

## Competitive Interactions between Cricket Frogs (*Acris blanchardi*) and Other Anurans

MELISSA B. YOUNGQUIST<sup>1</sup>, KEVIN DOWNARD, AND MICHELLE D. BOONE

Department of Biology, Miami University, Oxford, OH 45056, USA

**ABSTRACT:** In recent decades, created ponds have become one of the dominant aquatic habitats in anthropogenic landscapes. Understanding how competition between colonizing species influences community assembly in these new habitats is important for predicting species distributions across the landscape. The objective of this study was to examine competition between larval Cricket Frogs (*Acris blanchardi*), which are showing declines in parts of their range, and other anurans including Bullfrogs (*Lithobates catesbeianus*), Green Frogs (*Lithobates clamitans*), and Cope's Gray Treefrogs (*Hyla chrysoscelis*). Using two separate experiments, we examined competitive interactions between larvae of (1) Cricket Frogs and different size classes of Bullfrogs; and (2) Cricket Frogs and Green Frogs, Cricket Frogs and Cope's Gray Treefrogs, or all three species together. We found no effect of either recently hatched or overwintered Bullfrog larvae on Cricket Frog metamorphosis. However, we found that Green Frogs reduced Cricket Frog survival and that Cope's Gray Treefrogs increased Cricket Frog time to metamorphosis. Because Cricket Frog populations have an annual life cycle, they might be sensitive to factors that influence recruitment, including competition with some species. Dispersal and landscape connectivity could be vital for maintaining Cricket Frog populations in areas with high densities of competitors (i.e., Green Frogs and Treefrogs). Conversely, the lack of competition between Cricket Frogs and Bullfrogs could explain why both species are able to coexist.

**Key words:** Community; Hylidae; Mesocosm; Ranidae; Species interactions

SINCE the 1780s, the United States has lost over 50% of wetland habitat (Dahl 1990). The past decade has seen an increase in created freshwater ponds, many of which are used for irrigation and recreation and which provide habitat for numerous taxa (Cereghino et al. 2008; Babbitt et al. 2009; Dahl 2011). How communities are assembled in these habitats is an important question for predicting species distributions in anthropogenic landscapes, where created ponds are one of the most-abundant aquatic habitat types (Dahl 2011). Of the multiple biotic interactions that affect species presence, resource competition has long been acknowledged as an important driver of community assembly (Gause 1934; Connell 1961; Goldberg and Barton 1992).

Competition between individuals can reduce fitness or singular aspects of fitness such as growth or survival. These effects of competition on individuals can have population level consequences, resulting in reduced abundance within a community or, in extreme cases, exclusion (Gause 1934; Schoener 1983; Goldberg and Barton 1992). However, individuals can avoid competition by altering behaviors (e.g., diet, spatial habitat use, temporal activity patterns) to partition resources (Schoener 1974; Pacala and Roughgarden 1982). Ultimately, whether and how competition affects species abundance depends on species traits and environmental conditions, especially the availability of resources (Tilman 1977; Briones et al. 1998; Kiesecker et al. 2001; Aresco 2010). In freshwater habitats, where the composition and densities of resources and competitors are in constant flux, competition might be a prominent factor regulating population dynamics—especially for species with complex life histories whose larvae must reach metamorphosis within a single season.

Many amphibian species colonize newly created ponds in agricultural landscapes (e.g., Babbitt et al. 2009); understanding competitive interaction between larval could help explain observed patterns of community composition. While instances of competitive exclusion appear rare in the wild (but see Hairston 1980), competition can affect the quantity

and quality of individuals recruited into the population by altering the size and timing of metamorphosis and, thereby, influencing population dynamics and community structure (e.g., Morin 1983; Semlitsch et al. 1988; Chelgren et al. 2006). One important factor for larval competition is size: larger larvae are often competitively dominant and negatively affect smaller larval amphibians (e.g., Morin and Johnson 1988; Boone et al. 2007; Knight et al. 2009). Size differences can be the result of species-specific growth rates or priority effects (Lawler and Morin 1993; Knight et al. 2009). In addition to size differences, species with faster growth or feeding rates could exploit and quickly deplete resources to the detriment of others (e.g., Morin and Johnson 1988; Smith and Burgett 2012). Differences in growth rate can translate into differences in larval period and allow for release from competition; as individuals leave the environment via metamorphosis, they reduce the length in time of resource overlap (Lawler and Morin 1993). A final factor affecting the outcome of competition between amphibian larvae is a change in resource use throughout ontogeny because the strength of competition changes as the food preferences of individuals diverge (Werner and Gilliam 1984; Cereghino 2006).

The effects of competition could have subtle impacts on populations of long-lived species because of stochastic variation in competitive environments. For short-lived species, however, the negative effects of competition could affect population dynamics more dramatically. Blanchard's Cricket Frogs (*Acris blanchardi*) have an annual life history with very few individuals surviving more than 1 yr in the wild (Lehtinen and MacDonald 2011). While Cricket Frogs can be found in multiple habitat types, they generally prefer open-canopy ponds and streams (Lehtinen and Skinner 2006; Trumbo et al. 2012). Cricket Frogs are declining across much of their range and are listed as endangered or threatened in multiple states (Gray et al. 2005). Despite their conservation status, relatively little is known about the basic ecology and species interactions of Cricket Frogs.

<sup>1</sup> CORRESPONDENCE: e-mail, youngqmb@miamioh.edu

The objective of this study was to examine how Cricket Frog metamorphosis was affected by competition in the larval environment. Using outdoor mesocosms, we conducted two separate experiments using co-occurring species that breed synchronously with Cricket Frogs (Bullfrogs [*Lithobates catesbeianus*], Cope's Gray Treefrogs [*Hyla chrysoscelis*, hereinafter Treefrog] and Green Frogs [*Lithobates clamitans*]). We tested two hypotheses: (1) competition between Cricket Frogs and Bullfrogs is influenced by initial size of the Bullfrog competitor; and (2) Cricket Frogs compete with co-occurring summer-breeding species, i.e., Treefrogs and Green Frogs. In the first study, we predicted that Cricket Frogs would show reduced growth and survival when reared with large, overwintered Bullfrogs versus recently hatched Bullfrogs. In the second study, we predicted that Cricket Frogs would experience stronger competition with Green Frogs than with Treefrogs because the former has a longer larval period and would exert competitive pressures throughout the Cricket Frog larval period. Alternatively, because Treefrogs metamorphose faster and larger than Cricket Frogs, their rapid growth rate might enable them to deplete resources early in the experiment and cause them to compete more strongly with Cricket Frogs.

#### MATERIALS AND METHODS

##### Animal Collection and Care

For each experiment, we collected 10 amplexed Cricket Frog pairs on 20 and 21 May 2012 from Miami University's Ecology Research Center (ERC), Oxford, OH, USA. For the first experiment, we tested Cricket Frog competition with both recently hatched and overwintered Bullfrog larvae. To obtain recently hatched Bullfrogs, we collected a total of four partial Bullfrog egg masses on 21 and 25 May 2012 from the ERC. We collected overwintered Bullfrog tadpoles (Gosner Stages 27–36; Gosner 1960) from two locations in Oxford, OH: one location was a permanent residential pond and the other was from Four Mile Creek in the Miami University Natural Areas (MUNA). For the second experiment, we tested for Cricket Frog competition with Green Frogs and Treefrogs. We collected a total of three partial Green Frog egg masses on 22, 24, and 26 May 2012 from Boesel Pond in the MUNA. We collected a total of three amplexed Treefrog pairs on 25 and 29 May 2012 from Indian Creek Metro Park, Reily, OH. Eggs of each species were placed in artificial outdoor rearing ponds containing 1000 L water, leaf litter, and algal inoculate from a fishless pond. As with most anuran species, the species we used are opportunistic feeders and, depending on ontogeny and location, will feed on phytoplankton and invertebrates from the water column, periphyton, and sediments (Jenssen 1967; Johnson 1991; Schiesari et al. 2009; Ruibal and Laufer 2012).

##### Experimental Design

Both experiments were conducted simultaneously in outdoor 1300-L cattle tank mesocosms at the ERC. To each mesocosm we added 1000 L water, 1 kg leaf litter, and plankton from a fishless pond to establish zooplankton and algal communities. Mesocosms were filled 20 and 21 May 2012 and leaf litter added 21 and 22 May 2012 for

Experiment 1 and Experiment 2, respectively. Mesocosms were covered by a 2-mm mesh lid to prevent invasion by insects or other anurans and were inoculated with pond water three times per week until initiation of the experiment. For periphyton collection throughout the experiment, we placed five glass microscope slides that were attached to flotation noodles and submerged just below the water's surface into each mesocosm. The submerged surface area of the side of a slide was 13.75 cm<sup>2</sup>.

##### Experiment 1: Effects of size class on competition.—

To test for competitive interactions between Crickets Frogs, recently hatched Bullfrog, and overwintered Bullfrog tadpoles, we used 10 treatments: five species assemblages crossed with the presence or absence of two overwintered Bullfrog tadpoles. The species assemblages included: two controls with Cricket Frogs only (30 or 60 per mesocosm), two controls with recently hatched Bullfrogs only (30 or 60 per mesocosm), and both Cricket Frogs and two controls with recently hatched Bullfrogs (30 Bullfrogs and 30 Cricket Frogs per mesocosm). Ponds with only Cricket Frogs or only recently hatched Bullfrogs served as density controls for assemblages containing both species. Tadpole densities were representative of those found in nature (Turnipseed and Altig 1975; Kupferberg 1997; Casper and Hendricks 2005). While overwintered Bullfrogs can be found at higher densities, they were difficult to find at the start of this experiment because of an unusually warm spring resulting in early metamorphosis. All treatments were replicated five times. All tadpoles were added on 4 June 2012 (experimental Day 0).

We monitored mesocosms for phytoplankton, periphyton, and zooplankton abundance as well as water quality (dissolved oxygen, pH, and temperature) on experimental Days 8, 29, and 50. We collected periphyton by scraping 27.5 cm<sup>2</sup> from microscope slides. Samples were transferred to 0.7- $\mu$ m glass fiber filters (47 mm diameter) and immediately placed in 15 mL of buffered acetone solution. Phytoplankton was collected by filtering 100 mL of water taken from a 3-L composite water sample onto a glass fiber filter and placed in 15 mL of buffered acetone solution. Phytoplankton was sampled by taking three, 1-L samples from two sides and the center of each mesocosm. Periphyton and phytoplankton samples were stored overnight at 4°C for chlorophyll extraction. We estimated phytoplankton and periphyton abundance from chlorophyll *a* via fluorometry (10-AU fluorometer, Turner Designs, Sunnydale, CA). Zooplankton abundance was qualitatively ranked on a scale of 0–3 (low–high) after observation of the entire mesocosm for 1 min.

We monitored mesocosms daily for Cricket Frog and Bullfrog metamorph emergence. Cricket Frog response variables were survival, time to metamorphosis, and mass at metamorphosis. Bullfrog response variables were survival, Gosner stage (Gosner 1960), and tadpole mass at the end of the experiment. The experiment was terminated on experimental Day 59, when the majority of Cricket Frogs had metamorphosed (97% of surviving individuals), at which time all ponds were drained and remaining tadpoles collected.

Only mesocosms that had  $\geq 3$  Cricket Frog or Bullfrog survivors were included in the analyses, resulting in three to five replicates per treatment: low-density mesocosms containing Cricket Frogs and high-density mesocosms containing recently-hatched and overwintered Bullfrogs had five replicates; high-density mesocosms with Cricket

Frogs had three replicates; all other treatments had four replicates. Bullfrog and Cricket Frog data were analyzed separately. We used Shapiro-Wilk tests to examine if data were distributed normally and visualized normality of residuals using normal probability plots (see Supplemental Data available online). We transformed data that were nonnormal. For Bullfrogs, we rank-transformed Gosner stage because of highly skewed data and nonnormally distributed variances. We analyzed Bullfrog survival and mass using two-way analysis of variance (ANOVA) and rank-transformed Gosner stage using a Friedman test (for only main effects). For Cricket Frogs, we log transformed mass and time to metamorphosis. All Cricket Frog responses were analyzed using ANOVA. Relative chlorophyll *a* levels from periphyton and phytoplankton, temperature, dissolved oxygen, pH, and zooplankton relative abundance were analyzed using repeated-measure ANOVAs. We log transformed periphyton and phytoplankton for normality. All analyses were run in SAS (v 9.4, SAS Institute Inc., Cary, NC).

**Experiment 2: Competition with Green Frogs and Treefrogs.**—We created six different assemblage types using Cricket Frogs, Green Frogs, and Cope's Gray Treefrogs: three controls with Cricket Frogs only (20, 30, or 60 individuals per mesocosm), both Cricket Frogs and Green Frogs (30 of each species), both Cricket Frogs and Treefrogs (30 of each species), and all three species together (20 of each species). Assemblages with only Cricket Frogs served as density controls. The medium-density (30) was a control for the two-species assemblages and the low-density (20) was a control for the three-species assemblage; the high-density (60) was a control for all multispecies assemblages. All treatments were replicated four times. Tadpoles were added on 6 June 2012 (experimental Day 0).

Using procedures described in Experiment 1, we monitored algal abundance and water quality on experimental Days 8, 29, and 50. We searched ponds daily for metamorphs and the experiment was terminated on experimental Day 55 when the majority of Cricket Frogs had metamorphosed (96% of surviving individuals). Response variables were survival, time to metamorphosis, and mass at metamorphosis for Cricket Frogs and Treefrogs. Tadpole mass and Gosner stage (Gosner 1960) were recorded for Green Frogs at the end of the experiment.

We included all mesocosms that had  $\geq 3$  Cricket Frog survivors in the analyses, resulting in  $\geq 3$  replicates per assemblage: the low-density (20) Cricket Frog and both Cricket Frog and Green Frog assemblages had three replicates; all other assemblages had four replicates. We used Shapiro-Wilk tests to examine if data were distributed normally and visualized normality of residuals using normal probability plots (see Supplementary Material available online). We transformed data that were nonnormal: we xarsine square-root transformed survival. Because transformed survival was heteroscedastic, we used Welch's ANOVA, which corrects for heteroscedastic data in one-way ANOVAs. Mass and time to metamorphosis were analyzed with ANOVA. We also conducted an orthogonal contrast to detect differences between assemblages with a total of 60 tadpoles (Cricket Frog only, both Cricket Frogs and Green Frogs, both Cricket Frogs and Treefrogs, and all three species together). The first contrast tested for differences between only Cricket Frog

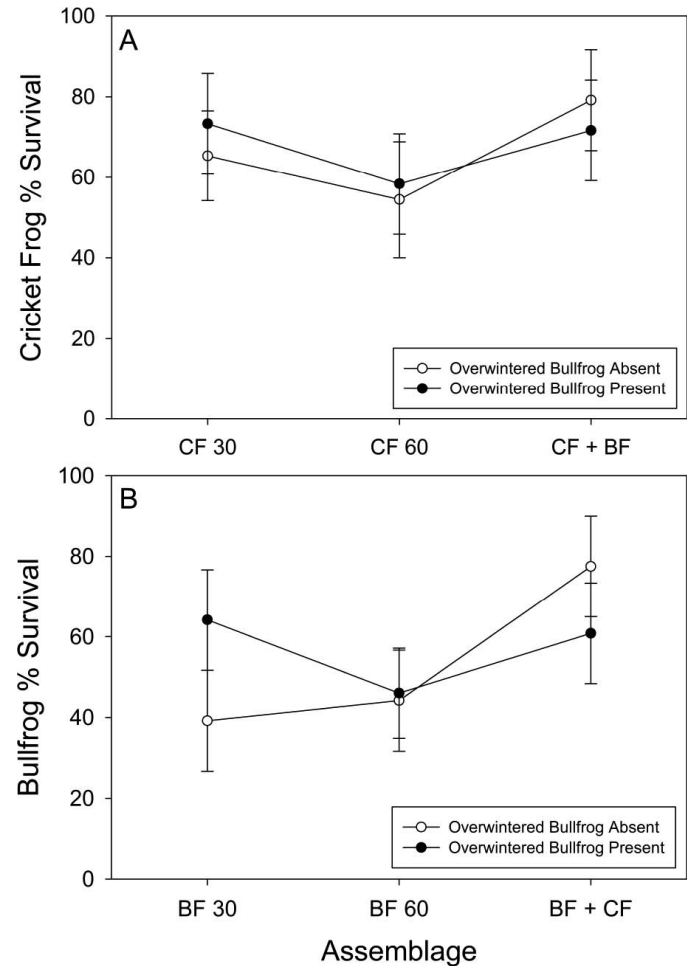


FIG. 1.—(A) Mean ( $\pm 1$  SE) Cricket Frog (CF) survival to metamorphosis and (B) mean Bullfrog (BF) survival to end of the experiment in Experiment 1. Both CF 30 and BF 30 indicate low-density, single-species controls; CF 60 and BF 60 indicate high-density, single-species controls; CF + BF indicates the two-species assemblage.

assemblages and the multispecies assemblages (testing for differences in intra- and interspecific competition). The second contrast tested for differences in effects of Treefrogs and Green Frogs on Cricket Frog tadpoles. Relative chlorophyll *a* levels from periphyton and phytoplankton, temperature, dissolved oxygen, pH, and zooplankton were analyzed using repeated-measure ANOVAs; we log transformed periphyton and phytoplankton for normality.

## RESULTS

### Experiment 1: Effects of Size Class on Competition

We found no evidence of competition between either recently hatched or overwintered Bullfrog tadpoles and the Cricket Frog tadpoles (Figs. 1 and 2). There were no effects of assemblage or overwintered Bullfrogs on Cricket Frog survival ( $F_{2,19} \leq 1.10$ ,  $P \geq 0.35$ ) or survival of recently hatched Bullfrogs ( $F_{2,19} \leq 2.05$ ,  $P \geq 0.16$ ). There were also no effects of assemblage or overwintered Bullfrogs on Cricket Frog time to metamorphosis ( $F_{2,18} \leq 1.19$ ,  $P \geq 0.32$ ), Cricket Frog mass ( $F_{1,19} \leq 2.15$ ,  $P \geq 0.16$ ), recently hatched Bullfrog Gosner stage ( $F_{2,21} \leq 2.23$ ,  $P \geq 0.15$ ), or recently hatched Bullfrog mass ( $F_{2,19} \leq 1.39$ ,  $P \geq$



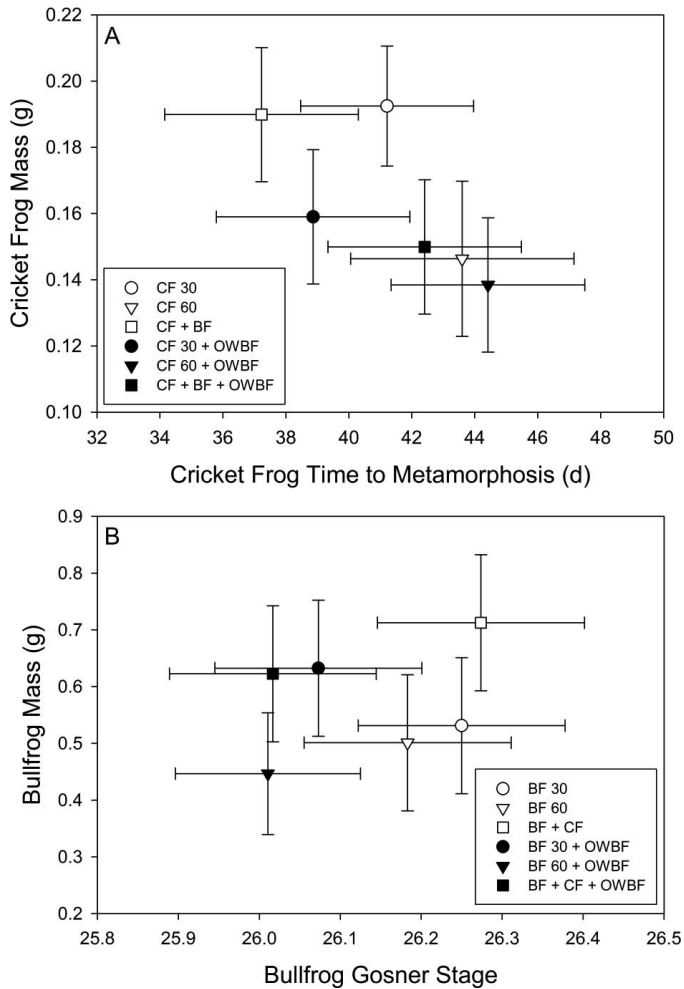


FIG. 2.—(A) Mean ( $\pm 1$  SE) growth of Cricket Frogs (CF) and (B) mean growth of Bullfrogs (BF) in Experiment 1. Both CF 30 and BF 30 indicate low-density, single-species controls; CF 60 and BF 60 indicate high-density, single-species controls; CF + BF indicates the two-species assemblage; OWBF indicates the presence of two overwintered bullfrog tadpoles.

0.27). There was a time by assemblage effect on relative levels of chlorophyll *a* for periphyton (Table 1; Fig. 3). While periphyton increased in the first 30 d, higher tadpole density reduced periphyton abundance relative to low-density treatments. The presence of overwintered Bullfrogs did not affect periphyton (Table 1). There were no effects of either assemblage or overwintered Bullfrogs on phytoplankton (Table 1) or other water quality measures ( $F_{4,31} \leq 1.32$ ,  $P \geq 0.29$ ).

#### Experiment 2: Competition with Green Frogs and Treefrogs

There was an overall effect of assemblage type on Cricket Frog survival ( $F_{5,16} = 7.95$ ,  $P = 0.01$ ; Fig. 4). An orthogonal contrast revealed a difference between the effects of Treefrogs and Green Frogs on Cricket Frog survival ( $F_{1,16} = 5.15$ ,  $P = 0.04$ ); Cricket Frog survival was lower in the presence of Green Frogs than in Treefrogs. The timing and size of Cricket Frog tadpoles at metamorphosis differed among assemblage types (Wilks' Lambda = 0.20,  $F_{10,30} = 2.45$ ,  $P = 0.03$ ; Fig. 5). Cricket Frogs did best alone at a density of 30 tadpoles per mesocosm; Treefrogs and Green Frogs negatively affected timing of metamorphosis and size at metamorphosis. Tree-

frogs metamorphosed earlier and larger than did Cricket Frogs (Treefrog average time  $\pm 1$  SE =  $26.75 \pm 0.16$  d; Treefrog average mass =  $0.421 \pm 0.007$  g). Only three Green Frogs reached metamorphosis. There were no effects of assemblage type on relative levels of chlorophyll *a* for periphyton and phytoplankton; however, periphyton abundance fluctuated over time (Table 2; Fig. 3). There were no effects on other water quality measures ( $F_{5,15} \leq 1.36$ ,  $P \geq 0.29$ ).

#### DISCUSSION

A regional species pool is filtered by abiotic and biotic factors, resulting in a local species assemblage. In addition to other species interactions, competition can be an important driver of community structure. Cricket Frogs breed in the late spring and summer in a variety of aquatic habitats with other amphibians, which could result in competition for food resources. We manipulated competition between Cricket Frogs and three co-occurring anurans species to assess if competition could be important for population dynamics and Cricket Frog distribution.

In the first experiment, we did not detect competition between Cricket Frogs and Bullfrogs, nor did we see an effect of overwintered Bullfrogs on growth and survival of recently hatched Cricket Frogs or Bullfrogs. The density of overwintered Bullfrogs used in this study is within the natural range (Kupferberg 1997; Mueller et al. 2006); however, it could be that the addition of two overwintered Bullfrogs was not enough to affect recently hatched tadpoles. Studies using higher densities show overwintered Bullfrogs can negatively impact growth of amphibian larvae (Kupferberg 1997; Boone et al. 2007). Additionally, there was no evidence of either intra- or interspecific competition between Cricket Frogs and Bullfrogs, despite lower levels of periphyton in high-density mesocosms as well as in the assemblages with Bullfrogs. While the absence of intraspecific competition might lead to the conclusion that no competition between tadpoles would be observed, its absence does not preclude interspecific competition between Bullfrogs and Cricket Frogs if either were a superior competitor.

The apparent disconnect between a depression of periphyton and lack of competition indicates either that the densities were not high enough to induce resource limitation or that tadpoles were able to feed from multiple sources. In particular, Bullfrog tadpoles appear to be opportunistic feeders that feed preferentially on high-quality food (Kupferberg 1997; Schiesari et al. 2009; Ruibal and Laufer 2012). Tadpoles could also switch resource use to avoid competition (Werner 1994). These behaviors could explain why recently hatched Bullfrog tadpoles were unaffected by Cricket Frog tadpoles. Cricket Frogs could also have increased activity levels in Bullfrog assemblages, as has been seen in other hylid species, to compensate for reduced resources (e.g., Monello et al. 2006), although we did not observe a change in activity. Cricket Frogs and Bullfrogs are commonly found breeding in the same habitats, and one study found a positive association between the presence of Cricket Frogs and Bullfrogs whereby Bullfrog abundance explained 75% of the variation in Cricket Frog abundance (Brodman 2008). Because both species frequently occur in

TABLE 1.—Repeated measures analysis of variance of the effect of species assemblage and overwintered Bullfrog larvae on periphyton and phytoplankton abundance in Experiment 1.

Response	Source of variation	df	F	P
Periphyton	Between-subject effects			
	Assemblage	4	2.37	0.07
	Overwintered Bullfrog	1	0.79	0.38
	Assemblage × overwintered Bullfrog	4	0.19	0.94
	Error	30		
	Within-subject effects			
	Time	2	59.76	<0.0001
	Time × assemblage	8	2.47	0.02
	Time × overwintered Bullfrog	2	0.71	0.46
	Time × assemblage × overwintered Bullfrog	8	1.67	0.14
Error	60			
Phytoplankton	Between-subject effects			
	Assemblage	4	0.8	0.53
	Overwintered Bullfrog	1	1.19	0.28
	Assemblage × overwintered Bullfrog	4	0.31	0.87
	Error	30		
	Within-Subject Effects			
	Time	2	104.02	<0.0001
	Time × assemblage	8	1.2	0.31
	Time × overwintered Bullfrog	2	0.66	0.52
	Time × assemblage × overwintered Bullfrog	8	0.9	0.52
Error	60			

open-canopy, permanent wetlands (Shulze et al. 2010; Trumbo et al. 2012), the apparent lack of competition in the larval stage could contribute to their coexistence.

In the second experiment, our results support the hypothesis that Cricket Frogs compete with co-occurring, summer-breeding anurans. The presence of Treefrogs increased time to metamorphosis for Cricket Frogs, suggesting resource limitation early in Cricket Frog development and subsequent competitive release as Treefrogs metamorphosed. There was an average of 17 d between Treefrog and Cricket Frog metamorphosis (~1/3 of the Cricket Frog larval period without Treefrogs). Audo et al. (1995) found that Treefrog (*Hyla chrysoscelis*) tadpoles starved early in development delayed their time to metamorphosis, but that there were no effects on size or survival. Similar results were found in damselflies that were starved early in development (Dmitriew and Rowe 2005). The lack of difference in Cricket Frog size indicates compensatory growth occurred after Treefrogs metamorphosed, which is common in species with complex life histories (e.g., Vonesh and Bolker 2005; Stoks and Cordoba-Aguilar 2012). Where food limitation early in development is concerned, our results and those of Audo et al. (1995) differ from other studies that found either no or opposite effects (Travis 1984; Alford and Harris 1988). Although we did not detect differences in algal resources between mesocosms with Treefrog present versus absent, there was a trend in which the mesocosms with Treefrogs had the lowest levels of periphyton on experimental Days 8 and 29, which coincides with the time when Treefrogs were present. Alternatively, we observed that Treefrog tadpoles were more active than Cricket Frog tadpoles, and they could have interfered with Cricket Frog feeding (interference competition). More activity by the larger Treefrog tadpoles could increase direct interactions between tadpoles and reduce feeding efficiency

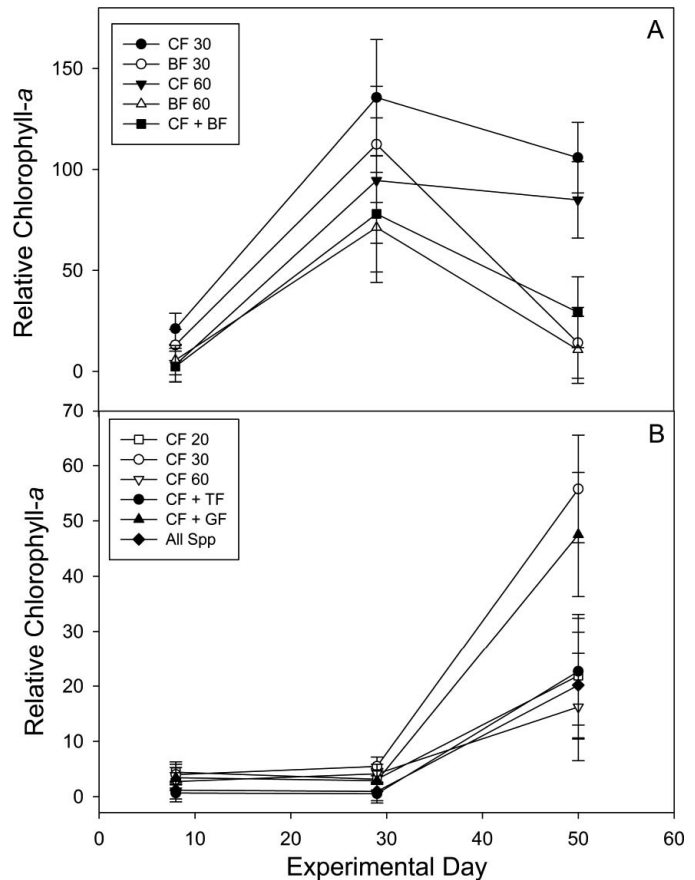


FIG. 3.—(A) Mean ( $\pm 1$  SE) relative levels of periphyton in Experiment 1 in Cricket Frog (CF) and Bullfrog (BF) assemblages. Both CF 30 and BF 30 indicate low-density, single-species controls; CF 60 and BF 60 indicate high-density, single-species controls; CF + BF indicates the two-species assemblage. (B) Mean relative levels of periphyton in Experiment 2. The CF 20, CF 30, and CF 60 indicate the low, medium, and high-density Cricket Frog controls; CF + TF indicates the assemblage with both Cricket Frogs and Treefrogs; CF + GF indicates the assemblage with both Cricket Frogs and Green Frogs; All Spp indicates the three-species assemblage.

of competitors (e.g., Wilbur 1977; Faragher and Jaeger 1998).

Green Frogs also had a strong negative effect on Cricket Frogs. They reduced Cricket Frog survival by up to 50% compared to assemblages with only Cricket Frogs at a density of 30 or 60 individuals. However, there were no differences in size and time to metamorphosis of Cricket Frogs between the high density (60) assemblages with only Cricket Frogs and the assemblages with Green Frogs (30 of each species), despite the decrease in Cricket Frog survival. The difference in competitive effects of Green Frogs and Bullfrogs on Cricket Frogs might indicate a more similar diet between Cricket Frogs and Green Frogs than between Cricket Frogs and Bullfrogs. Stable isotope analyses indicate niche differentiation in feeding between Bullfrogs and Green Frogs (Schiesari et al. 2009), and studies on competition between Bullfrogs and Green Frogs also indicate possible resource differentiation (Werner 1994). We did not attempt to determine the exact nature of diet overlap. Audo et al. (1995) found that tadpoles starved later in development had lower survival and smaller size at metamorphosis but found no impacts on time to metamorphosis. This pattern matches

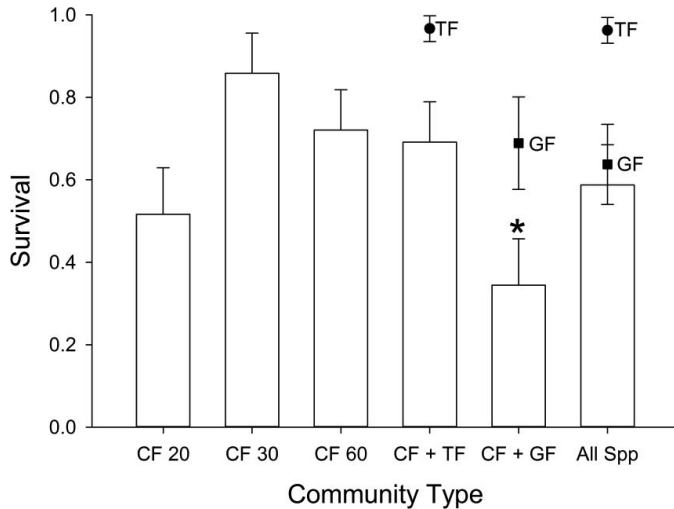


FIG. 4.—Mean ( $\pm 1$  SE) Cricket Frog (CF) survival from Experiment 2. Filled circles are mean Treefrog survival; Filled squares are mean Green Frog survival. The CF 20, CF 30, and CF 60 indicate the low, medium, and high-density Cricket Frog controls; CF + TF indicates the assemblage with both Cricket Frogs and Treefrogs; CF + GF indicates the assemblage with both Cricket Frogs and Green Frogs; All Spp indicates the three-species assemblage. \*Indicates Cricket Frog survival in CF + GF assemblage was less than in the CF + TF assemblage.

the trend of Cricket Frogs in the presence of Green Frogs. It might be that, as Green Frog tadpoles grew, they gained a competitive advantage over Cricket Frog tadpoles late in the experiment and hindered resource acquisition by Cricket Frogs. Because Cricket Frogs function as an annual species, reductions in juvenile recruitment over successive years and in the absence of migrants could result in an increased risk of extirpation.

Finally, we did not detect any differences in survivorship or metamorphosis between the low-density (20) Cricket Frog assemblage, which acted as a density control for Cricket Frogs in three-species assemblage, and the three-species assemblage. This indicates that direct competition

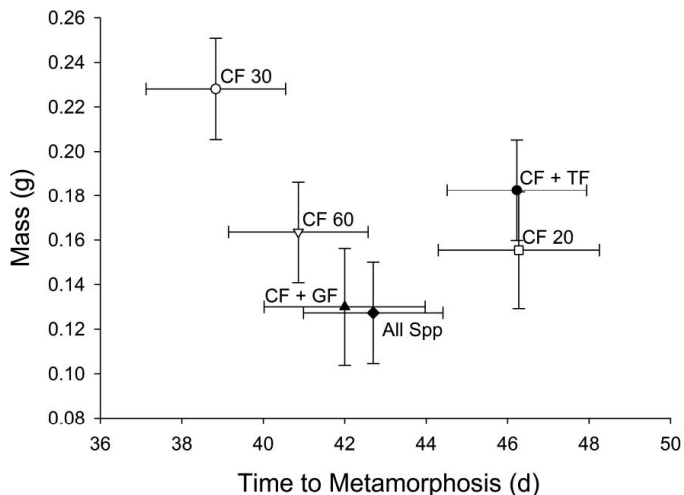


FIG. 5.—Mean ( $\pm 1$  SE) Cricket Frog mass and time to metamorphosis in Experiment 2 by assemblage type. The CF 20, CF 30, and CF 60 indicate the low, medium, and high-density Cricket Frog controls; CF + TF indicates the assemblage with both Cricket Frogs and Treefrogs; CF + GF indicates the assemblage with both Cricket Frogs and Green Frogs; All Spp indicates the three-species assemblage.

TABLE 2.—Repeated measures analysis of variance of the effect of species assemblage on periphyton and phytoplankton abundance in Experiment 2.

Response	Source of variation	df	F	P
Periphyton	Between-subject effects			
	Assemblage	5	2.31	0.09
	Error	15		
	Within-subject effects			
	Time	2	40.81	<0.0001
Phytoplankton	Between-subject effects			
	Assemblage	5	0.26	0.93
	Error	16		
	Within-subject effects			
	Time	2	58.66	<0.0001
	Time $\times$ assemblage	10	1.09	0.4
	Error	32		

may be reduced in complex communities with more than two species interacting. These results are in contrast to the observed differences between the medium-density (30) controls and the two-species assemblages, which indicates competitive effects of Treefrogs and Green Frogs on Cricket Frogs. Our study indicates that Cricket Frogs likely perform best when alone at medium to high densities. The low survival, low mass, and long larval period found in the low-density (20) treatment was surprising because we expected Cricket Frogs to experience the least amount of competition and highest access to resources in this assemblage. These results could indicate a nonlinear response between density and growth or survival; Cricket Frog tadpoles might facilitate each other at medium densities and experience Allee effects at low densities, as demonstrated in other species (Wilbur 1977; Smith-Gill and Gill 1978; Smith and Burgett 2012).

Conclusions

Our study shows that the growth and survival of Cricket Frog tadpoles can be negatively affected by heterospecific competitors and that competitive interactions are species specific. The four species tested are sympatric and all combinations, from a single species to all four, have been observed at ponds in the wild (Brodman 2008; MBY, personal observation); therefore, the experimental assemblages and competitive effects are ecologically relevant. Because the competitive effects were relatively minor and species specific, however, Cricket Frog recruitment and population persistence might not be strongly affected by larval competition in resource-rich environments within the range of densities studied. In resource-poor environments or in habitats where densities of Green Frogs and Treefrogs are high, Cricket Frog recruitment might be reduced. High variation in recruitment across the landscape attributable to differences in community assemblage means Cricket Frogs might need to rely on immigration to maintain regional populations across a landscape. Further studies on source-sink dynamics and competitor presence would be needed to assess the importance of competition for species presence and distribution. Finally, Bullfrogs can negatively affect other larval anurans, including Green Frogs (Werner 1994; Kiesecker and Blaustein 1998; Boone et al. 2007), which would indirectly benefit Cricket Frogs. Because



Cricket Frogs and Bullfrogs are likely to colonize similar types of ponds, our results indicate that Bullfrog tadpoles will not hinder, and could indirectly facilitate, Cricket Frog colonization across a landscape.

**Acknowledgments.**—We thank S. Rumschlag and T. Hoskins for comments on previous versions of this manuscript. Funding was provided by the Miami University Undergraduate Summer Scholars Program. Animal collection was approved by the Ohio Department of Natural Resources (Wild Animal Permit: Scientific Collection 14-80). All protocols were approved by the Miami University Institutional Animal Care & Use Committee (protocol #827).

#### SUPPLEMENTARY MATERIAL

Supplementary material associated with this article can be found online at <http://dx.doi.org/10.1655/Herpetologica-D-14-00049.S1>.

#### LITERATURE CITED

- Alford, R.A., and R.N. Harris. 1988. Effects of larval growth history on anuran metamorphosis. *American Naturalist* 131:91–106.
- Aresco, M.J. 2010. Competitive interactions of two species of freshwater turtles, a generalist omnivore and an herbivore, under low resource conditions. *Herpetologica* 66:259–268.
- Audo, M.C., T.M. Mann, T.L. Polk, C.M. Loudenslager, W.J. Diehl, and R. Altig. 1995. Food deprivation during different periods of tadpole (*Hyla chrysoscelis*) ontogeny affects metamorphic performance differently. *Oecologia* 103:518–522.
- Babbitt, K.J., M.J. Baber, D.L. Childers, and D. Hocking. 2009. Influence of agricultural upland habitat type on larval anuran assemblages in seasonally inundated wetlands. *Wetlands* 29:294–301.
- Boone, M.D., R.D. Semlitsch, E.E. Little, and M.C. Doyle. 2007. Multiple stressors in amphibian communities: Effects of chemical contamination, bullfrogs, and fish. *Ecological Applications* 17:291–301.
- Briones, O., C. Montaña, and E. Ezcurra. 1998. Competition intensity as a function of resource availability in a semiarid ecosystem. *Oecologia* 116:365–372.
- Brodman, R. 2008. A 14-year study of amphibian populations and metacommunities. *Herpetological Conservation and Biology* 4:106–119.
- Casper, G.S., and R. Hendricks. 2005. *Rana catesbeiana*. Shaw 1802 American Bullfrog. Pp. 540–546 in *Amphibian Declines: The Conservation Status of United States Species* (M.J. Lannoo, ed.). University of California Press, USA.
- Cereghino, R. 2006. Ontogenetic diet shifts and their incidence on ecological processes: A case study using two morphologically similar stoneflies (Plecoptera). *Acta Oecologia* 30:33–38.
- Cereghino, R., A. Ruggiero, P. Marty, and S. Angelibert. 2008. Biodiversity and distribution patterns of freshwater invertebrates in farm ponds of a south-western French agricultural landscape. *Hydrobiologia* 597:43–51.
- Chelgren, N.D., D.K. Resenberg, S.S. Heppell, and A.I. Gitelman. 2006. Carryover aquatic effects on survival of metamorphic frogs during pond emigration. *Ecological Applications* 16:250–261.
- Connell, J.H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42:710–723.
- Dahl, T.E. 1990. Wetland Losses in the United States 1780s to 1980s. Fish and Wildlife Service, U.S. Department of the Interior, USA.
- Dahl, T.E. 2011. Status and Trends of Wetlands in the Conterminous United States 2004 to 2009. Fish and Wildlife Service, U.S. Department of the Interior, USA.
- Dmitriew, C., and L. Rowe. 2005. Resource limitation, predation risk, and compensatory growth in a damselfly. *Oecologia* 142:150–154.
- Faragher, S.G., and R.G. Jaeger. 1998. Tadpole bullies: Examining mechanisms of competition in a community of larval anurans. *Canadian Journal of Zoology* 76:144–153.
- Gause, G.F. 1934. *The Struggle for Existence*. Williams and Wilkins, USA.
- Goldberg, D.E., and A.M. Barton. 1992. Patterns and consequences of interspecific competition in natural communities: A review of field experiments with plants. *American Naturalist* 139:771–801.
- Gosner, K.L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* 16:183–190.
- Gray, R.H., L.E. Brown, and L. Blackburn. 2005. *Acris crepitans* Baird 1854(b): Northern cricket frog. Pp. 441–443 in *Amphibian Declines: The Conservation Status of United States Species* (M.J. Lannoo, ed.). University of California Press, USA.
- Hairton, N.G. 1980. The experimental test of an analysis of field distributions: Competition in terrestrial salamanders. *Ecology* 1980:817–826.
- Jenssen, T.A. 1967. Food habits of the green frog, *Rana clamitans*, before and during metamorphosis. *Copeia* 1967:214–218.
- Johnson, L.M. 1991. Growth and development of larval northern cricket frogs (*Acris crepitans*) in relation to phytoplankton abundance. *Freshwater Biology* 25:51–59.
- Kiesecker, J.M., and A.R. Blaustein. 1998. Effects of introduced bullfrogs and smallmouth bass on microhabitat use, growth, and survival of native red-legged frogs (*Rana aurora*). *Conservation Biology* 12:776–787.
- Kiesecker, J.M., A.R. Blaustein, and C.L. Miller. 2001. Potential mechanisms underlying the displacement of native red-legged frogs by introduced bullfrogs. *Ecology* 82:1964–1970.
- Knight, C.M., M.J. Parris, and W.H.N. Gutzke. 2009. Influence of priority effects and pond location on invaded larval amphibian communities. *Biological Invasions* 11:1033–1044.
- Kupferberg, S.J. 1997. Bullfrog (*Rana catesbeiana*) invasion of a California river: The role of larval competition. *Ecology* 78:1736–1751.
- Lawler, S.P., and P.J. Morin. 1993. Temporal overlap, competition, and priority effects in larval anurans. *Ecology* 74:174–182.
- Lehtinen, R.M., and M.C. MacDonald. 2011. Live fast, die young? A six year field study of longevity and survivorship in Blanchard's cricket frog (*Acris crepitans blanchardi*). *Herpetological Review* 42:504–507.
- Lehtinen, R.M., and A.A. Skinner. 2006. The enigmatic decline of Blanchard's cricket frog (*Acris crepitans blanchardi*): A test of the habitat acidification hypothesis. *Copeia* 2006:159–167.
- Monello, R.J., J.J. Dennehy, D.L. Murray, and A.J. Wirsing. 2006. Growth and behavioral response of tadpoles of two native frogs to an exotic competitor, *Rana catesbeiana*. *Journal of Herpetology* 40:403–407.
- Morin, P.J. 1983. Predation, competition, and the composition of larval anuran guilds. *Ecological Monographs* 53:119–138.
- Morin, P.J., and E.A. Johnson. 1988. Experimental studies of asymmetric competition among anurans. *Oikos* 53:398–407.
- Mueller, G.A., J. Carpenter, and D. Thornbrugh. 2006. Bullfrog tadpole (*Rana catesbeiana*) and red swamp crayfish (*Procambarus clarkii*) predation on early life stages of endangered razorback sucker (*Xyrauchen texanus*). *Southwestern Naturalist* 51:258–261.
- Pacala, S., and J. Roughgarden. 1982. Resource partitioning and interspecific competition in two two-species insular *Anolis* lizard communities. *Science* 217:444–446.
- Ruibal, M., and G. Laufer. 2012. Bullfrog *Lithobates catesbeianus* (Amphibia: Ranidae) tadpole diet: Description and analysis for three invasive populations in Uruguay. *Amphibia-Reptilia* 33:355–363.
- Schiesari, L., E.E. Werner, and G.W. Kling. 2009. Carnivory and resource-based niche differentiation in anuran larvae: Implications for food web and experimental ecology. *Freshwater Biology* 54:572–586.
- Schoener, T.W. 1974. Resource partitioning in ecological communities. *Science* 185:27–39.
- Schoener, T.W. 1983. Field experiments on interspecific competition. *American Naturalist* 122:240–285.
- Semlitsch, R.D., D.E. Scott, and J.H.K. Pechmann. 1988. Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum*. *Ecology* 69:184–192.
- Shulse, C.D., R.D. Semlitsch, K.M. Trauth, and A.D. Williams. 2010. Influences of design and landscape placement parameters on amphibian abundance in constructed wetlands. *Wetlands* 30:915–928.
- Smith, G.R., and A.A. Burgett. 2012. Interaction between two species of tadpoles mediated by nutrient enrichment. *Herpetologica* 68:174–183.
- Smith-Gill, S.J., and D.E. Gill. 1978. Curvilinearities in the competition equations: An experiment with ranid tadpoles. *American Naturalist* 112:557–570.
- Stoks, R., and A. Cordoba-Aguilar. 2012. Evolutionary ecology of Odonata: A complex life cycle perspective. *Annual Review of Entomology* 57:249–265.
- Tilman, D. 1977. Resource competition between planktonic algae: An experimental and theoretical approach. *Ecology* 58:338–348.
- Travis, J. 1984. Anuran size at metamorphosis: Experimental test of a model based on intraspecific competition. *Ecology* 65:1155–1160.
- Trumbo, D.R., A.A. Burgett, R.L. Hopkins, E.G. Biro, J.M. Chase, and J.H. Knouft. 2012. Integrating local breeding pond, landcover, and climate factors in predicting amphibian distributions. *Landscape Ecology* 27:1183–1196.

- Turnipseed, G., and R. Altig. 1975. Population density and age structure of three species of hylid tadpoles. *Journal of Herpetology* 9:287–291.
- Vonesh, J.R., and B.M. Bolker. 2005. Compensatory larval responses shift trade-offs associated with predator-induced hatching plasticity. *Ecology* 86:1580–1591.
- Werner, E.E. 1994. Ontogenetic scaling of competitive relations: Size-dependent effects and responses in two anuran larvae. *Ecology* 75:197–213.
- Werner, E.E., and J.F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* 15:393–425.
- Wilbur, H.M. 1977. Density-dependent aspects of growth and metamorphosis in *Bufo americanus*. *Ecology* 58:196–200.

**Accepted on** 12 August 2015  
**Associate Editor:** Sarah Woodley