

HABITAT SEGREGATION IN TWO SISTER TAXA OF HYLID TREEFROGS

MARGARET S. GUNZBURGER^{1,2}

Department of Biological Science, Florida State University, Tallahassee, Florida 32306-1100, USA

ABSTRACT: One of the basic tenets of ecological niche theory is that closely-related, ecologically similar species do not coexist. When such species co-occur over large portions of their geographic ranges, they often are segregated by habitat. The objective of this study was to evaluate experimentally the roles of abiotic habitat characteristics and competition in the habitat segregation of two sister taxa of Hylid treefrogs. These species co-occur throughout the southeastern United States, but *Hyla cinerea* typically breeds in permanent ponds, while *H. gratiosa* breeds in temporary ponds. I conducted a reciprocal transplant experiment using enclosures in natural ponds to compare survival, larval period, and size at metamorphosis for both species in temporary and permanent ponds. While the overall survival of *H. cinerea* was higher than *H. gratiosa* and survival varied among localities, there were no significant distinctions in survival between temporary and permanent ponds. *Hyla cinerea* tadpoles had longer larval period and larger size at metamorphosis in temporary ponds relative to permanent ponds. *Hyla gratiosa* tadpoles were significantly larger at metamorphosis in temporary ponds than permanent ponds, and had longer larval periods when encountering only conspecifics than when raised with *H. cinerea*. The results of these experiments, in conjunction with other work, suggest that a combination of factors is likely responsible for the habitat segregation between these two species.

Key words: Anura; Competition; Field experiment; Florida; Georgia; Habitat distribution; *Hyla cinerea*; *Hyla gratiosa*; Larval period; Predation; Reciprocal transplant experiment; Tadpole

MANY sets of related taxa segregate along the hydroperiod gradient from temporary to permanent ponds (Wellborn et al., 1996). This gradient includes variation in predation pressure, the prevalence and intensity of competition, and a variety of abiotic environmental effects (Wellborn et al., 1996). One of the most prevalent divisions in these habitat types is the predator community composition, with ephemeral ponds having few predators, temporary ponds characterized by odonate predators, and permanent ponds characterized by predatory fish (Gunzburger and Travis, 2004; Wellborn et al., 1996; Werner and McPeck, 1994). Predation influences the distribution of prey species across the gradient, with a general shift from larger, more active to smaller, less active prey species as hydroperiod increases (Wellborn et al., 1996). Predation may also interact with competition through a trade-off in predator avoidance and competitive ability: actively foraging species tend to be competitively dominant but also suffer higher predation rates than less mobile, competitively inferior species (Kats et al., 1988; Morin,

1983; Skelly, 1995; Wilbur, 1997). Predator density may increase or decrease across the hydroperiod gradient (Gunzburger and Travis, 2004; Skelly, 1995). In addition to predation and competition, other environmental factors may covary across this habitat gradient, including primary production and water chemistry, and these factors may have opposing effects on different species (Wellborn et al., 1996; Werner and Anholt, 1996; Whiles and Goldowitz, 2001). Understanding the role of these factors in the distribution of species across this gradient requires detailed experimental interspecific comparisons in order to tease apart the hypothesized reasons for habitat segregation. Mechanisms resulting in habitat segregation of closely-related species may be difficult to detect because these species are often ecologically very similar. Studies of competing species have demonstrated that species employ various mechanisms, including niche partitioning, to reduce interspecific competition (Krivan and Sirot, 2002; MacArthur, 1958; Schoener, 1968).

The effects of predation and competition across the hydroperiod have been extensively studied in anuran larvae because there are several groups of closely-related taxa that

¹ PRESENT ADDRESS: Nokuse Plantation, 13292 Co Hwy 3280, Bruce, Florida 32455, USA.

² CORRESPONDENCE: e-mail, gunzburger@nokuse.org

occur across this gradient (Kats et al., 1988; Morin, 1983; Skelly, 1995; Wellborn et al., 1996). To determine if anuran larval phenotype is more similar between closely-related species or species that share similar habitats, Richardson (2001a) calculated Euclidean distances between tadpoles of several anuran taxa using standardized trait values. In 22 within-family but different-habitat taxa comparisons of species pairs, only 2 comparisons found taxa to be more phenotypically similar than predicted by chance: *Hyla cinerea* was more similar to *Hyla squirella* and *Hyla gratiosa*.

These species present an interesting system in which to evaluate the factors contributing to habitat segregation because despite their similarities, the two most closely-related species, *H. cinerea* and *H. gratiosa*, show strong habitat segregation. *Hyla cinerea* occurs in permanent ponds while *H. gratiosa* occurs in long-hydroperiod, but fishless, temporary ponds (Gunzburger, 2005; Hedges, 1986; Lamb and Avise, 1987; Maxson and Wilson, 1975; Mount, 1975). *Hyla gratiosa* tadpoles have a relatively deeper tail fin, grow to larger sizes, and have longer larval periods than *H. cinerea* (Leips and Travis, 1994; Leips et al., 2000). *Hyla cinerea* is the only species of its genus in the southeastern United States that regularly breeds in large permanent ponds with fish predators (Mount, 1975; Richardson, 2001b).

Previous studies of *H. cinerea* and *H. gratiosa* have demonstrated that these species do not differ in traits associated with competitive ability which might be expected to differ for species inhabiting different habitat types (Leips and Travis, 1994; Leips et al., 2000). Neither species shows an adaptive response to pond drying, such as increased rate of metamorphosis, as may be expected for the temporary pond breeder, *H. gratiosa* (Leips et al., 2000). In addition, both species have similar levels of larval plasticity in response to changing food levels (Leips and Travis, 1994). Richardson's (2001a) study demonstrated similarities between *H. cinerea* and *H. gratiosa* in phenotypic traits associated with predator avoidance, yet other studies have suggested that predation rates differ for these species. *Hyla cinerea* tadpoles face higher

predation pressure in temporary ponds than permanent ponds (Gunzburger and Travis, 2004), and each species of tadpole has higher survival with the dominant predator type it encounters in nature (Blouin, 1990; Gunzburger, 2005). The objective of this study was to evaluate the relative roles of competition and environmental habitat characteristics on the habitat distribution of *H. cinerea* and *H. gratiosa* using a field reciprocal transplant experiment. Each species of tadpole is predicted to have higher performance under the conditions of its natural habitat type.

MATERIALS AND METHODS

Study Sites

I performed a reciprocal transplant experiment to evaluate the influence of competition and habitat characteristics on the performance of larval *H. cinerea* and *H. gratiosa*. I used two pairs of temporary and permanent ponds, one pair at Pebble Hill Plantation in southern Grady Co., Georgia, U.S.A.: 7-Up Pond (temporary, 30.774 N, 84.096 W) and Beaver Pond (permanent, 30.785 N, 84.089 W), and two ponds at Lake Jackson in northern Leon Co., Florida: Cool View Pond (temporary, 30.524 N, 84.355 W) and Little Lake Jackson (permanent, 30.526 N, 84.359 W). The ponds differed in plant communities and underlying soil type. Both Pebble Hill ponds had clay soil substrates. 7-Up Pond had buttonbush (*Cephalanthus occidentalis*), almost no submergent aquatic vegetation, and a layer of leaf litter on the bottom; Beaver Pond had water lilies (*Nymphaea odorata*), bog rush (*Juncus* sp.), and maidencane (*Panicum* sp.). The substrate at the two Lake Jackson ponds was comprised of organic sediment over sand; Little Lake Jackson had duck potato (*Sagittaria lancifolia*) and invasive exotic water hyacinth (*Eichhornia crassipes*) and water fern (*Salvinia* sp.); Cool View Pond was completely dominated by duckweed (*Lemna valdiviana*) and the invasive exotic submergent macrophyte *Hydrilla verticillata*.

I evaluated the potential biotic and abiotic differences between these ponds to provide correlations to any observed differences in tadpole response variables. I quantified predator community composition in the four ponds

during the experiment on 1 July 2004 using a 0.5 m² aluminum box sampler (Gunzburger and Travis, 2004). The two temporary ponds contained invertebrate tadpole predators (libellulid odonates, notonectids, and crayfish) but no fish, while the two permanent ponds contained both invertebrate predators (including libellulid odonates) and fish (Centrarchidae, Fundulidae, and Poeciliidae). I also attempted to quantify productivity at each pond using algae growth plates (Aresco, 2005), but water level fluctuations prevented accurate measurements. However, based on preliminary results, algae and periphyton growth rate appeared to be higher in the two permanent ponds than in the temporary ponds in this study. Cool View Pond receives significant input of runoff from a nearby residential community.

Reciprocal Transplant Experiment

At each pond, there were three replicate blocks of three tadpole treatments: 20 *H. cinerea* tadpoles, 20 *H. gratiosa* tadpoles and 10 *H. cinerea* and 10 *H. gratiosa* combined, a total of nine cages in each of four ponds, for a grand total of 36 cages. Previous studies have shown that at the densities used in this experiment (56 tadpoles/m², 0.093 tadpoles/l), as well as at lower densities, tadpoles of several species show effects of competition (Gascon and Travis, 1992; Travis and Trexler, 1986; Warner et al., 1993). The substitutive design of this experiment evaluates the competitive equivalence of these species across the habitat gradient by holding tadpole density constant in all treatments. Cages were constructed of fiberglass window screen (2-mm mesh) sewn into a tall cube with mesh on all six sides (60 cm on a side, 90 cm tall) and supported with frames made of PVC pipes. The frames held the cages with the mesh bottom flush with the pond substrate and kept the top of the cage well above the water level to allow tadpoles to surface and breathe air and metamorphs to emerge. The mesh window screen allowed free flow of water into the cages so tadpoles were exposed to competitor and predator chemical cues present in each pond. The top of each cage was attached with Velcro to allow cages to be opened and resealed during censuses. Cages

were placed into ponds 2 June 2004 at Little Lake Jackson, 3 June 2004 at Cool View Pond, and 9 June 2004 at 7-Up Pond and Beaver Pond. Water levels in ponds fluctuated throughout the course of this experiment and cages were moved as necessary to maintain a water depth of 50–80 cm. Cages were not stocked with vegetation from the ponds to prevent introduction of predators or other tadpoles into the cages.

Amplexed pairs of *H. cinerea* and *H. gratiosa* were collected in the early morning of 16 June 2004 to provide eggs to raise into tadpoles for the experiment. In order to avoid confounding local adaptation to a specific pond with my experimental treatments, I did not collect adults from the localities to be used for the caging experiment. I collected four *H. gratiosa* pairs from Kit Pond (30.375 N, 84.371 W) and six *H. cinerea* pairs from Innovation Pond (30.324 N, 84.324 W), both over 10 km from the ponds in the experiment. Amplexed pairs were maintained overnight in buckets filled with well water in which to oviposit eggs. After oviposition, all eggs from each species were mixed and transferred to three large aquaria (76 cm × 32 cm × 46 cm) at the Florida State University greenhouse facility in Tallahassee, Leon Co., FL, U.S.A. Partial water changes were performed daily and tadpoles were fed a mixture of ground rabbit chow and fish flakes ad libitum after hatching. Tadpoles were haphazardly selected, counted, and stocked into cages on 29 June 2004 at Pebble Hill and 30 June 2004 at Lake Jackson.

Ten censuses were performed throughout the experiment, every five to seven days, to monitor tadpole survival, remove metamorphs, and remove any nonexperimental animals that had invaded the cages. Very few nonexperimental animals were found in the cages, and those that did invade, including odonate naiads, fish (*Heterandria formosa*), crawfish, leeches, and hatchling tadpoles (*Hyla femoralis*), were very small in size and thus probably did not interact with the tadpoles in the experiment. Metamorphs (identified as having at least one front leg emerged, stage 42, Gosner, 1960) were removed from each cage and returned to the laboratory. Upon completion of metamorpho-

sis (defined as complete tail resorption), each metamorph was patted dry with a paper towel, weighed, and released at the pond from which amplexed pairs were collected for that species. The experiment ended on 6 September 2004 when all surviving tadpoles had completed metamorphosis. Three response variables were recorded for each cage at the end of the experiment: proportion tadpoles surviving to metamorphosis, \bar{x} larval period (days between oviposition on 16 Jun 2004 and complete tail resorption), and \bar{x} size at metamorphosis (g).

This experiment crossed three levels of a tadpole treatment within a pond with a hierarchical organization of pond effects. The highest level of pond effect was geographic location, Pebble Hill or Lake Jackson, which is a random effect because there are many groups of permanent and temporary ponds throughout the landscape. Habitat type, temporary or permanent, nested within geographic location, is a fixed effect because each geographic location contains one pond of each habitat type. Within each habitat type are three blocks, and within each block are the two tadpole treatments: single or combined species. Survival data were analyzed comparing the two tadpole species, but because these two species were known a priori to differ in both size and larval period length, size at metamorphosis and larval period were analyzed separately within each tadpole species.

Proportion of tadpoles surviving was first compared using ANOVA with tadpole species, habitat type, and the interaction term as main effects. Habitat type and habitat type \times tadpole species were nonsignificant in this analysis, so the interaction term was removed from the analysis and geographic location was added as a main effect. Second, for each species separately, size at metamorphosis and larval period length was compared using ANOVA. The main effects were treatment (single or combined species), habitat type, and geographic location. The interaction effect of treatment by habitat type determined if the interactions of the two species vary by habitat type. The block nested within habitat type nested within geographic location identified any block effects for each variable. The analysis was modified for *H. gratiosa* due to

100% mortality of this species at Cool View Pond within the first nine days of the experiment. Size at metamorphosis and larval period were compared with an ANOVA with main effects of treatment (single or combined species), habitat type, geographic location and an interaction effect of treatment by habitat type. To examine the potential covariation of the response variables, I conducted linear regression analyses to determine if there was a relationship between proportion surviving and size at metamorphosis or larval period for each species. Because this was a substitutive experiment, this analysis also allowed me to determine if any differences in response variables in single and combined treatments is due simply to a change in density of conspecifics or a change in density of heterospecifics. To better fit the assumptions of normality, data for proportion surviving were subjected to arcsin-square-root transformation and size at metamorphosis and larval period were subjected to natural-logarithm transformation before analysis.

RESULTS

Growth and survival of tadpoles varied widely across treatments, pond types, and geographic locations (Fig. 1). Survival of *H. cinerea* (overall \bar{x} survival = 0.63 ± 0.06) was significantly higher than survival of *H. gratiosa* (0.42 ± 0.07) (ANOVA $F_{1,44} = 6.32$, $P = 0.016$) (Fig. 1, Table 1). In 8 cages, all *H. gratiosa* tadpoles died (6 of which were at Cool View Pond), whereas 2 cages of *H. cinerea* experienced 100% mortality. There was no significant effect of habitat type or habitat type \times tadpole species interaction as would be expected if each species has higher survival in its natural habitat type. Tadpole survival was higher in the Pebble Hill ponds than at the Lake Jackson ponds (ANOVA $F_{1,44} = 4.29$, $P = 0.044$).

Overall, larval period of *H. gratiosa* was longer and size at metamorphosis was larger than for *H. cinerea* (Fig. 1). However, larval period and size at metamorphosis were influenced by different factors for the two species. *Hyla cinerea* tadpoles were larger at metamorphosis and had longer larval periods in temporary ponds relative to permanent ponds (Fig. 1, Table 2). In addition, there was

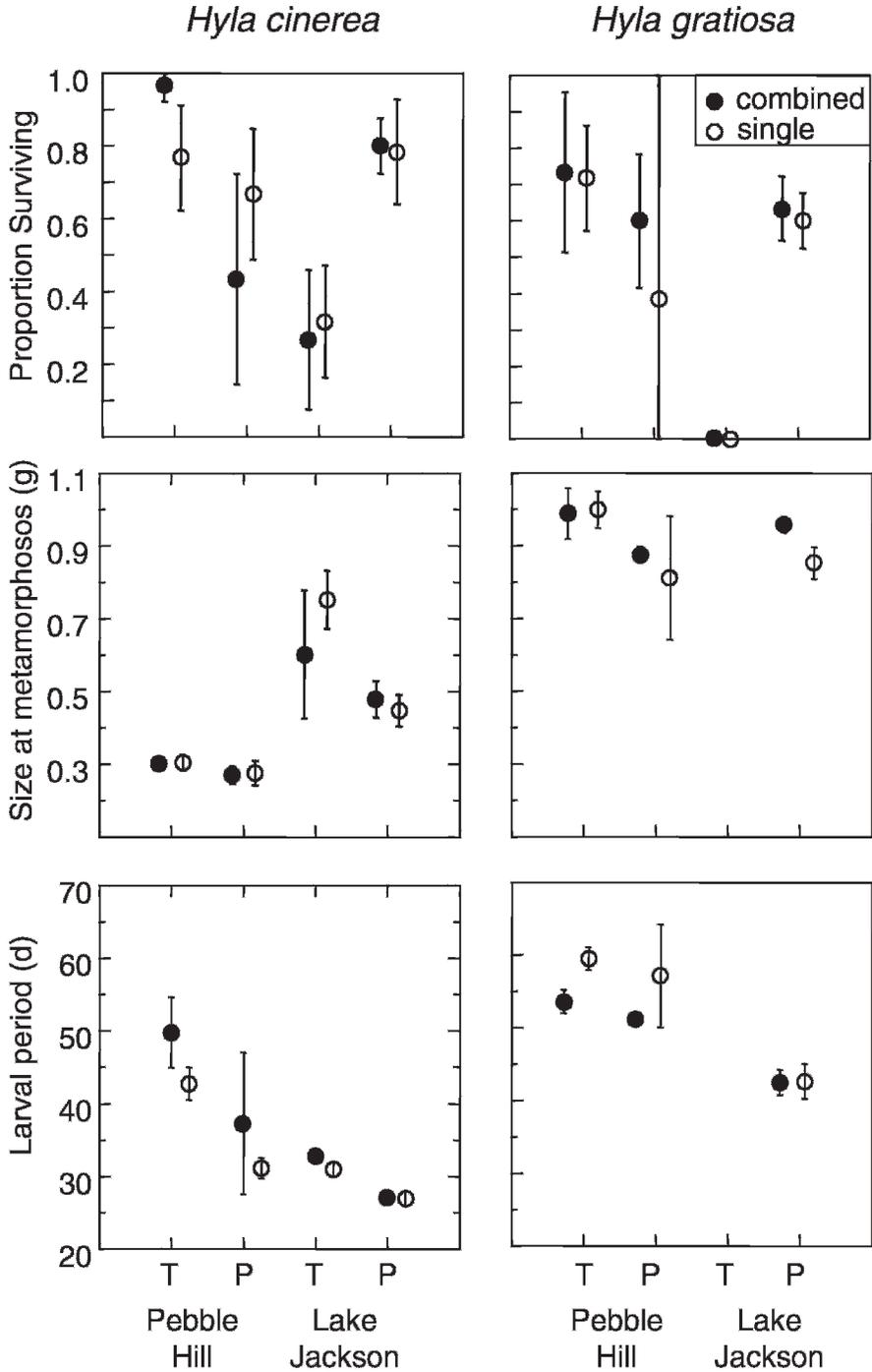


FIG. 1.—Proportion surviving, size at metamorphosis, and larval period of *Hyla cinerea* and *H. gratiosa* in four localities, temporary (T) and permanent (P) ponds at Pebble Hill and Lake Jackson, in combined (both species) and single (one species) treatments. Each dot is the mean of the three cages in that treatment at that pond with standard error.

TABLE 1.—ANOVA results for proportion surviving (subjected to arcsin-square-root transformation) of *Hyla cinerea* and *H. gratiosa* in the reciprocal transplant experiment.

Source	Survival ($n = 48$)				
	SS	df	MS	F-ratio	P
Species	1.23	1	1.23	6.32	0.016
Habitat type	0.20	1	0.20	1.02	0.318
Geographic location	0.83	1	0.83	4.29	0.044
Error	8.55	44	0.19		

a significant effect of geographic location on *H. cinerea* tadpoles, with tadpoles from Lake Jackson ponds having larger size at metamorphosis and shorter larval periods than those from Pebble Hill ponds (Fig. 1, Table 2). There was also a marginally significant treatment effect on larval period: *H. cinerea* tended to have longer larval periods when raised with *H. gratiosa*. *Hyla gratiosa* tadpoles were significantly larger in temporary ponds relative to permanent ponds and had longer larval periods in single species treatments relative to combined species treatments (Fig. 1, Table 3). Thus, when raised together in combined species treatments, *H. cinerea* has a longer larval period and *H. gratiosa* has a shorter larval period relative to their respective single species treatments. There was also evidence of geographic variation in performance of *H. gratiosa* tadpoles, with longer larval period at Pebble Hill than at Lake Jackson (Table 3).

TABLE 2.—ANOVA results for *Hyla cinerea* in the reciprocal transplant experiment, data subjected to ln transformation.

Source	Size at Metamorphosis ($n = 22$)				
	SS	df	MS	F-ratio	P
Treatment	0.01	1	0.01	0.50	0.498
Habitat type	0.22	1	0.22	11.4	0.010
Geographic location	1.93	1	1.93	100	0.000
Treatment × Habitat type	0.05	1	0.05	2.4	0.160
Treatment × Geographic location	0.02	1	0.02	0.92	0.365
Block(Habitat type(Geographic location))	0.21	8	0.03	1.38	0.331
Error	0.15	8	0.02		
Source	Larval Period ($n = 22$)				
	SS	df	MS	F-ratio	P
Treatment	0.06	1	0.06	4.97	0.056
Habitat type	0.25	1	0.25	21.9	0.002
Geographic location	0.45	1	0.45	39.0	0.000
Treatment × Habitat type	0.00	1	0.00	0.00	0.993
Treatment × Geographic location	0.03	1	0.03	2.19	0.177
Block(Habitat type(Geographic location))	0.03	8	0.004	0.35	0.923
Error	0.091	8	0.01		

Linear regression analyses indicated that the only significant covariation in response variables was a negative relationship between size at metamorphosis and proportion surviving for *H. cinerea* (Fig. 2). Addition of survival as a factor into the ANOVA of size at metamorphosis for this species did not alter the results. The decrease in *H. gratiosa* larval period in the combined species treatments could be either due to a response to the decrease in density of conspecifics (from 20 total *H. gratiosa* to 10) or an increase in the density of *H. cinerea* (from 0 to 10) (Smith, 2005). However, the correlation between *H. gratiosa* larval period and the total number of *H. gratiosa* surviving in each cage across all treatments was not significant ($r^2 = 0.025$, $P = 0.56$, $n = 16$; Fig. 2).

DISCUSSION

The results of this field reciprocal transplant experiment provide evidence that each species has higher performance in its natural habitat type. Tadpoles of both species were found to be capable of surviving to metamorphosis in both pond types while exposed to ambient competitor and predator cues. However, *H. cinerea* had higher survival overall than *H. gratiosa*, and *H. gratiosa* tended to transform later and at larger sizes than *H. cinerea* in both pond types. Both species of treefrog metamorphosed at larger sizes in temporary ponds, and *H. cinerea* had

TABLE 3.—A summary of ANOVA results for *Hyla gratiosa* in the reciprocal transplant experiment, data subjected to ln transformation.

Size at Metamorphosis ($n = 16$)					
Source	SS	df	MS	F-ratio	P
Treatment	0.01	1	0.01	1.30	0.279
Habitat type	0.07	1	0.07	11.17	0.007
Geographic location	0.01	1	0.01	2.08	0.177
Treatment \times Habitat type	0.01	1	0.01	2.13	0.173
Error	0.07	11	0.01		
Larval Period ($n = 16$)					
Treatment	0.02	1	0.02	6.22	0.030
Habitat type	0.01	1	0.01	1.42	0.259
Geographic location	0.14	1	0.14	40.12	0.000
Treatment \times Habitat type	0.003	1	0.003	0.97	0.347
Error	0.04	11	0.003		

a longer larval period in temporary ponds. Larger size at metamorphosis in amphibians is generally positively correlated with increased post-metamorphic fitness, including increased juvenile survival, decreased time to maturity, and increased reproductive success (Semlitsch et al., 1988). Thus both species of treefrogs appear to have higher performance in temporary ponds. However, *H. cinerea* takes 10 d longer to metamorphose in temporary ponds than permanent ponds and thus is potentially exposed to predation for a longer period of time. Previous research has shown that *H. cinerea* can be expected to suffer much higher predation rates in temporary ponds than permanent ponds due to the high density of predatory odonate naiads (Gunzburger and Travis, 2004). Tadpoles are sensitive to waterborne cues and have been demonstrated to alter foraging rates and activity levels in response to chemical cues from nearby predators (Werner, 1991; Werner and Anholt, 1996). It may be that *H. cinerea* tadpoles do not recognize predator cues in temporary ponds as readily as those in permanent ponds, and thus do not begin metamorphosis immediately once a minimum size has been reached. *Hyla gratiosa* are larger at metamorphosis in temporary ponds, but the larval period is similar in both pond types. Therefore *H. gratiosa* tadpoles have higher growth rates in temporary ponds, indicating they may better assimilate nutrients in temporary ponds than permanent ponds.

Tadpoles of *Hyla gratiosa* appear to be stronger competitors than those of *H. cinerea*.

Hyla cinerea tadpoles tended to have longer larval periods when raised with *H. gratiosa* relative to with conspecifics, while *H. gratiosa* tadpoles reached larger sizes at metamorphosis when raised with *H. cinerea* instead of conspecifics. This difference was not merely due to a decrease in density of conspecifics, because size at metamorphosis was unrelated to total number of *H. gratiosa* surviving in each cage (Fig. 2). In addition, size at metamorphosis for *H. cinerea* decreased with increased tadpole density (Fig. 2). Thus, for *H. gratiosa*, the effect of one *H. cinerea* tadpole is less than the effect of one *H. gratiosa* tadpole, but for *H. cinerea*, the effect of one *H. gratiosa* tadpole is greater than the effect of one *H. cinerea* tadpole.

The relative roles of predation and competition in the habitat distribution of anuran larvae has been the subject of considerable research. Most studies concluded that a combination of these factors through a trade-off in competitive ability and predator avoidance allows anuran species to partition habitat (Skelly, 1995; Werner, 1991; Werner and Anholt, 1996). These two closely-related species of treefrogs are found as larvae in distinct habitat types and each species has somewhat higher survival with the predator regime of its natural habitat type (Blouin, 1990; Gunzburger, 2005). However, these species also share many phenotypic traits that might be expected to influence survival differentially in the two habitat types (Leips et al., 2000; Leips and Travis, 1994; Richardson, 2001a). This field study, although limited

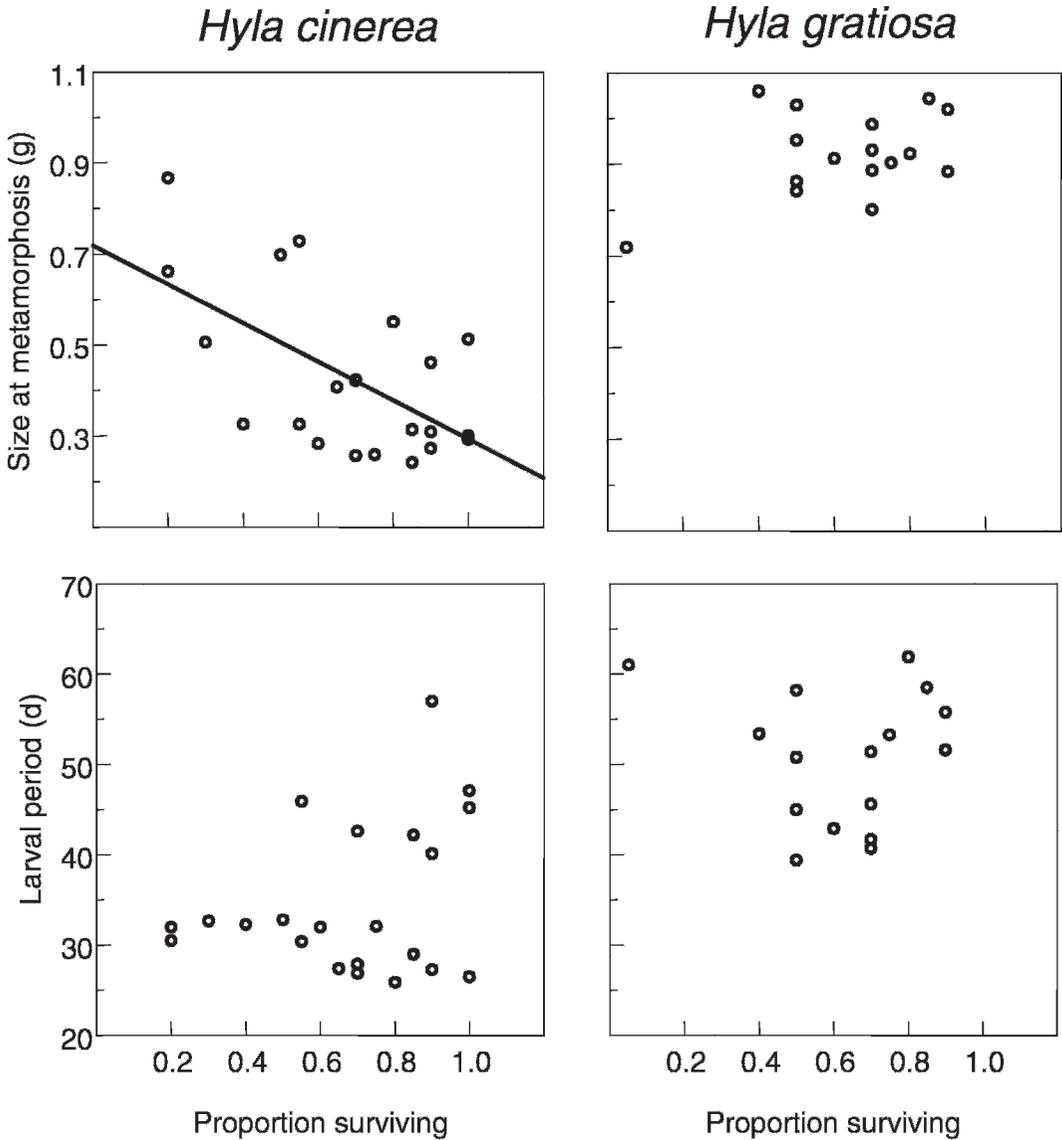


FIG. 2.—Relationship between proportion surviving and size at metamorphosis and larval period for *H. cinerea* and *H. gratiosa*. Each dot is the result from one cage. Linear regression analysis of each plot revealed one significant relationship indicated by the line in the upper left panel ($r^2 = 0.25$, $P = 0.018$, $n = 22$).

in power due to small sample size, in combination with previous mesocosm experiments (Gunzburger, 2005; Gunzburger and Travis, 2004) suggests that the habitat distributions of these two species are influenced by different factors. *Hyla cinerea* has a relatively short larval period resulting in smaller size at metamorphosis, which suggests that its primary antipredator adaptation in permanent

ponds may be to escape the larval habitat as soon as possible. Moreover, a combination of high densities of odonate predators and competitive inferiority to *H. gratiosa* likely keeps *H. cinerea* from temporary ponds. In contrast, *H. gratiosa* has a longer larval period and achieves much larger sizes at metamorphosis. Predation by fish likely keeps *H. gratiosa* out of permanent ponds (Gunzbur-

ger, 2005). This study presents, by necessity, an oversimplified system of direct comparisons of performance of two sister taxa of hylid treefrogs without considering the direct effects of predators or other competitors. In reality, temporary ponds in the southeastern United States are often occupied by many additional anuran species, including at least four other species of hylids (*H. squirella*, *H. femoralis*, *H. chrysoscelis*, and *Acris gryllus*, Mount, 1975). The presence of these additional species may lend additional support to the conclusion of this study that *H. cinerea* avoids temporary ponds due to competitive exclusion. Numerous mesocosm studies have been conducted evaluating the interspecific interactions of anuran larvae, but fewer field studies exist, and none have captured the true complexity of natural systems. The effects of these additional species on the outcome of species interactions should be the subject of further research.

Acknowledgments.—I thank J. Travis for advice throughout this study and support through National Science Foundation grant DEB 99-03925. R. Fuller, R. Hale, and K. McGhee assisted in cage construction. J. Cox, C. Martin, and R. Masters of Tall Timbers Research Station provided access to Pebble Hill Plantation. E. Gunzburger, A. Deyle, and M. Aresco assisted during the field experiment. J. Travis, F. James and T. Miller provided helpful comments on earlier drafts of this manuscript. I acknowledge the support of the Amphibian Research and Monitoring Initiative of the United States Geological Survey during the preparation of this manuscript. Experiments were performed under FSU ACUC Protocol #0115.

LITERATURE CITED

- ARESCO, M. J. 2005. Ecological relationships of turtles in northern Florida lakes: A study of omnivory and the structure of a lake food web. Ph.D. Dissertation, Florida State University, Tallahassee, Florida, U.S.A.
- BLOUIN, M. S. 1990. Evolution of palatability differences between closely-related treefrogs. *Journal of Herpetology* 24:309–311.
- GASCON, C., AND J. TRAVIS. 1992. Does the spatial scale of experimentation matter? A test with tadpoles and dragonflies. *Ecology* 73:2237–2243.
- GOSNER, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* 16:183–190.
- GUNZBURGER, M. S. 2005. Differential predation on tadpoles influences the potential effects of hybridization between *Hyla cinerea* and *Hyla gratiosa*. *Journal of Herpetology* 39:682–687.
- GUNZBURGER, M. S., AND J. TRAVIS. 2004. Evaluating predation pressure on green treefrog larvae across a habitat gradient. *Oecologia* 140:422–429.
- HEDGES, S. B. 1986. An electrophoretic analysis of Holarctic frog evolution. *Systematic Zoology* 35:1–21.
- KATS, L. B., J. W. PETRANKA, AND A. SIH. 1988. Antipredator defenses and the persistence of amphibian larvae with fishes. *Ecology* 69:1865–1870.
- KRIVAN, V., AND E. SIROT. 2002. Habitat selection by two competing species in a two-habitat environment. *American Naturalist* 160:214–234.
- LAMB, T., AND J. C. AVISE. 1987. Morphological variability in genetically defined categories of anuran hybrids. *Evolution* 41:157–165.
- LEIPS, J., AND J. TRAVIS. 1994. Metamorphic responses to changing food levels in two species of Hylid frogs. *Ecology* 75:1345–1356.
- LEIPS, J., M. G. McMANUS, AND J. TRAVIS. 2000. Response of treefrog larvae to drying ponds: Comparing temporary and permanent pond breeders. *Ecology* 81:2997–3008.
- MACARTHUR, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* 36:533–536.
- MAXSON, L. R., AND A. C. WILSON. 1975. Albumin evolution and organismal evolution in tree frogs (Hylidae). *Systematic Zoology* 24:1–15.
- MORIN, P. J. 1983. Predation, competition, and the composition of larval anuran guilds. *Ecological Monographs* 53:119–138.
- MOUNT, R. H. 1975. *The Reptiles and Amphibians of Alabama*. Auburn Printing Co., Auburn, Alabama, U.S.A.
- MURPHY, C. G. 1994. Chorus tenure of male barking treefrogs, *Hyla gratiosa*. *Animal Behaviour* 48:763–777.
- RICHARDSON, J. M. L. 2001a. The relative roles of adaptation and phylogeny in determination of larval traits in diversifying anuran lineages. *American Naturalist* 157:282–299.
- RICHARDSON, J. M. L. 2001b. A comparative study of activity levels in larval anurans and response to the presence of different predators. *Behavioral Ecology* 12:51–58.
- SCHOENER, T. W. 1968. The *Anolis* lizards of Bimini: Resource partitioning in a complex fauna. *Ecology* 49:704–726.
- 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.
- SKELLY, D. K. 1995. A behavioral trade-off and its consequences for the distribution of *Pseudacris* treefrog larvae. *Ecology* 76:150–164.
- SMITH, K. G. 2005. Effects of nonindigenous tadpoles on native tadpoles in Florida: Evidence of competition. *Biological Conservation* 123:433–441.
- TRAVIS, J., AND J. C. TREXLER. 1986. Interactions among factors affecting growth, development, and survival in experimental populations of *Bufo terrestris* (Anura: Bufonidae). *Oecologia* 69:110–116.
- WARNER, S. C., J. TRAVIS, AND W. A. DUNSON. 1993. Effect of pH variation on interspecific competition between two species of hylid tadpoles. *Ecology* 74:183–194.
- 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.
- WERNER, E. E. 1991. Nonlethal effects of a predator on competitive interactions between two anuran larvae. *Ecology* 72:1709–1720.
- WERNER, E. E., AND B. R. ANHOLT. 1996. Predator-induced indirect effects: Consequences to competitive interactions in anuran larvae. *Ecology* 77:157–169.
- WERNER, E. E., AND M. A. MCPEEK. 1994. Direct and indirect effects of predators on two anuran species across an environmental gradient. *Ecology* 75:1368–1382.
- WHILES, M. R., AND B. S. GOLDOWITZ. 2001. Hydrologic influences on insect emergence production from central Platte River wetlands. *Ecological Applications* 11:1829–1842.
- WILBUR, H. M. 1997. Experimental ecology of food webs: Complex systems in temporary ponds. *Ecology* 78:2279–2302.

Accepted: 23 April 2007
Associate Editor: Dean Adams