Larval Development Varies Across Pond Age and Larval Density in Cope's Gray Treefrogs, *Hyla chrysoscelis*

Author(s): Matthew R. Pintar and William J. Resetarits, Jr.
Source: Herpetologica, 73(4):291-296.
Published By: The Herpetologists' League
https://doi.org/10.1655/Herpetologica-D-17-00027.1
URL: http://www.bioone.org/doi/full/10.1655/Herpetologica-D-17-00027.1

Herpetologica, 73(4), 2017, 291–296

Larval Development Varies Across Pond Age and Larval Density in Cope's Gray Treefrogs, *Hyla chrysoscelis*

MATTHEW R. PINTAR[1] AND WILLIAM J. RESETARITS, JR.

Department of Biology and Center for Water and Wetlands Resources, University of Mississippi, University, MS 38677, USA

ABSTRACT: Ovipositing amphibians select breeding sites that determine their offspring's larval habitat. Preference–performance theory predicts that adults will select habitat patches that match the expected performance of their offspring in those patches. Many amphibians breed in temporary ponds immediately after they fill, and one species, *Hyla chrysoscelis* (Cope's Gray Treefrogs), selects between breeding sites based on patch age differences of as little as 7 d. Prior work established that *H. chrysoscelis* have better larval performance in more recently filled ponds, but not in ponds less than 15 d after filling or among ponds that differed in age by less than 65 d. Our objective was to determine experimentally whether larval *H. chrysoscelis* performance varies across short time scales after filling (3- and 23-d-old ponds) and across two larval densities (15 and 30 larvae per mesocosm). Higher larval densities reduced metamorph mass and body condition, but did not otherwise affect larval performance. There were lower survival, shorter larval periods, and slightly lower mass and body condition among larvae from 3-d-old ponds than those in 23-d-old ponds. These mixed performance differences across our two levels of habitat age might not necessarily be representative of what happens in natural systems, however, where older ponds have more established communities of competitors and predators.

Key words: Larval period; Metamorphosis; Preference–performance; Priority effects; Temporary ponds

THE DEVELOPMENT of new habitat patches, and disturbances to existing patches, initiate the processes of colonization, competition, and succession that generate the habitat mosaics and patterns of species abundances and richness that are observed across natural landscapes (Connell 1978; Sousa 1984; Resh et al. 1988; Chesson 2000). In both newly created habitats (e.g., via disturbances) or newly available habitats (e.g., seasonal colonization of temperate breeding habitats by migratory birds), benefits gained from early arrival at new patches stem from being able to secure breeding sites that optimize available resources, predator avoidance, and competition (Alve 1999; Kokko 1999). In freshwater systems, the transition from permanent to temporary water bodies is a defining characteristic, generating large differences in community composition across this gradient of hydroperiod (Wellborn et al. 1996). The filling of temporary ponds initiates a myriad of processes that transform these seasonally terrestrial habitats into freshwater systems with a diverse array of organisms (Wellborn et al. 1996; Wilbur 1997; Fairchild et al. 2000). Many temporary pond organisms have not only complex life cycles, but also considerable phenotypic plasticity, both of which allow them to take advantage of the variable conditions in temporary ponds and escape impending desiccation (Wilbur and Collins 1973; Semlitsch and Wilbur 1988; Sibly 1995; Laurila et al. 2002).

Habitat selection is a response to variation in habitat quality, and adults select oviposition sites that maximize offspring performance (Fretwell and Lucas 1970; Resetarits 1996; Morris 2003). Many anurans breed in ponds immediately after they fill (Woodward 1983; Duellman and Trueb 1986; Pintar and Resetarits 2017), and earlier breeding provides offspring with an advantage over later breeders because of priority effects (Alford and Wilbur 1985; Wilbur and Alford 1985). Dead biomass in a pond basin releases nutrients that, upon pond filling, produce blooms of early successional periphyton and phytoplankton that are more palatable for anuran larvae than later successional filamentous algae and macrophytes (Seale 1980). Abundances of competitors and predators increase as ponds age, and resources for larval anurans decline as nutrients are assimilated in unpalatable biomass or exported from a pond (Wellborn et al. 1996; Wilbur 1997; Kraus and Vonesh 2012). Thus, priority effects occur when earlier breeders can obtain more resources under less competition early in development, enabling them to outcompete later colonizers (Alford and Wilbur 1985; Wilbur and Alford 1985; Facelli and Pickett 1991; Shorrocks and Bingley 1994). The priority advantage of selecting newly filled ponds derives from the reduced mortality risk via desiccation and predation, decreased competition, and increased resource availability (Alford and Wilbur 1985; Wilbur 1987).

Hyla chrysoscelis Cope 1880 (Cope's Gray Treefrogs) shows preference for newly filled ponds that differ in the age of their water by as little as 7 d (Pintar and Resetarits 2017). Prior work established *H. chrysoscelis* as having better larval performance (increased survival, larger body size, shorter larval periods) in newer ponds, but these new ponds had been established for 15 d when larvae were added, whereas the old ponds were 80 d old (Wilbur and Alford 1985). Because *H. chrysoscelis* prefers newer ponds and has demonstrated oviposition site preference across smaller timescales of pond establishment, we asked if larval performance differs across these smaller timescales (matching the resolution of oviposition preferences) and if intraspecific competition differentially affects growth and development across a gradient of patch age. To determine whether development differs across smaller differences in the age of temporary ponds (3 and 23 d after filling), we investigated the effects of patch age on the growth and development of *H. chrysoscelis* with two densities of larvae ($n = 15$ or 30 per 110 L) in mesocosms in a natural landscape.

---

[1] CORRESPONDENCE: e-mail, matthew.pintar@gmail.com

TABLE 1.—Results for (a) analyses of variance (ANOVA) on survival and days to metamorphosis, (b) multivariate ANOVA on body size (snout–urostyle length, head width, tibiofibula length), and (c) ANOVAs for mass, body condition, and growth rates of *Hyla chrysoscelis* (Cope's Gray Treefrogs). The Age factor was the age of mesocosms at the time larvae were added: New (3 d), Old (23 d). The Density factor was the number of larvae added to each 110-L mesocosm ($n = 15$ or 30). There were no Age × Density interactions ($P > 0.3$), so they were excluded from analyses. Data that were the basis for these analyses are presented in Table S1 in the Supplemental Materials available online.

(a) ANOVAs	SS	df	*F*	*P*
Survival				
Age	14.28	1	52.90	<0.0001
Density	0.39	1	1.46	0.24
Residuals	5.67	21		
Days to metamorphosis				
Age	8.00	1	126.31	<0.0001
Density	0.06	1	0.99	0.33
Residuals	1.33	21		
(b) MANOVA	Wilks' λ	df	*F*	*P*
Body size				
Age	0.01	3,19	0.1	0.98
Density	0.06	3,19	0.4	0.74
(c) ANOVAs	SS	df	*F*	*P*
Mass				
Age	0.34	1	5.34	0.03
Density	0.92	1	14.55	0.001
Residuals	1.33	21		
Body condition				
Age	4.79	1	7.34	0.01
Density	11.00	1	16.86	0.001
Residuals	13.70	21		
Growth rate (mass)				
Age	3.36	1	23.79	<0.0001
Density	2.15	1	15.23	0.001
Residuals	2.96	21		
Growth rate (length)				
Age	7.74	1	113.06	<0.0001
Density	0.11	1	1.63	0.22
Residuals	1.44	21		

MATERIALS AND METHODS

We conducted our experiment in a natural landscape at the University of Mississippi Field Station (UMFS) in Lafayette County, Mississippi, USA. On 2 June 2015, we set up an array of 12 mesocosms (plastic wading pools: 1-m diameter, 110 L), each filled with well water, and added 0.5 kg of dry hardwood leaf litter (predominantly *Quercus* spp.) as a nutrient base. Mesocosms were covered with tight-fitting fiberglass screens (pore size = 1.3 mm^2) to prevent the escape of metamorphs and entry of unwanted colonizers. On 22 June we established 12 additional mesocosms in the same manner as, and directly adjacent to, the original 12 mesocosms. Thus, our patch age treatment consisted of two treatments: mesocosms established on 2 June (Old) and 22 June (New). In the absence of sufficient rainfall, we maintained volumes of all mesocosms by refilling with well water as needed (usually once weekly) throughout the experiment. Pools were blocked by spatial position from south to north in three linear rows.

On 22 June, we collected *H. chrysoscelis* eggs that had been laid at various sites (other mesocosms) at UMFS the previous night. These eggs were kept in the lab until they hatched and were added to mesocosms on 25 June. We sorted larvae into groups of five individuals, with all five individuals sourced from the same collection site. We then combined these groups of 5 larvae into groups of 15 and 30, ensuring that, at most, one-third of all larvae in the aggregate groups were sourced from a single site. This was done to reduce potential biases attributable to maternal effects, such as oviposition preference differences. These groups of 15 and 30 larvae were our initial density treatments (per 110 L mesocosms), which we randomly assigned to Old and New mesocosms (with equal distribution of 15 and 30 among Old and New). Each density/age combination in the 2 × 2 factorial design had six replicates, for a total of 24 mesocosms. After larvae were added to mesocosms, we checked daily for metamorphs. When present, metamorphs were collected, weighed (±0.001 g), photographed, and released at UMFS. The position of each metamorph was standardized in photographs, including a scale for calibration in Image J, which we used to measure the snout–urostyle length (SUL), head width, and tibiofibula length of metamorphs (±0.001 mm; Schneider et al. 2012). Mesocosms remained in place until late September, but the last metamorph emerged on 28 August 2015, and there were no remaining larvae when the mesocosms were later drained.

Data Analysis

We analyzed survival, time to metamorphosis, size at metamorphosis, body condition, and growth rate to metamorphosis to assess the effects of patch age and conspecific density on larval *H. chrysoscelis* (untransformed data are presented in Table S1 in the Supplemental Materials available online). We included patch age and initial larval density as factors in all analyses of variance (ANOVA) or multivariate ANOVAs (MANOVA). Using observed larval survival (number of metamorphs produced in each mesocosm) rather than initial density (15 or 30) did not produce differences in statistical significance or result in different conclusions, so we kept initial density as one of the two primary factors of interest. To assess survival, we used a factorial ANOVA on the proportion of individuals that survived to metamorphosis in each mesocosm. Similarly, we analyzed time to metamorphosis with a factorial ANOVA. We analyzed individual body size with a factorial MANOVA on SUL, tibiofibula length, and head width. Mass and growth rates (grams/day and millimeters/day) were similarly analyzed, but with separate ANOVAs. Growth rate was calculated based on individual size (mass or SUL) at metamorphosis and days to metamorphosis. Metamorph body condition (size-independent mass) was analyzed by mean-scaling mass to decouple variance from the measurement scale and means, regressing against SUL, and using the residuals in the ANOVA with age and density as factors (Berner 2011). All analyses used type III sums of squares and a significance level of $\alpha = 0.05$, and were conducted in R v3.3.3 (R Core Team 2017) with the car package v2.1.4 (Fox and Weisberg 2011). Block (row) was not significant in any analyses ($P > 0.25$), and it was incorporated into the error term. Days to metamorphosis were square root transformed ($\sqrt{X + 0.5}$), and body measurements were log transformed.

RESULTS

We observed an effect of patch age on survival, with 54.7 ± 4.0% (mean ± 1 SE) survival to metamorphosis in New mesocosms and 88.3 ± 2.3% survival in Old mesocosms, but

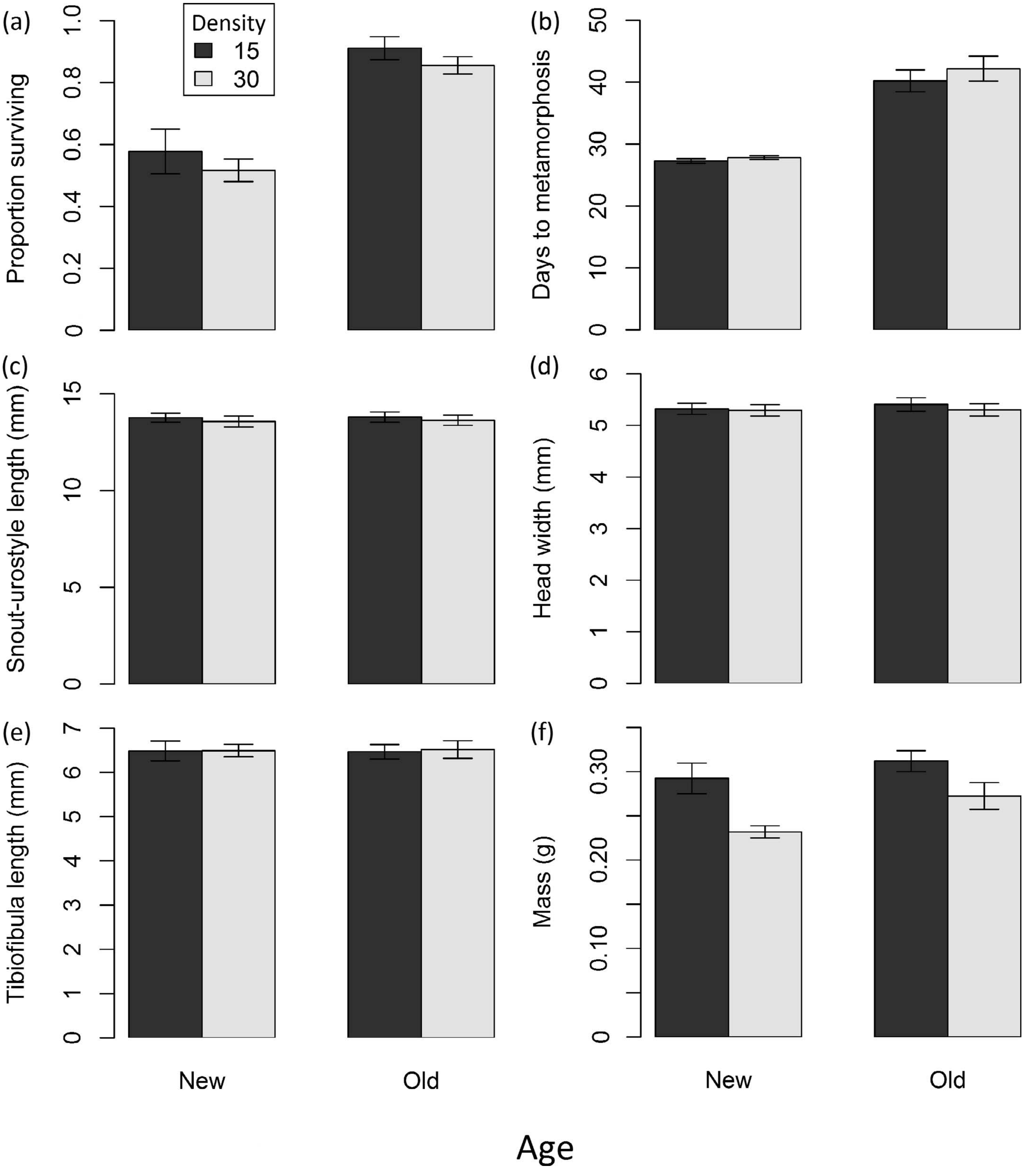

FIG. 1.—Mean (±1 SE) survival (a), days to metamorphosis (b), and metamorph snout–urostyle length (c), head width (d), tibiofibula length (e), and mass (f) of *Hyla chrysoscelis* (Cope's Gray Treefrogs) per mesocosm. Age indicates the age of mesocosms at the time larvae were added: New (3 d), Old (23 d). Density indicates the number of larvae added to each mesocosm.

no effect of initial density (Table 1a, Fig. 1a). We also observed an effect of patch age on days to metamorphosis, with individuals in New mesocosms taking 27.5 ± 0.2 d to reach metamorphosis and individuals in Old mesocosms taking 41.2 ± 1.3 d, but again there was no effect of initial density (Table 1a, Fig. 1b). We observed no effects of either patch age or initial density in the MANOVA (Table 1b) on SUL, head width, and tibiofibula length (Fig. 1c–e). There

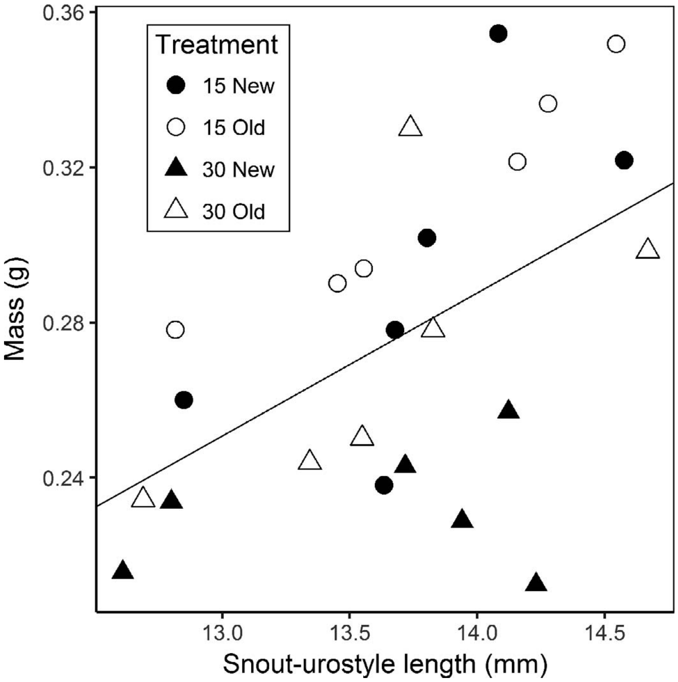

FIG. 2.—Average mass versus average snout–urostyle length for metamorphs of *Hyla chrysoscelis* (Cope's Gray Treefrogs) in each mesocosm, with patch age and density as factors ($R^2 = 0.69$, $P < 0.0001$). Treatment symbols represent the combination of larval density ($n = 15$ or 30) per mesocosm and the age of each mesocosm on the day larvae were added: New (3 d), Old (23 d). The regression line provides an indication of body condition, with higher body condition above the line and lower body condition below.

were effects of both patch age and initial density on metamorph mass and body condition (Table 1c). Metamorphs had greater mass at Low density and in Old patches (Fig. 1f), which, when coupled with the equivalent SUL at metamorphosis among all treatments, meant that body condition varied similarly to mass (Fig. 2). There were similar effects on growth rate to metamorphosis, with effects of both age and density on Δ mass, with the fastest growth in New and Low density mesocosms (Table 1c, Fig. 3a). There was only an effect of age on Δ length, with faster growth in New mesocosms (Table 1c, Fig. 3b). There were no interactions between age and density in any analysis ($P > 0.3$), so the interaction terms were excluded from our models.

DISCUSSION

Preference–performance theory predicts matching between oviposition site preference and larval performance. In assemblages of multiple anuran species, early breeding is beneficial because of reduced competition and priority effects gained from earlier access to resources (Alford and Wilbur 1985; Wilbur and Alford 1985). Some species of oviparous frogs, particularly *H. chrysoscelis*, have preferences that match those performance differences, providing their offspring with the best habitat for the duration of their larval stage (Resetarits and Wilbur 1989; Pintar and Resetarits 2017). By manipulating conspecific density and patch age over short time scales, we were able to test whether such small differences in oviposition preferences have consequences for offspring. Over the smaller differences in patch age that we tested, we observed mixed performance differences between our Old and New mesocosms across our two larval densities.

Larval density only affected mass and body condition, as might be expected, because more competitors result in fewer per capita resources, regardless of age treatment. Neither initial density nor patch age affected other morphometrics at metamorphosis (SUL, head width, tibiofibula length; Fig. 1c–e), indicating that larvae needed to reach a critical body

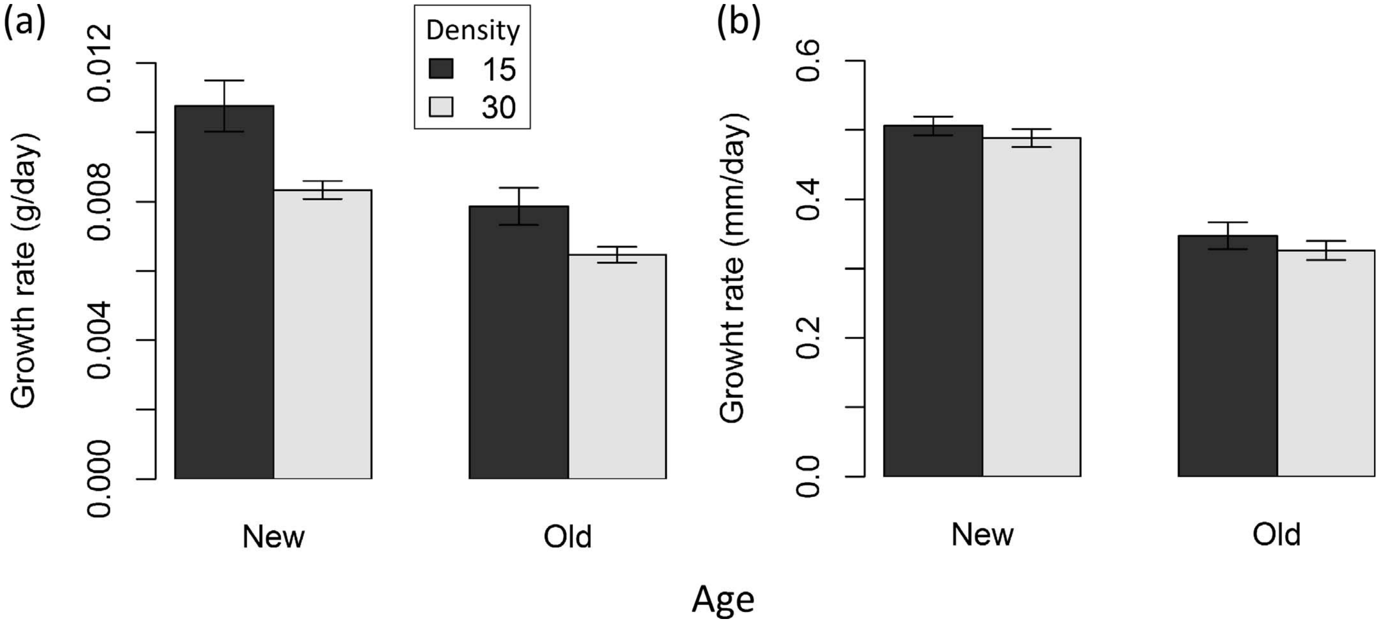

FIG. 3.—Mean (±1 SE) growth rates for metamorphs of *Hyla chrysoscelis* (Cope's Gray Treefrogs) in terms of (a) mass gained per day and (b) length gained per day per mesocosm. Age indicates the age of mesocosms at the time larvae were added: New (3 d), Old (23 d). Density indicates the number of larvae added to each mesocosm.

size at which metamorphosis occurred, regardless of mass (Wilbur and Collins 1973). Increased mass and better body condition are important components of future fitness, as larger individuals have a higher probability of overwinter survival, have a higher likelihood of breeding, breed sooner, and produce larger clutches (Smith 1987; Scott 1994; Beck and Congdon 2000; Morey and Reznick 2001; Scott et al. 2007). Ovipositing *H. chrysoscelis* have been shown to avoid habitat patches with conspecifics (Resetarits and Wilbur 1989), indicating that this is one component of preference–performance matching in amphibians.

Although we observed lower overall mass in New compared to Old mesocosms, initial density had a larger effect on mass than did patch age. The dominant effects of patch age were on survival and time to metamorphosis: overall survival was lower and time to metamorphosis shorter in New mesocosms than in Old (Fig. 1a–b). The shorter time to metamorphosis was not at the expense of size at metamorphosis, as is often expected with shorter larval periods (Scott 1994; Morey and Reznick 2001), and it only resulted in slightly smaller mass. Requiring an average of 14 fewer days to complete metamorphosis, yet doing it at very similar sizes, should produce a fitness benefit. Shorter larval periods allow larvae to escape deteriorating conditions in temporary ponds by moving into the terrestrial habitat and continue growth in preparation for the ensuing winter and following breeding season.

Although we observed high survival in Old mesocosms (88.3%), the lower survival in New mesocosms (54.7%) might call into question the benefits of breeding immediately after ponds fill, at least from the perspective of ovipositing adults or the entire *H. chrysoscelis* population. Our experiment was a simplified system in which all of our mesocosms were closed to colonizing and ovipositing insects, frogs, and other organisms that could not fit through the small mesh of our screen lids. In natural systems we would expect 23-d-old ponds to have established communities, with zooplankton and periphyton, as well as competitors and predators, which would put frogs breeding in these patches later at a much larger disadvantage than what we observed in our experiment. In older ponds open to colonization by other organisms, we would expect smaller body sizes attributable to the pressures of competition and predation, and also perhaps shorter times to metamorphosis caused by these added stressors (Wilbur and Collins 1973; Resetarits 1998; Day and Locke 2002).

Whereas our results in a simplified experimental system show that there are both costs and benefits for larval performance when adults breed in ponds immediately after they fill, the costs would likely be offset by community assembly dynamics in natural systems (Resetarits et al. 2005; Kraus and Vonesh 2010). Selection has matched adult oviposition preferences with larval performance differences in landscapes of habitat patches that vary in quality. *Hyla chrysoscelis* has served as a model organism in this regard, with oviposition and performance differences that have been observed across a range of patch characteristics (Wilbur and Alford 1985; Resetarits and Wilbur 1989; Resetarits et al. 2004; Rieger et al. 2004; Binckley and Resetarits 2007; Pintar and Resetarits 2017). Considering the functionally diverse responses of assemblages of many species (e.g., Resetarits and Pintar 2016; Resetarits and Silberbush 2016), integration of habitat selection and larval performance across landscapes of habitat patches will help to predict species distribution and abundance, and local and regional patterns of species diversity.

Acknowledgments.—Support was provided by the University of Mississippi Graduate Student Council, the Henry L. and Grace Doherty Foundation, and the University of Mississippi Field Station. This research was approved by the University of Mississippi's Institutional Animal Care and Use Committee (Protocol 14-027) and the Mississippi Department of Wildlife, Fisheries, and Parks (Permit 0624141). J. Bohenek and T. Breech commented on a previous draft of the manuscript.

SUPPLEMENTAL MATERIALS

Supplemental material associated with this article can be found online at http://dx.doi.org/10.1655/Herpetologica-D-17-00027.S1; http://dx.doi.org/10.1655/Herpetologica-D-17-00027.S2.

LITERATURE CITED

Alford, R.A., and H.M. Wilbur. 1985. Priority effects in experimental pond communities: Competition between *Bufo* and *Rana*. Ecology 66:1097–1105. DOI: http://dx.doi.org/10.2307/1939161

Alve, E. 1999. Colonization of new habitats by benthic foraminifera: A review. Earth-Science Reviews 46:167–185. DOI: http://dx.doi.org/10.1016/S0012-8252(99)00016-1

Beck, C.W., and J.D. Congdon. 2000. Effects of age and size at metamorphosis on performance and metabolic rates of southern toad, *Bufo terrestris*. Functional Ecology 14:32–38. DOI: http://dx.doi.org/10.1046/j.1365-2435.2000.00386.x

Berner, D. 2011. Size correction in biology: How reliable are approaches based on (common) principal component analysis? Oecologia 166:961–971. DOI: http://dx.doi.org/10.1007/s00442-011-1934-z

Binckley, C.A., and W.J. Resetarits, Jr. 2007. Effects of forest canopy on habitat selection in treefrogs and aquatic insects: Implications for communities and metacommunities. Oecologia 153:951–958. DOI: http://dx.doi.org/10.1007/s00442-007-0780-5

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31:343–366. DOI: http://dx.doi.org/10.1146/annurev.ecolsys.31.1.343

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302–1310. DOI: http://dx.doi.org/10.1126/science.199.4335.1302

Cope, E.D. 1880. On the zoological position of Texas. Bulletin of the United States National Museum 17:1–51.

Day, T., and R. Locke. 2002. Developmental thresholds and the evolution of reaction norms for age and size at life-history transitions. American Naturalist 159:338–350. DOI: http://dx.doi.org/10.1086/338989

Duellman, W.E., and L. Trueb. 1986. Biology of Amphibians. McGraw Hill, USA.

Facelli, J.M., and S.T.A. Pickett. 1991. Plant litter: Its dynamics and effects on plant community structure. Botanical Review 57:1–32. DOI: http://dx.doi.org/10.1007/BF02858763

Fairchild, G.W., A.M. Faulds, and J.F. Matta. 2000. Beetle assemblages in ponds: Effects of habitat and site age. Freshwater Biology 44:523–534. DOI: http://dx.doi.org/10.1046/j.1365-2427.2000.00601.x

Fox, J., and S. Weisberg. 2011. An {R} Companion to Applied Regression, 2nd edition. Sage, USA.

Fretwell, S.D., and H.L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16–36. DOI: http://dx.doi.org/10.1007/BF01601953

Kokko, H. 1999. Competition for early arrival in migratory birds. Journal of Animal Ecology 68:940–950. DOI: http://dx.doi.org/10.1046/j.1365-2656.1999.00343.x

Kraus, J.M., and J.R. Vonesh. 2010. Feedbacks between community assembly and habitat selection shape variation in local colonization. Journal of Animal Ecology 79:795–802. DOI: http://dx.doi.org/10.1111/j.1365-2656.2010.01684.x

Kraus, J.M., and J.R. Vonesh. 2012. Fluxes of terrestrial and aquatic carbon by emergent mosquitoes: A test of controls and implications for cross-ecosystem linkages. Oecologia 170:1111–1122. DOI: http://dx.doi.org/10.1007/s00442-012-2369-x

Laurila, A., S. Karttunen, and J. Merilä. 2002. Adaptive phenotypic plasticity and genetics of larval life histories in two *Rana temporaria* populations. Evolution 56:617–627. DOI: http://dx.doi.org/10.1111/j.1420-9101.2004.00744.x

Morey, S.R., and D.N. Reznick. 2001. Effects of larval density on postmetamorphic spadefoot toads (*Spea hammondii*). Ecology 82:510–522. DOI: http://dx.doi.org/10.1890/0012-9658(2001)082[0510:EOLDOP]2.0.CO;2

Morris, D.W. 2003. Toward an ecological synthesis: A case for habitat selection. Oecologia 136:1–13. DOI: http://dx.doi.org/10.1007/s00442-003-1241-4

Pintar, M.R., and W.J. Resetarits, Jr. 2017. Out with the old, in with the new: Oviposition preference matches larval success in Cope's gray treefrog, *Hyla chrysoscelis*. Journal of Herpetology 51:186–189. DOI: http://dx.doi.org/10.1670/16-019

R Core Team. 2017. R: A Language and Environment for Statistical Computing, Version 3.3.3. Available at https://www.R-project.org. R Foundation for Statistical Computing, Austria.

Resetarits, W.J., Jr. 1996. Oviposition site choice and life history evolution. American Zoologist 36:205–215. DOI: http://dx.doi.org/10.1093/icb/36.2.205

Resetarits, W.J., Jr. 1998. Differential vulnerability of *Hyla chrysoscelis* eggs and hatchlings to larval insect predators. Journal of Herpetology 32:440–443. DOI: http://dx.doi.org/10.2307/1565462

Resetarits, W.J., Jr., and M.R. Pintar. 2016. Functional diversity of non-lethal effects, chemical camouflage, and variation in fish avoidance in colonizing beetles. Ecology 97:3517–3529. DOI: http://dx.doi.org/10.1002/ecy.1593

Resetarits, W.J., Jr., and A. Silberbush. 2016. Local contagion and regional compression: Habitat selection drives spatially explicit, multiscale dynamics of colonisation in experimental metacommunities. Ecology Letters 19:191–200. DOI: http://dx.doi.org/10.1111/ele.12553

Resetarits, W.J., Jr., and H.M. Wilbur. 1989. Choice of oviposition site by *Hyla chrysoscelis*: Role of predators and competitors. Ecology 70:220–228. DOI: http://dx.doi.org/10.2307/1938428

Resetarits, W.J., Jr., J.F. Rieger, and C.A. Binckley. 2004. Threat of predation negates density effects in larval gray treefrogs. Oecologia 138:532–538. DOI: http://dx.doi.org/10.1007/s00442-003-1466-2

Resetarits, W.J., Jr., C.A. Binckley, and D.R. Chalcraft. 2005. Habitat selection, species interactions, and processes of community assembly in complex landscapes. Pp. 374–398 in Metacommunities: Spatial Dynamics and Ecological Communities (M. Holyoak, M.A. Leibold, and R.D. Holt, eds.). University of Chicago Press, USA.

Resh, V.H., A.V. Brown, A.P. Covich, . . .R.C. Wissmar. 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society 7:433–455. DOI: http://dx.doi.org/10.2307/1467300

Rieger, J.F., C.A. Binckley, and W.J. Resetarits, Jr. 2004. Larval performance and oviposition site preference along a predation gradient. Ecology 85:2094–2099. DOI: http://dx.doi.org/10.1890/04-0156

Schneider, C.A., W.S. Rasband, and K.W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. Nature Methods 9:671–675. DOI: http://dx.doi.org/10.1038/nmeth.2089

Scott, D.E. 1994. The effect of larval density on adult demographic traits in *Ambystoma opacum*. Ecology 75:1383–1396. DOI: http://dx.doi.org/10.2307/1937462

Scott, D.E., E.D. Casey, M.F. Donovan, and T.K. Lynch. 2007. Amphibian lipid levels at metamorphosis correlate to post-metamorphic terrestrial survival. Oecologia 153:521–532. DOI: http://dx.doi.org/10.1007/s00442-007-0755-6

Seale, D.B. 1980. Influence of amphibian larvae on primary production, nutrient flux, and competition in a pond ecosystem. Ecology 61:1531–1550. DOI: http://dx.doi.org/10.2307/1939059

Semlitsch, R.D., and H.M. Wilbur. 1988. Effects of pond drying time on metamorphosis and survival in the salamander *Ambystoma talpoideum*. Copeia 1988:978–983. DOI: http://dx.doi.org/10.2307/1445721

Shorrocks, B., and M. Bingley. 1994. Priority effects and species coexistence: Experiments with fungal-breeding *Drosophila*. Journal of Animal Ecology 63:799–806. DOI: http://dx.doi.org/10.2307/5257

Sibly, R.M. 1995. Life-history evolution in spatially heterogeneous environments, with and without phenotypic plasticity. Evolutionary Ecology 9:242–257. DOI: http://dx.doi.org/10.1007/BF01237771

Smith, D.C. 1987. Adult recruitment in chorus frogs: Effects of size and date at metamorphosis. Ecology 68:344–350. DOI: http://dx.doi.org/10.2307/1939265

Sousa, W.P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15:353–391. DOI: http://dx.doi.org/10.1146/annurev.es.15.110184.002033

Wellborn, G.A., D.K. Skelly, and E.E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. Annual Review of Ecology and Systematics 27:337–363. DOI: http://dx.doi.org/10.1146/annurev.ecolsys.27.1.337

Wilbur, H.M. 1987. Regulation of structure in complex systems: Experimental temporary pond communities. Ecology 68:1437–1452. DOI: http://dx.doi.org/10.2307/1939227

Wilbur, H.M. 1997. Experimental ecology of food webs: Complex systems in temporary ponds. Ecology 78:2279–2302. DOI: http://dx.doi.org/10.1890/0012-9658(1997)078[2279:EEOFWC]2.0.CO;2

Wilbur, H.M., and R.A. Alford. 1985. Priority effects in experimental pond communities: Responses of *Hyla* to *Bufo* and *Rana*. Ecology 66:1106–1114. DOI: http://dx.doi.org/10.2307/1939162

Wilbur, H.M., and J.P. Collins. 1973. Ecological aspects of amphibian metamorphosis. Science 182:1305–1314. DOI: http://dx.doi.org/10.1126/science.182.4119.1305

Woodward, B.D. 1983. Predator–prey interactions and breeding-pond use of temporary-pond species in a desert anuran community. Ecology 64:1549–1555. DOI: http://dx.doi.org/10.2307/1937509

Accepted on: 14 August 2017
Associate Editor: Chris Gienger