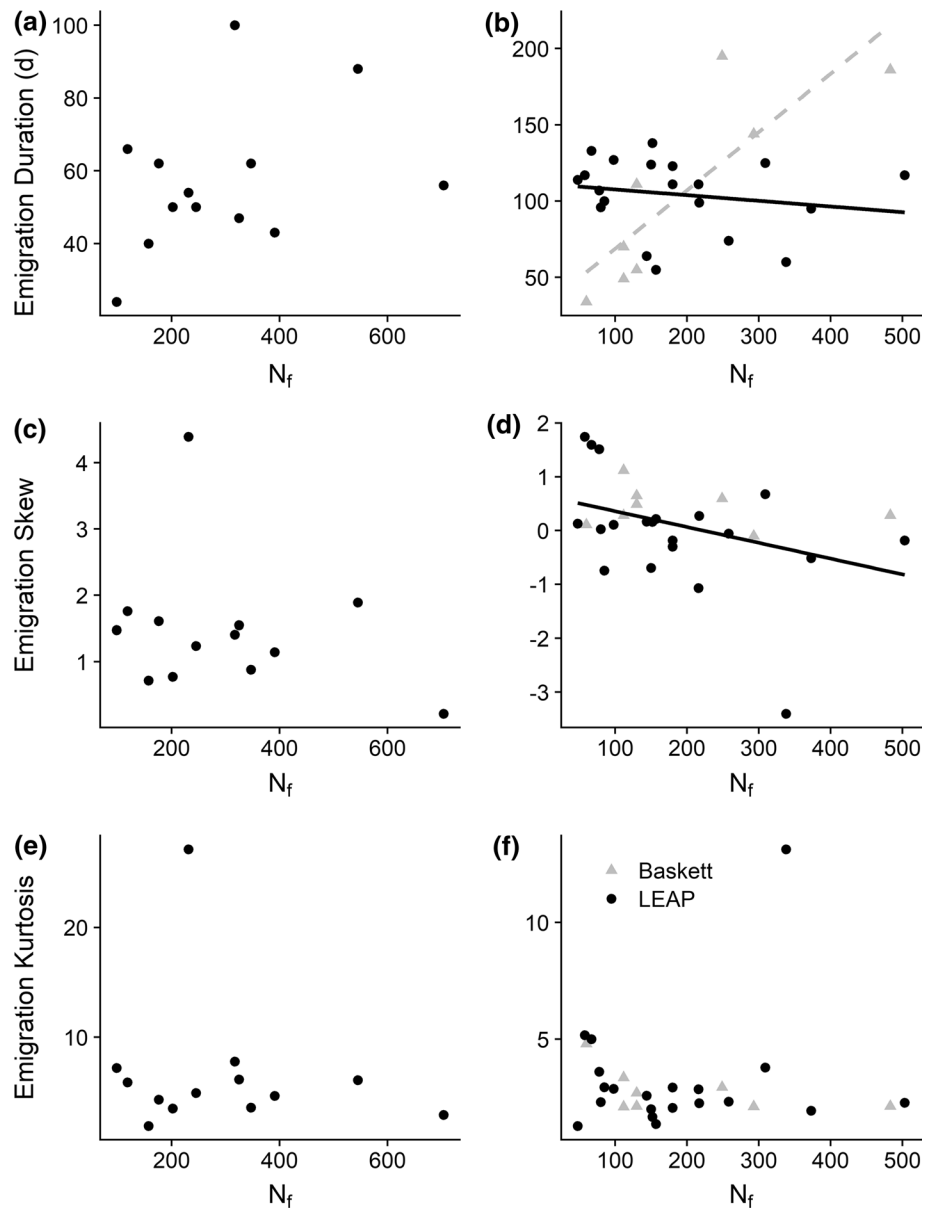
Juvenile emigration

Models of emigration skewness in ringed salamanders using N_f and breeding skewness as covariates converged using both pond and year as random effects (Online Resource 3, Table S1). Emigration duration included only year as a random effect, and emigration kurtosis was best modeled as a GLM (Online Resource 3, Table S1). Emigration duration did not vary with either N_f ($\chi^2=1.30$, $df=1$, $P=0.25$; Fig. 2A) or breeding duration ($\chi^2=0.18$, $df=1$, $P=0.67$ $R_m^2=0.05$; $R_c^2=0.60$; Fig. 3A). Ponds with more females tended to have to higher emigration skewness ($\chi^2=3.60$, $df=1$, $P=0.06$; $R_m^2=0.22$; $R_c^2=0.91$; Fig. 2C). For each increase in female abundance, skewness decreased by a value of 0.004 (Online Resource 3, Table S2). This would translate into a decrease of 1.19 in skewness at the average

observed number of females ($N_f=297$). Emigration kurtosis was not predicted by either N_f ($F_{1,9}=0.38$, $P=0.74$; Fig. 2E) or breeding kurtosis ($F_{1,9}=4.09$, $P=0.29$; Fig. 3E) and generally explained very little of the variation (adj. $R^2=-0.05$).

For spotted salamanders, all three models (duration, skewness and kurtosis) used only pond as a random effect (Online Resource 3, Table S1). There was an interaction of location and N_f that predicted emigration duration ($\chi^2=13.59$, $df=1$, $P=0.0002$; $R_m^2=0.43$; $R_c^2=0.69$; Fig. 2B). Emigration duration at Basket increased by 0.37 d per female, whereas at the LEAP ponds, duration remained relatively constant. Emigration duration was also negatively related to breeding duration ($\chi^2=3.93$, $df=1$, $P=0.05$), though this result was not significant after correcting for multiple tests using false discovery

Fig. 2 Relationships of juvenile emigration duration (**a, b**), skewness (**c, d**), and kurtosis (**e, f**) with number of breeding females (N_f) for ringed salamanders (left column; $N=13$) and spotted salamanders (right column; $N=28$). In **b, d** and **f**, gray triangles correspond to the Baskett ponds and the black circles correspond to the LEAP ponds. The relationships in **b** (with an interaction between N_f and location) and **d** are significant. The relationship in **d** is significant even if the outlier point at $\sim(325, -3.2)$ is removed

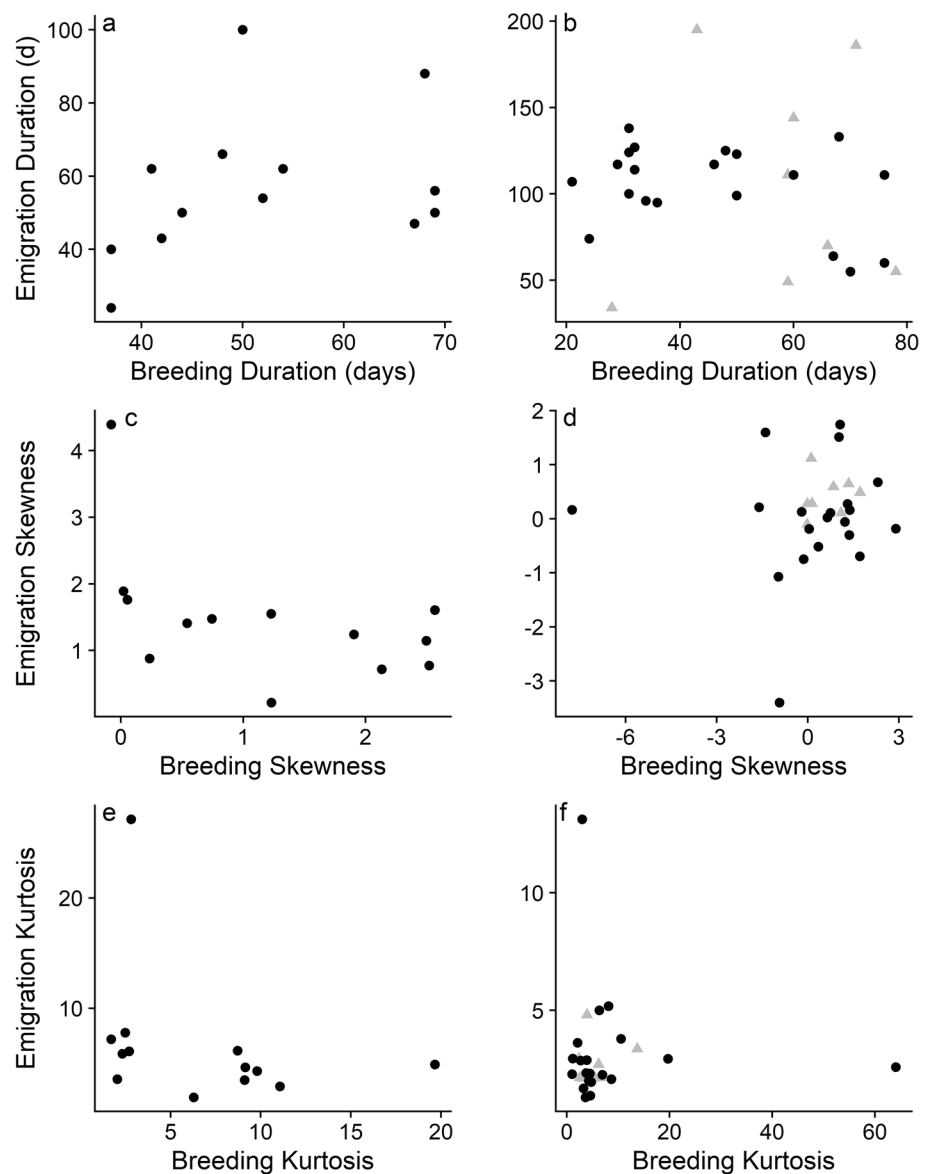


rate methods. Emigration skewness was not predicted by breeding skewness ($\chi^2=0.29$, $df=1$, $P=0.59$; $R_m^2=0.16$; $R_c^2=0.26$, Fig. 3D), and emigration kurtosis was not explained by breeding kurtosis ($\chi^2=0.0001$, $df=1$, $P=0.99$; $R_m^2=0.02$; $R_c^2=0.02$; Fig. 3F). There was a significant effect of N_f on breeding skewness ($\chi^2=4.33$, $df=1$, $P=0.04$; Fig. 2D), where skewness decreased by 0.003 for each increase in abundance (Online Resource 2, Table S2). This would translate into a decrease in skewness of 0.57 at the average population size ($N_f=190$). However, after correcting for multiple tests, this result became non-significant, so caution should be applied to interpretation of this result. The number of breeding females was not related to emigration kurtosis ($\chi^2=0.13$, $df=1$, $P=0.72$; Fig. 2F).

Survival

The variance of random effects was zero for survival index of all ringed salamander models, and thus we fit GLMs for each metric (Online Resource 3, Table S1). The number of breeding females was not a significant predictor of survival index in any model for ringed salamanders (all $P>0.72$; Fig. 4A). Survival index of ringed salamanders was also not statistically related to breeding duration ($F_{1,10}=0.01$, $P=0.92$; Fig. 4C), skewness ($F_{1,10}=1.68$, $P=0.22$; Fig. 4E) or kurtosis ($F_{1,10}=1.83$, $P=0.21$; Fig. 4G). None of these models explained much of the variation (adj. R^2 range = $-0.20 - -0.02$).

Fig. 3 Relationships of juvenile emigration phenology for ringed salamanders (left columns; $N=13$) and spotted salamanders (right columns; $N=28$). In **b**, **d** and **f**, gray triangles correspond to the Baskett ponds and the black circles correspond to the LEAP ponds. The relationship in **b** and **d** were significant at $P < 0.05$, though these results were not significant after correcting for multiple tests



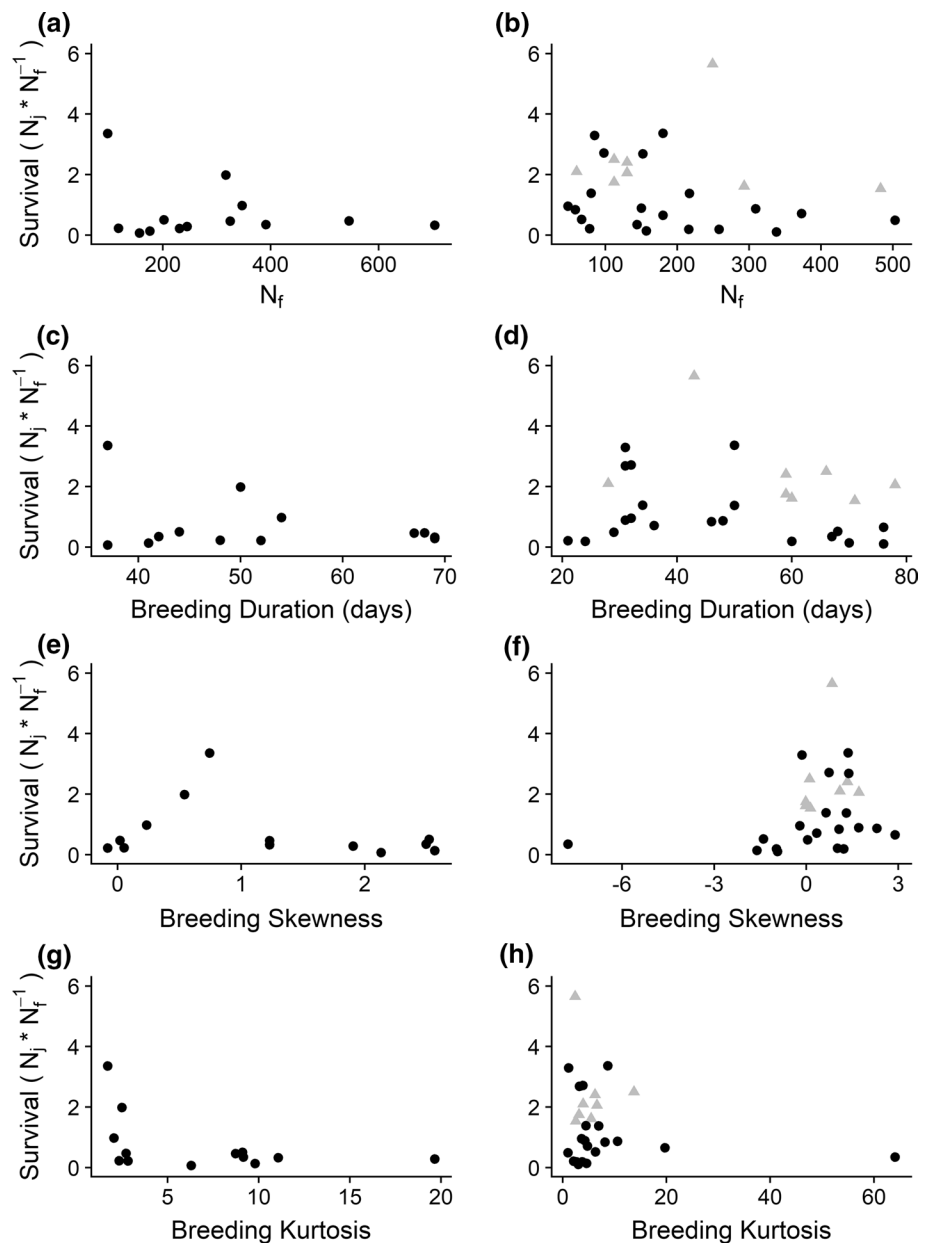
Pond and year were included as random effects in models of spotted salamander survival index that included breeding duration and skewness as covariates, but only year could be included with breeding kurtosis (Online Resource 3, Table S1). The only significant predictor of survival index was location. Average survival index was more than two times higher at Baskett than the LEAP sites for spotted salamanders, though relatively similar between species at the LEAP sites (Online Resource S3, Table S1). Breeding duration ($\chi^2 = 0.64$, $df = 1$, $P = 0.42$; Fig. 4D), skewness ($\chi^2 = 1.12$, $df = 1$, $P = 0.29$ Fig. 4F) and kurtosis ($\chi^2 = 0.08$, $df = 1$, $P = 0.78$; Fig. 4H) were

all not significant, nor was N_f in any of the models (all $P > 0.14$; Fig. 4B).

Discussion

Understanding how phenology influences demography is a critical goal, as many species worldwide are exhibiting phenological shifts (Parmesan 2006, 2007). Evaluating different aspects of phenology beyond the first or mean date of an event are especially critical, as other metrics like phenological variability have historically been underappreciated (Inouye et al. 2019; Miller-Rushing et al. 2010) and could potentially affect demography and species interactions in

Fig. 4 Relationships of survival index (metamorphs per female; $N_j \times N_f^{-1}$) with number of breeding females (**a, b**), breeding duration (**c, d**), breeding skewness (**e, f**), and breeding kurtosis (**g, h**) for ringed salamanders (left columns; $N=13$) and spotted salamanders (right column; $N=28$). In **b, d, f,** and **h**, gray triangles correspond to the Basket ponds and the black circles correspond to the LEAP ponds. Survival was higher at Basket than LEAP, but no significant relationships existed with breeding variability or breeding females (N_f)



unexpected ways. Here, we examined relationships of phenological variability between life stages in natural populations of two pond-breeding salamander species, whether variability impacted survival rates, and how density dependence changed phenological relationships. We found that phenological distributions of our focal species differed in each ontogenetic event. We also found that survival and emigration variability of our two focal species were largely unrelated to female breeding variability and had weak relationships with female abundance, a proxy for larval density. Overall, our study is one of the first to quantify the skewness and kurtosis of phenological distributions and their potential impacts on demography.

Documentation of current phenological patterns can provide a benchmark against which future changes in phenology can be compared (Visser and Both 2005). We observed both species- and stage-specific differences in the degree of phenological variability. Specifically, species were similar in breeding except for the degree of skewness, where ringed salamanders more often had a right-tailed distribution than spotted salamanders. Additionally, emigration phenology was different across species for all three metrics tested. Ringed salamanders had shorter emigration durations and were more often right-skewed with larger peaks and tails (leptokurtic). In contrast, spotted salamanders had longer emigration durations that were not skewed (normally distributed) and more uniform in shape (platykurtic). Use of these

metrics to characterize phenology has not been performed for amphibians to our knowledge and could be a fruitful way to further examine changes in phenology occurring with climate change (Blaustein et al. 2001). However, connecting such distributions to demographic rates is also needed to show that they have biological consequences (Forrest and Miller-Rushing 2010); we did not find such relationships here with survival of eggs/larvae. Additionally, the exact mechanism of these contrasting distributional patterns is not known, though weather likely contributes at least in part to the shape, given that most amphibian movement is tied to suitable rainfall and temperature patterns (Todd and Winne 2006). Comparing contemporary patterns of phenology across species, as we have here, is critical, because not all species are responding to climate change in similar ways (Parmesan 2007). However, a more thorough cross-taxon comparison is needed, as we were only able to compare two species, which limits identification of the traits that explain species differences. For example, different sensitivities to the environmental drivers of phenology among life stages may elicit greater phenological shifts (Inouye et al. 2019). Our study also highlights that phenological variability can vary between stages within species, as well as within stages across species. Given numerous taxa exhibit complex life cycles (Wilbur 1980), further consideration of such stage-specific phenological variability likely requires greater scrutiny to predict its effects on demography and species interactions (Yang and Rudolf 2010).

Whether the phenology of different life stages of the same species are correlated has received limited attention (Augspurger 1981; Carter and Rudolf 2019; Rasmussen and Rudolf 2015). Therefore, it is difficult to predict when or for which species such relationships may manifest, which would be important to understand in the context of species' whose phenologies are shifting with climate change. We found no relationships between breeding and emigration phenology for either of our focal species. One potential explanation for this difference in phenological coupling among species is the time length separating breeding and emigration. For example, Rasmussen and Rudolf (2015) found in an experimental study that breeding and emigration synchrony were linked in Gulf Coast toads (*Bufo nebulifer* [*Incilius nebulifer*]). However, that species has a larval period of only a few weeks, whereas it is at least ~2–4 months for spotted salamanders and 6–9 months for ringed salamanders. When phenological processes occur closer together and are strongly dictated by weather, as is amphibian phenology (Todd and Winne 2006), they may be more likely to be related than when they are more temporally separated, as weather data exhibits persistent behavior. For species with shorter larval periods like American toads (*Anaxyrus americanus*), it would be more likely for suitable weather conditions to be more correlated because of the shorter time windows between breeding and

metamorphosis, increasing the likelihood of phenological coupling between life stages. For species with longer larval periods, there would be reduced autocorrelation in weather drivers that would initiate each phenological event, increasing the chance of decoupled phenologies. Thus, phenological coupling across ontogenetic stages may be time-dependent, occurring only for taxa when each process is temporally close.

Two metrics of emigration phenology (duration and skewness) were better explained by larval density than breeding phenology for spotted salamanders at the Baskett site, supporting the idea that species interactions can play a critical and potentially mediating role in determining the shape of a phenological distribution. It is already well known that increases in larval density can lengthen larval periods via competition (Scott 1990; Semlitsch and Caldwell 1982), but we show more specifically how it affects the emigration distribution: higher densities had longer duration, as well as less right skewed distributions. We previously found that intraspecific competition in ringed salamanders lengthened their larval period, increasing their emigration phenology window and temporal overlap with spotted salamanders in ponds (Anderson and Semlitsch 2014). Density dependence may also build on the above arguments for time-scale dependencies: when more time elapses between phenological processes, there would be increased potential for interactions like competition or predation to disrupt phenological relationships by altering population densities. If phenological rates are density-dependent, factors that alter species densities may change the degree to which phenologies of different life stages are related.

We observed location-specific patterns for survival of spotted salamanders at two locations separated by 67 km at approximately the same latitude. Thus, the two sites should experience approximately the same weather conditions that would drive demographic patterns. Yet, survival index of spotted salamanders was on average more than twice as high at Baskett than at the LEAP sites. We cannot distinguish the exact mechanism of the location differences, because the data sets are spatiotemporally separated, and causation cannot be entirely determined from observational data. However, there are several possible explanations. Notably, fall-breeding ambystomatids are not present at the Baskett ponds (Hocking et al. 2008), whose larvae can prey on spotted salamander larvae (Anderson et al. 2016; Urban 2007) and thus variation in intraguild predation pressure could be driving the differences in survival. The survival outcome is at least consistent with experimental results on these two species (Anderson and Semlitsch 2014). Pond community structure may vary across locations, specifically predator assemblages. The LEAP ponds had more slightly more sun exposure due to logging (Semlitsch et al. 2009), which can result in higher dragonfly densities (French and McCauley

2018). However, differences in dragonfly densities would have to be specific to individuals in the family Aeshnidae, which are the only effective dragonfly predator of salamanders (Stretz et al. 2019). Data from other field sites in Missouri indicate Aeshnidae densities do not vary with canopy cover (Anderson et al. 2021). Finally, the Baskett ponds were slightly smaller in area and at least one of them dried more often than the LEAP sites, which could again drive differences in community structure of a variety of predators, including the ones discussed above.

Overall, our study shows that investigation of metrics that involve the entire phenological distribution – here as different measures of the degree of phenological variability – can provide important insights into how phenology differs across life stages and species. As we focused primarily on intraspecific patterns, extending our approach to test whether phenological variability impacts interspecific interactions will help unravel their role in shaping community dynamics; such work is currently in its infancy (Carter and Rudolf 2019; Rasmussen and Rudolf 2015). We previously tested whether mean dates of breeding and interspecific interactions affected survival of our focal species using the LEAP data (Anderson et al. 2015), finding that the timing of ringed salamander breeding and emigration positively and negatively affected spotted salamander survival, respectively. This indicates combinations of different aspects of phenological distributions, such as the mean and variability in phenology, may help explain dynamics of species interactions, as has been documented in other taxa (CaraDonna et al. 2014; Carter and Rudolf 2019; Rasmussen and Rudolf 2016). Exploration of different phenological metrics in combination may help further our understanding of how species interactions may change if climate change continues to alter species' phenologies. In particular, pairing experiments with field observations that test how community structure (i.e., the presence of predators) influences the importance of multiple phenological metrics would be a powerful approach. Further tests of whether phenology can be linked across life stages are also needed, which is important to understand in the context of climatic change: if one life stage is changing, it may have ramifications on the phenology of other life stages if they are coupled. While our data here are not temporally sufficient to test for effects of climatic change, future studies that have such long-term data may provide greater insights as to whether these effects are already occurring.

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