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Variation in Pond Hydroperiod Affects Larval Growth in Southern Leopard Frogs, *Lithobates sphenocephalus*

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Size at metamorphosis is an important correlate of amphibian fitness. Several, often interrelated factors, such as hydroperiod, competition, and food availability, determine metamorph size. Hydroperiod is a defining characteristic of ponds, but pond drying is not always a deterministic process, and refilling can occur prior to complete drying. We conducted an experiment to test if a recurring four-week partial drying/filling cycle affected amphibian growth and size using a population of overwintering larval *Lithobates sphenocephalus* (Southern Leopard Frogs). Effects of the drying/filling cycle varied over time on larval mass, but this cycle had no overall effect on other measures of larval or metamorph size. Metamorph size covaried with both survival and larval period length: individuals were larger at metamorphosis when survival was lower and among individuals with longer larval periods. We observed the first reported instance of prolonged larval periods across multiple winters in *L. sphenocephalus*, wherein some of our larvae exposed to the drying/filling cycle required 18 months to reach metamorphosis. Individuals that overwintered as larvae for a second winter were larger at metamorphosis than those that metamorphosed at the end of the previous summer. *Lithobates sphenocephalus* maximize metamorphic size rather than optimize metamorphic timing, and metamorph size can also be affected by larval survival.

MANY amphibians selectively breed in temporary ponds, which support higher primary productivity and fewer predators (particularly fish) than permanent ponds (Wassersug, 1975; Woodward, 1983; Resetarits and Wilbur, 1989; Wilbur, 1997). However, there is a tradeoff in that metamorphosis must occur prior to drying. Depending on the developmental model, poor conditions in aquatic habitats can result in metamorphosis as soon as a minimal size is reached, or later, often at larger sizes, due to acquisition of resources over a longer period of time (Wilbur and Collins, 1973; Newman, 1987; Alford and Harris, 1988; Scott, 1990; Day and Locke, 2002). Amphibian life cycles and the timing of successive life history events are also tightly linked to temperature, and larval anuran overwintering occurs in species and populations that breed either in autumn or in geographic areas with cooler climates.

Environmental temperature is an important factor in determining larval growth and differentiation, with growth increasing and differentiation proceeding as temperature increases, until growth-inhibiting temperatures are reached (Berven et al., 1979; Berven, 1982; Harkey and Semlitsch, 1988). By reducing larval growth and differentiation, lower temperatures increase the length of the larval period (Smith-Gill and Gill, 1978): in much of the temperate zone it is too cold for metamorphosis to occur in winter, making larval overwintering obligatory (Berven et al., 1979; Collins and Lewis, 1979). However, in many species larval overwintering is not possible as death occurs once temperatures drop to a critical thermal minimum, which often occurs at temperatures several degrees above freezing (Cowles and Bogert, 1944; McDiarmid and Altig, 1999). Larval overwintering has been linked to greater intraspecific competition (Morin et al., 1983), but regardless of the cause, species that overwinter as larvae tend to reach larger metamorphic size vs. metamorphosing earlier and smaller (Parris, 2000; Ryan and Winne, 2001). Metamorph size is an important determinant of individual fitness (Earl and Whiteman, 2015): individuals that are larger at metamorphosis have increased resistance to parasites, greater lipid stores, higher probability of overwinter survival, higher likelihoods of breeding, earlier breeding, and larger clutch sizes (Smith, 1987; Semlitsch et al., 1988; Scott, 1994; Beck and Congdon, 2000; Morey and Reznick, 2001; Scott et al., 2007). Timing life history events in response to temperature changes involves tradeoffs that affect larval development and potential overwintering success.

The Ranidae are the most widely distributed frogs in the world, with at least 15 species native to the United States and Canada known to have overwintering larvae. Of these, only five (*Lithobates catesbeianus*, *L. grylio*, *L. heckscheri*, *Rana aurora*, and *R. muscosa*) are known to overwinter as larvae for more than one winter (Altig and McDiarmid, 2015). Larval *Lithobates sphenocephalus* (=*Rana sphenocephala*; Southern Leopard Frogs) overwinter across much of this species' range when sufficient rainfall encourages fall breeding (McCallum et al., 2004). In temporary ponds, fall breeding can reduce the desiccation risk. Variation in pond water levels is often minimal during winter, especially in the Southeastern United States, where precipitation and lowered evapotranspiration maintain consistent water levels. However, this does not eliminate all risk, and habitat variability in turn influences other abiotic parameters, such as temperature and conductivity, as well as intraspecific density. Studies on the effects of hydroperiod have treated it as a one-way process, but this is not necessarily the case as precipitation and flooding can refill drying ponds and alter the developmental trajectory of organisms living therein.

Our goal was to assess the influence of pond hydroperiod and flooding on overwintering larval development, length of the larval period, size at metamorphosis, and survival in *L. sphenocephalus*. We conducted a field mesocosm experiment raising larvae of a natural population of fall breeding *L. sphenocephalus* and manipulating habitat variability using a simulated drying/filling cycle. We hypothesized that this drying/filling cycle would reduce survival and individual body size due to increased competition in smaller water volumes, whereas the length of the larval period would increase.

MATERIALS AND METHODS

Our experiment was conducted at the University of Mississippi Field Station (UMFS) near Oxford in north-central

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Mississippi, USA. A seasonally-large rainfall event in early October 2014 refilled many of the dry ponds at UMFS. Egg masses of *Lithobates sphenocephalus* were laid on the night of 7 October 2014, and we collected eight egg masses from two adjacent, recently filled ponds the following morning. Egg masses were held in the lab for seven days until embryos hatched. We randomly assigned groups of 25 larvae from each egg mass to individual mesocosms on 14 October such that each mesocosm received a total of 200 larvae sourced from eight different egg masses.

Mesocosms (plastic cattle tanks, 2.7 m diameter) held ~1200 L at a depth of 50 cm, which was the maximum used in this experiment. Adjustable standpipes were affixed to mesocosms to allow regulation of water levels. Mesocosms were established in a field at UMFS on 13 October 2014 and filled with unchlorinated well water. Mesocosms were provisioned with 4 kg of dry hardwood leaf litter as a nutrient base and 1 L aliquots of water from fishless ponds to inoculate zooplankton, algae, and periphyton. No supplemental food was added, and mesocosms were left uncovered, as metamorphs were unable to escape.

Two treatments were randomly assigned to mesocosms: Constant, which had stable water levels throughout the experiment (depth of 50 cm; $n = 5$), and Fluctuating, which underwent a four-week drying/filling cycle (depth ranged from 20–50 cm; $n = 5$). Fluctuating mesocosms had water level lowered by 10 cm once every seven days for three weeks to a minimum depth of 20 cm before refilling to a depth of 50 cm with well water and the cycle repeated. Refilling of each mesocosm lasted approximately 20 minutes and disturbed fine debris in mesocosms, but did not otherwise generate high amounts of water movement. While the rate of water loss from our mesocosms is greater than what we typically observe for a pond of this depth, it is not unrealistic, and the rapid rate of refilling is well within the limits of what we have observed at UMFS.

Water levels were first lowered on 21 October 2014, one week after larvae were added; screens covering standpipe openings prevented the loss of larvae from mesocosms while water was being discharged. From 21 January–7 March 2015 and 22 November 2015–15 March 2016 standpipes were removed to prevent ice damage, and water levels in all mesocosms were maintained at full depths for the duration of these periods. This time of the year (winter) is also the season when we typically observe the most stable water levels in ponds at UMFS. With the exception of when standpipes were removed, water levels were always being manipulated via the four-week drying/filling cycle.

From November 2014 until May 2015 we sampled larvae from each mesocosm on five dates (11 November, 12 January, 7 March, 8 April, and 9 May), collecting 16 individuals from each mesocosm on each sampling date. Sampling was conducted every other month in winter because of minimal growth during cold temperatures, but we increased sampling frequency to once per month when temperatures increased in spring; larval sampling stopped once metamorphs began to emerge. We weighed and photographed larvae before returning them to their mesocosm of origin; larvae were measured (total length, body depth) from photos in ImageJ (Schneider et al., 2012). In May–October 2015 and May–June 2016 we checked mesocosms daily for metamorphs, which were collected, weighed, and photographed. Outside of these time periods, mesocosms were checked at least once weekly, but no metamorphs were observed. Metamorph measurements (snout–urostyle length, head width, tibiofibula length) were also taken from photos in ImageJ. Positioning of both larvae and metamorphs was standardized in photos to minimize variance, and all photos contained scales to calibrate measurements. The experiment was terminated after the last individual metamorphosed on 8 June 2016. All metamorphs were released near egg collection sites at UMFS.

Data analysis.—We analyzed the effect of treatment over time using repeated-measures MANOVA on average larval body size (mass, total length, and body depth) in each mesocosm. We also analyzed the effect of treatment over time on larval body condition (size independent mass). Body condition was determined by mean-scaling mass to decouple variance from the measurement scale and means, regressing against total length, and using the residuals in repeated-measures ANOVA (Berner, 2011).

We used ANOVA on the average length of the larval period per mesocosm. Survival was analyzed with logistic regression on the proportion of metamorphs in each mesocosm, using a binomial error distribution with mesocosm as a random effect (Warton and Hui, 2011). Metamorph body size was analyzed with MANCOVA on mass, snout–urostyle length, head width, and tibiofibula length with survival to metamorphosis and larval period length as covariates. Survival (number of metamorphs produced from each mesocosm) and length of the larval period provide indicators of potential intraspecific competition/density dependence and time spent acquiring resources in the larval stage, respectively. We analyzed the effect of treatment on metamorph body condition in a similar manner to that of larval body condition, by regressing mean-scaled mass against snout–urostyle length and using the residuals in ANCOVA with survival and larval period length as covariates. We assessed if water depth (20, 30, 40, 50 cm) in the Fluctuating treatment had an effect on the production of metamorphs. To do this, we analyzed the proportion of individuals that metamorphosed while mesocosms were at each of the four depths using logistic regression with water depth as a fixed effect and mesocosm as a random effect.

We also assessed temporal variation in the production of metamorphs and the average mass of metamorphs across the duration of the experiment. Metamorphs were grouped based on the month they emerged (May–September 2015 and May–June 2016), and the number of metamorphs and their average mass in each mesocosm were determined for each month. One metamorph that emerged on 1 October 2015 was included in the September 2015 group. Not all mesocosms produced metamorphs each month, and only Fluctuating mesocosms had any metamorphs in 2016. Thus, we lacked adequate replication to effectively analyze the effect of treatment over time on metamorph size, so we analyzed mass with repeated-measures ANOVA that excluded treatment. The number of metamorphs produced over time was analyzed with repeated-measures ANOVA including treatment. We present the data over time grouped by treatment for both mass and number of metamorphs in the figures.

All analyses were conducted in R v 3.4.2 (R Core Team, 2017) using type III SS, $\alpha = 0.05$, the car package v 2.1-5 for type III analyses (Fox and Weisberg, 2011), and the lme4 package v 1.1-14 for mixed effects models (Bates et al., 2015). Body measurements were log-transformed and count data (survival, time (days) to metamorphosis) were square root transformed ($\sqrt{X + 0.5}$). Means of all individuals in each mesocosm were used for both larval and metamorph analyses.

Table 1. Larval repeated measures *F* statistics and *P* values for (A) MANOVA on body size (mass, total, length, body depth) and (B) follow-up ANOVAs on body size measures and ANOVA on body condition.

	Between pools		Within pool			
	Treatment df (1,8)		Time (4,32)		Treatment × time (4,32)	
	F	*P*	*F*	*P*	*F*	*P*
(A) MANOVAs						
Body size	1.77	0.2521	16.89	<0.0001	2.94	0.0020
(B) ANOVAs						
Mass	7.08	0.0288	79.67	<0.0001	4.43	0.0058
Total length	1.07	0.332	48.69	<0.0001	2.06	0.110
Body depth	0.68	0.432	38.38	<0.0001	0.59	0.673
Body condition	1.16	0.312	0.001	1.000	1.96	0.124

RESULTS

Larval responses.—There was a significant treatment × time interaction in the body size MANOVA and the follow-up ANOVA on mass, but no effect on total length or body depth (Table 1). Larvae in Fluctuating mesocosms were ~20% larger than those in Constant mesocosms early in the experiment (on the first two larval sampling dates), whereas larvae in Constant mesocosms were ~50% larger than those in Fluctuating mesocosms on the last two sampling dates (Fig. 1A). Significant effects of time in all larval body size analyses were due to growth over time. There were no significant effects in the larval body condition ANOVA (Table 1).

Metamorph responses.—Treatment had no effect on survival to metamorphosis ($\chi^2 = 0.017$, $P = 0.8975$) or larval period length ($F_{1,8} = 3.117$, $P = 0.1155$; Fig. 2A, B). Metamorph body size covaried with both survival and larval period in the body size MANCOVA (Table 2A) and follow-up ANCOVAs on mass, snout–urostyle length, and tibiofibula length, but there were no effects of treatment (Table 2B, Fig. 2C, D). Head width covaried with survival, with a marginal effect of larval period length and no effect of treatment (Table 2B). Overall, metamorphs were larger in mesocosms that produced fewer metamorphs and among those that took longer to reach metamorphosis. In the body condition ANCOVA, there were no effects of treatment or covariance with survival and larval period length (Table 2C). Water depth had an effect on number of metamorphs produced from Fluctuating mesocosms ($\chi^2 = 17.317$, $P = 0.0006$), with the most produced from mesocosms at a depth of 50 cm (17.0±5.54 individuals; mean ± SE) and the fewest from those at a depth of 40 cm (9.8±2.96). *Post-hoc* Holm-adjusted Tukey results showed differences between the number of metamorphs produced between mesocosms at a depth of 40 and 50 cm ($P = 0.0019$) and 30 and 50 cm ($P = 0.0035$), with all other comparisons being non-significant.

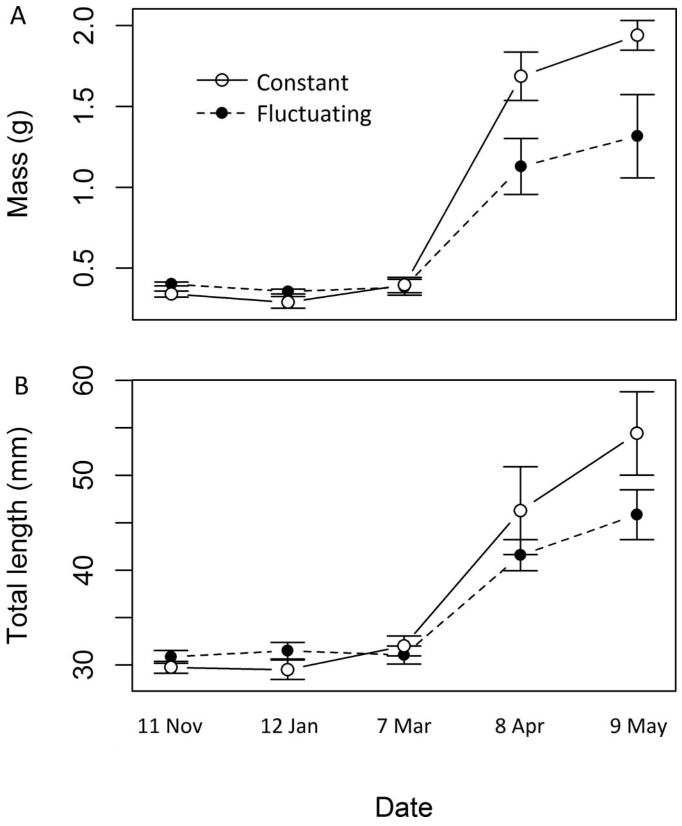

Fig. 1. Average (A) mass and (B) total length of larvae in Constant and Fluctuating mesocosms on sampling dates over time from 11 November 2014 until 9 May 2015 (means ± SE).

The number of metamorphs produced varied over time ($F_{6,48} = 3.887$, $P = 0.0031$) but did not interact with treatment ($F_{6,48} = 1.554$, $P = 0.1813$), with the most metamorphs produced in June and July 2015 (Fig. 3A). A total of 663 individuals survived to metamorphosis (27.6% survival), with 637 individuals metamorphosing in 2015. Only 26 individuals metamorphosed in 2016 (3.9% of all metamorphs), and all of these metamorphs were in Fluctuating mesocosms. The average mass of metamorphs also varied over time ($F_{6,17} = 13.85$, $P < 0.0001$; Fig. 3B), with the earliest (in May 2015) and latest (in May–June 2016) emerging metamorphs being larger than those that metamorphosed throughout the summer of 2015 (June–September).

DISCUSSION

Hydroperiod and habitat variability are important characteristics of freshwater systems that can change environmental conditions and shift competitive and density-dependent interactions among and between species. Here, we asked how a four-week partial drying/filling cycle affected development of *L. sphenocephalus* throughout the larval stage and at metamorphosis. Although larval size interacted over time with treatment in our experiment, survival, metamorph size, and length of larval period were not affected by habitat variability, while metamorph size covaried with survival and larval period length. Variation in patch size can compound

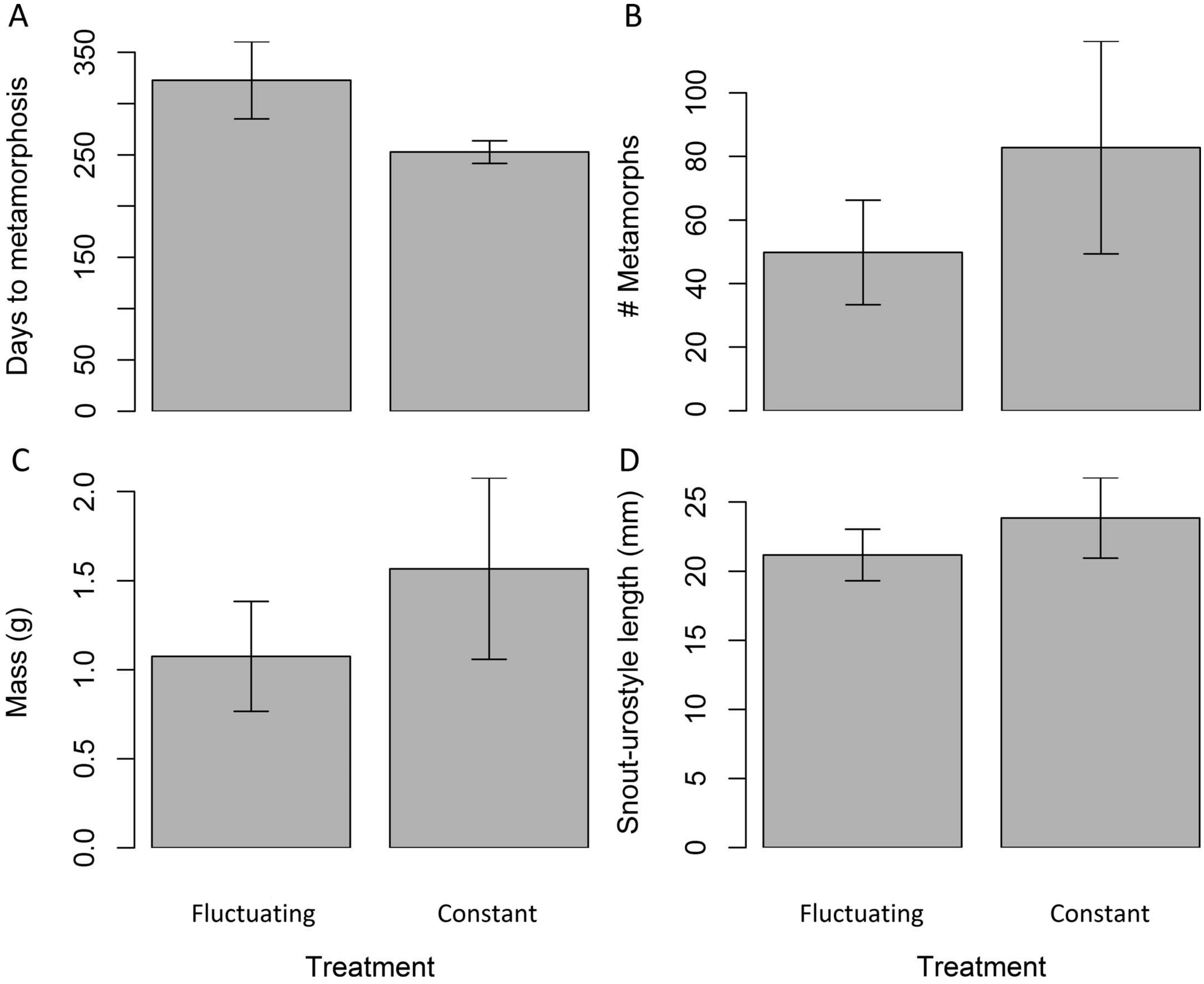

Fig. 2. Average (A) larval period length, (B) survival, (C) mass, and (D) snout–urostyle length of metamorphs from Constant and Fluctuating treatments (means ± SE).

the effects of larval density, as decreasing pond volumes typically lead to higher density (unless it induces early metamorphosis). Conversely, pond drying is not always a one-way process, and increasing volumes can temporarily relieve density-induced stress. Precipitation can refill ponds and change the trajectory of communities by obviating the need for immediate metamorphosis to escape desiccation and/or competition from increasing conspecific density. *Lithobates sphenocephalus* remain in the larval stage until reaching a critical metamorphic size, and this can necessitate larval overwintering (Morin et al., 1983; Ryan and Winne, 2001; Richter et al., 2009). The interconnected effects of hydroperiod and density are important for understanding patterns of individual growth, larval survival, and life history strategies such as overwintering in anurans, but these effects may vary based on the taxa studied (Ryan and Winne, 2001; Rogers and Chalcraft, 2008; Richter et al., 2009; Székely et al., 2010; Amburgey et al., 2012; Brady and Griffiths, 2012).

In previous experimental studies of *L. sphenocephalus*, longer hydroperiod increased the length of the larval period and number of metamorphs, but did not affect metamorph size, whereas increased larval density (controlling for per capita food availability), reduced the length of the larval period but did not affect survival or size (Ryan and Winne, 2001; Richter et al., 2009). Our overall metamorph sizes conform to these results—no effect of habitat variability on size at metamorphosis. Size of our metamorphs covaried with survival, which serves as a potential indicator of larval density and competition in the absence of direct counts. Thus, while habitat variability did not affect metamorph size in our experiment, density reduced metamorph size and likely affected per capita food availability. The most metamorphs emerged from Fluctuating mesocosms while they were at depths of 50 cm, which could indicate that flooding provides a stimulus encouraging metamorphosis, contrary to our expectation that more metamorphs would be produced at the lowest depths. However, our Fluctuating mesocosms reached a minimum depth of 20 cm (40% of maximum), which may not have been sufficiently stressful to elicit metamorphosis (Denver et al., 1998).

Interestingly, while treatment did not affect metamorph size, it did affect larval size. The significant time × treatment interaction on larval size may indicate that larvae in Fluctuating mesocosms were cued by variable conditions to

Table 2. Metamorph results for (A) MANCOVA body size, (B) follow-up ANCOVAs on body size measurements, and (C) ANCOVA on body condition. See also Figures 2, 3.

	df	*F*	*P*
(A) Body size MANCOVA			
Survival	1	9.35	0.0483
Larval Period	1	74.06	0.0025
Treatment	1	0.65	0.6641
(B) Body size ANCOVAs			
Mass			
Survival	1	64.749	0.0002
Larval period	1	16.985	0.0062
Treatment	1	0.972	0.3622
Residuals	6		
Snout–urostyle			
Survival	1	54.136	0.0003
Larval period	1	15.467	0.0077
Treatment	1	0.642	0.4534
Residuals	6		
Head width			
Survival	1	54.990	0.0003
Larval period	1	5.718	0.0539
Treatment	1	2.224	0.1865
Residuals	6		
Tibiofibula			
Survival	1	54.110	0.0003
Larval period	1	20.414	0.0040
Treatment	1	1.114	0.3318
Residuals	6		
(C) Body condition ANCOVA			
Survival	1	0.172	0.6929
Larval period	1	0.269	0.6225
Treatment	1	0.677	0.4421
Residuals	6	3.566	

acquire more resources early in development when small size precluded intraspecific competition. Later, when larvae were larger, stable volumes in Constant mesocosms may have allowed acquisition of more resources than in Fluctuating mesocosms due to lower size-specific competition. Given no observed differences in metamorph size, differences between treatments in larval size must have converged later in the experiment after we stopped larval measurements. Similarly, we saw no effect of treatment or any covariates on larval or metamorph body condition. We would expect this indicates that, developmentally, resources are allocated towards maintaining body condition prior to increasing length, and that metamorphosis occurs after a critical size is reached.

In our analysis of metamorphs over time, the first individuals to metamorphose in each year were larger than those throughout the mid- and late-summer. Larvae that metamorphosed in 2016 (all in Fluctuating mesocosms) were approximately twice as large as those that metamorphosed in late summer 2015 from Fluctuating mesocosms. Individuals that survived until 2016 may have gained advantages over those metamorphosing late the previous year due to larger size. When environmental conditions allow, *L. sphenocephalus* has the developmental plasticity to remain in the larval stage across multiple winters. Although we had only 26 individuals (3.9% of all metamorphs) metamorphose in 2016 and this was an experimental system, this is the first record of multiple-year larval overwintering in *L. sphenocephalus*. Our last individual metamorphosed on 8 June 2016, 608 days after oviposition.

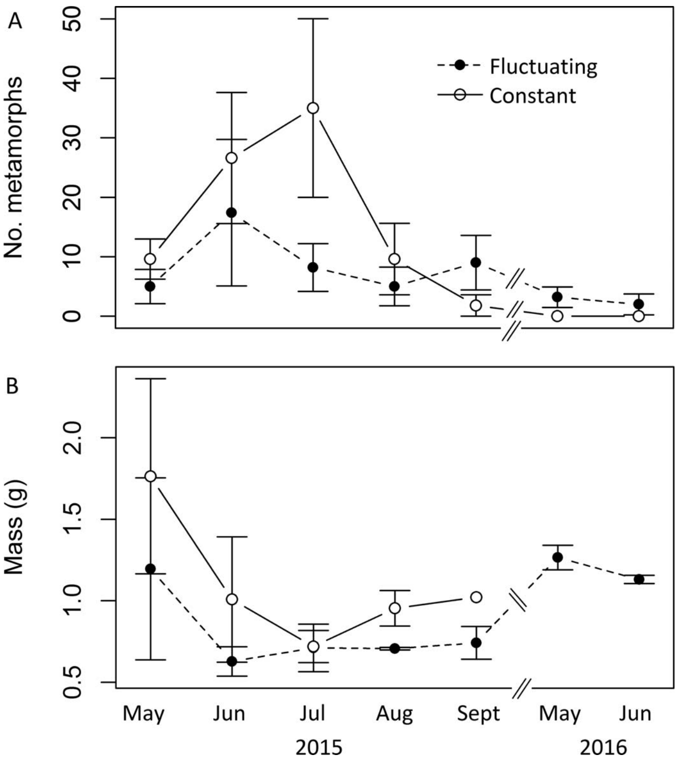

Fig. 3. Average (A) number of metamorphs and (B) metamorph mass per Fluctuating and Constant mesocosm during each month throughout the duration of the experiment (means ± SE).

Taking advantage of recently filled ponds in fall, adult frogs introduce their offspring into an environment with fewer competitors and predators (Wassersug, 1975; Woodward, 1983; Wellborn et al., 1996; Wilbur, 1997), and gain competitive size-related advantages over spring-breeding frogs (Alford and Wilbur, 1985; Wilbur and Alford, 1985). Because *L. sphenocephalus* also breed in permanent ponds, the fitness advantage of fall breeding can be compounded if fall breeders actively select recently filled ponds over preexisting ones, since the latter would contain established communities of both predators and competitors (Wellborn et al., 1996; Pintar and Resetarits, 2017).

Fall breeding by *L. sphenocephalus* is tied to large rainfall events accompanied by relatively warm temperatures (McCallum et al., 2004). At UMFS a major rainfall event in early October 2014 refilled many dry ponds and led to a large fall breeding event (used here). In 2015 ponds did not refill until late October, producing very limited fall breeding. Following extreme drought in 2016, ponds did not begin to refill until late November, and there was no breeding throughout the latter half of the year. Major rainfall events and unseasonably warm temperatures in mid-January 2017 produced oviposition by *L. sphenocephalus* that rivaled the event observed in October 2014 (see Appendix 1). This magnitude of shifts in weather-driven breeding across only three years has implications for populations and community assembly dynamics (Benard, 2004; Klaus and Lougheed, 2013). Drought-restricted breeding may impede a female's ability to produce multiple clutches in a year, and timing of breeding events can interact with hydrology, determining the time available for offspring to metamorphose before ponds dry (Miller-Rushing et al., 2010; Yang and Rudolf, 2010). Thus, abiotic factors, particularly hydroperiod and temperature, remain important drivers of intraspecific and interspecific interactions, as well as population dynamics and community structure in temporary ponds (Wellborn et al., 1996; Wilbur, 1997).

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APPENDIX 1

A note on fall versus winter breeding.—Our observations of seasonal oviposition patterns of *L. sphenocephalus* conform with those others have reported (Caldwell, 1986; McCallum et al., 2004). In warm weather (fall) egg masses are oviposited individually throughout ponds, isolated from other egg masses, and in a range of water depths (up to about 0.5 m). In cool weather (winter and early spring) egg masses are oviposited communally, typically in shallower areas. What makes our observation noteworthy is the proximity of communal breeding sites at UMFS. While other studies have reported one communal breeding site per pond per night, studies have often been of individual or isolated ponds. UMFS was originally a fish farm, so ponds are separated from each other by <5 m. We surveyed 19 ponds (in two contiguous clusters of ponds) ranging in size from 0.03 to 0.24 ha at UMFS in January 2017 following this breeding event. Each pond contained a single communal breeding site (occupying a circular area with a radius of ~1 m), and some breeding sites in adjacent ponds were closer to each other than to other parts of the same pond. In particular, one site contained 63 egg masses and was >50 m from the distant end of its own pond, yet only 20 m from another communal breeding site in an adjacent pond that contained 47 egg masses. There are ample shallow areas for oviposition around most of these ponds, so the use of a single breeding site suggests that these frogs may recognize each pond as a contiguous unit and focus their mate-finding efforts in proximity to one another in colder breeding conditions.