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NATIVE WHITE-LIPPED FROG LARVAE (*LEPTODACTYLUS ALBILABRIS*) OUTCOMPETE INTRODUCED CANE TOAD LARVAE (*RHINELLA MARINA*) UNDER LABORATORY CONDITIONS

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Abstract.—**Invasive species are a major focus within conservation biology. The widely introduced Cane Toad, *Rhinella marina*, has attracted particular interest in studies of the effects of invasive species on native communities. In this study, we examined the effects of competition with invasive Cane Toad larvae on the growth, development, and survival of native White-lipped Frog (*Leptodactylus albilabris*) larvae. We conducted two experiments; the first was a food calibration experiment to determine appropriate high and low food concentrations, and the second was a competition experiment in which we varied species compositions and food availability. In the food calibration experiment, lower food levels reduced the survival of both species. In the competition experiment, the presence of *R. marina* reduced the proportion of *L. albilabris* that survived to metamorphosis under the high food treatment. Otherwise, the introduced species had little negative impact on the native species. In contrast, larvae of *R. marina* experienced severe reductions in growth and survival in the presence of *L. albilabris*. Significant effects of the presence of *L. albilabris* on *R. marina* development were observed as early as the first two weeks, and continued up to metamorphosis. We conclude that *L. albilabris* larvae outcompete *R. marina* larvae when their numbers are approximately equal. Adaptations to life in ephemeral habitats may have provided *L. albilabris* with a competitive advantage over *R. marina*. Further studies are needed to determine if these patterns persist under natural conditions.**

Key Words.—*Bufo marinus*; competition; food availability; introduced species; invasive species; tadpoles

INTRODUCTION

Invasive species are a significant threat to biodiversity. Introduced species disturb native ecosystems and may have detrimental effects on native biota (Lampo and De Leo 1998; Crossland 2000; Mack et al. 2000). Invasive species can also modify inter- and intraspecific interactions in native species through both direct and indirect mechanisms (Crossland 2000; Crossland et al. 2008; Pizzatto and Shine 2009; Crossland et al. 2009). Although invasive species are known for their devastating effects on populations, communities, and ecosystems, many reports of such effects are based on circumstantial evidence (Crossland 2000; Mack et al. 2000). Little is known about the mechanisms by which invasive species impact native species, and a detailed understanding of these mechanisms is needed to improve conservation efforts (Smith 2005; Crossland et al. 2008, 2009; Pizzatto and Shine 2009; Crossland and Shine 2010).

Invasive species may impact native species by means of interspecific competition if their niches overlap. Niche overlap is particularly common in amphibians that undergo metamorphosis because they appear to be limited in their use of breeding sites by abiotic and biotic constraints on their larvae (Dayton and Fitzgerald 2001; Crawford et al. 2009). Smith (2005) reported that tadpole communities are frequently characterized by high population densities in temporally and spatially restricted aquatic habitats, making them vulnerable to competition with invasive species.

The Cane Toad, *Rhinella marina* (also known as *Bufo marinus*), is an invasive species that has attracted substantial interest among herpetologists and conservation biologists. Several traits appear to have contributed to the success of *R. marina* as an invader. Females can lay up to 35,000 eggs in long strings that hatch after approximately 36 hours (Rivero 1998). Tadpoles metamorphose from between 16 days (Crossland et al. 2009) to eight weeks post-hatching (Zug and Zug 1979). It has been suggested that they are aggressive feeders, a trait that may provide a competitive advantage (Alford 1999). Indeed, they are highly cannibalistic on conspecific eggs (Crossland and Shine 2011). They are also toxic (Crossland 2000; Smith 2005; Pizzatto and Shine 2009) and adaptable (Zug and Zug 1979). Larval characteristics of *R. marina* such as potential competition with native species (Smith 2005), toxicity of eggs (Crossland et al. 2008; Crossland and Shine 2010), and toxicity of larvae (Crossland 2000) suggest that this species may impact native tadpole communities (Smith 2005). It is not surprising, then, that several studies have examined the effects of *R.*

marina on native amphibians (Williamson 1999; Crossland et al. 2008; Cabrera-Guzmán et al. 2013a, 2013b; Shine 2013). The Cane Toad was introduced to Puerto Rico from Jamaica and Barbados in 1920, 1924, and 1926 as a biological control agent for May beetles (*Phyllophaga* spp.; Rivero 1998). In spite of its potential to harm native animals, there is scarce information concerning its impact on native herpetofauna in Puerto Rico, particularly in the larval phase. Platenberg (2007) mentions that tadpoles probably compete for limited freshwater resources with the White-lipped Frog, *Leptodactylus albilabris* (Anura: Leptodactylidae), but no studies have been conducted to evaluate this hypothesis.

Leptodactylus albilabris is native to Puerto Rico and the U.S. and British Virgin Islands (Henderson and Powell 2009). Tadpoles of this species hatch in approximately four days from eggs laid in terrestrial foam nests. Larvae develop in temporary ponds or channels after being washed away by water runoff during heavy rains (Rivero 1998). Metamorphosis occurs from 21 to 35 days after hatching (Dent 1956; Joglar 2005). In Puerto Rico, both *R. marina* and *L. albilabris* breed throughout the year, with peaks of activity during the wet season (June-November; Rivero 1998). Although *Leptodactylus albilabris* is one of the most abundant anurans in Puerto Rico, studies of its larval development are scarce. Existing reports describe its larval metabolism (Candelas et al. 1961), heat tolerance (Heatwole et al. 1968), and tolerance to salinity (Ríos-López 2008). In Puerto Rico, this is the only native anuran species that is not endangered and possesses a larval stage (Rivero 1998), making it the ideal species for testing the impacts of *R. marina* on native anuran larvae.

We conducted laboratory experiments to assess the impact of larval *R. marina* on the growth, development, and survival of larval *L. albilabris*. First, we determined the relationship between food availability and survival for each species separately (hereafter, the "food calibration experiment"). Next, we tested the effects of food availability and species composition on larval growth and development ("competition experiment"). We tested whether competition with *R. marina* larvae negatively affected the growth, development, and survival of larval *L. albilabris*. If the effect was mediated by competition for food, we predicted it would be stronger when food was limited.

MATERIALS AND METHODS

Tadpole collection and aquarium design.—We collected tadpoles of both species from wild populations in and around Caguas, Hormigueros, Mayagüez, and Añasco, Puerto Rico, at an early developmental stage (Gosner stage 25; Gosner 1960). We kept tadpoles in Sterilite® plastic containers (Sterilite Corporation, Fitchburg, Massachusetts, USA; 34.3 cm × 20.3 cm × 12.7 cm; 5.7 L) filled with 2 L of aged tap water. We cut 5 mm holes in the topmost part of the container to prevent water from overflowing during rainfall. Hagen Elite © fish-tank air pumps (Hagen Inc., Montreal, Quebec, Canada) maintained oxygen levels. We removed the center of the lid and replaced it with metallic screening. We cleaned each aquarium every three days to prevent accumulation of metabolic waste and colonization of potential food resources (e.g., algae). Throughout the experiment, aquaria sat on a shelving unit in a covered balcony, where they were exposed to ambient light cycles and temperature. We changed their locations every three days to balance position among treatment groups.

Food calibration experiment.—We conducted the food calibration experiment over 88 days, spanning May through August 2011. The purpose of the food calibration experiment was to determine the relationship between food availability and tadpole survival under the conditions to be used in the competition experiment. We used the results to select a low food level that would result in ~45% survival and a high food level that would result in ~75% survival for the competition experiment.

We conducted the food calibration experiment separately for each of the two species. We used four treatments consisting of different amounts of tadpole chow (3:1 ground rabbit pellets (Alimentos Agronutre, Mayagüez, Puerto Rico; 17% protein) and commercial fish flakes (TetraFin®, Tetra Holding US, Inc.; 42% protein) following guidelines established by Smith (2005). Treatments were as follows: 0.12 g, 0.23 g, 0.45 g, and 0.90 g per aquarium. We applied tadpole chow to all treatments every three days. Tadpoles were assigned to treatments at Gosner stage 26–28 (Gosner 1960). Each aquarium (experimental unit) contained twelve tadpoles that were randomly assigned to one of the four experimental treatments. There were three replicates of each treatment for a total of 24 aquaria, 12 for *L. albilabris* and 12 for *R. marina*.

We monitored tadpoles daily for survival and metamorphosis, and recorded the number of individuals that had matured. Metamorphosis was defined as the emergence of both forelimbs (Gosner stage 42). We removed and documented metamorphosed and dead tadpoles.

We constructed sigmoidal regression models to determine the effect of food treatment on the response variable, percent matured, in each species. We chose a sigmoidal regression because we expected survivorship to be uniformly low below some threshold food level, to increase with food availability over intermediate levels of food, and to plateau at high food levels, as food availability ceased to be a limiting factor.

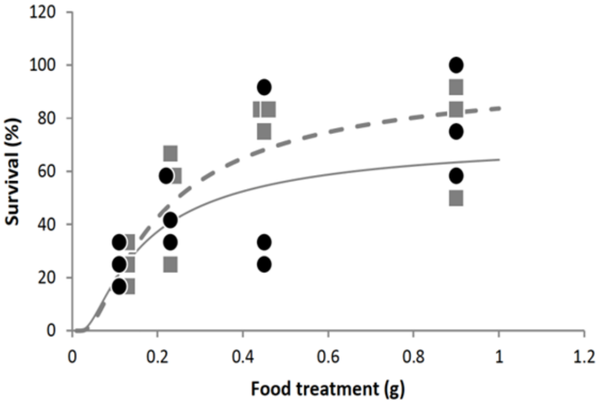

FIGURE 1. Food treatment effects on survival to metamorphosis for *Leptodactylus albilabris* (black circles) and *Rhinella marina* (gray squares) in the food calibration experiment. The trendlines were generated with sigmoidal regression (solid for *L. albilabris*; broken for *R. marina*). Some symbols have been offset so that all data are visible.

Competition experiment.—We conducted the competition experiment over 96 days spanning September 2011 to January 2012. At the beginning of the competition experiment, we randomly assigned tadpoles to one of eight experimental treatments following a 2 × 4 factorial design. The factors were food and species composition. Based on the results of the food calibration experiment, aquaria subjected to low food treatments received 0.23 g every three days, and those subjected to high food treatments received 0.68 g every three days. Species composition had four levels: 12 L: 0 R (12 *Leptodactylus* larvae and 0 *Rhinella* larvae), 0 L: 12 R, 6 L: 6 R, and 4 L: 8 R. We chose to run the 4 L: 8R treatment because *R. marina* are more fecund than *L. albilabris* (see Discussion), so we expected they would often occur at higher densities where the two species co-occur *in-situ*. We applied each of the eight experimental treatments to six replicates for a total of 48 aquaria (12 tadpoles per aquarium; 576 tadpoles in total). The independent sampling unit was the aquarium; therefore, we averaged individual-level data over each aquarium prior to analysis.

We determined Gosner stage, mass (g), and body length (mm) for each tadpole at the beginning of the experiment. For body length measurements, we placed tadpoles in a Petri dish with water over a ruler and photographed them. We then used these photos to determine total length and body length (excludes tail). After the beginning of the experiment, we measured Gosner stage, body length, and mass for each tadpole once a week and monitored tadpoles daily for survival and metamorphosis. Dead and metamorphosed tadpoles were measured and removed from the experiment.

We ran statistical analyses separately for each species. In addition to analyzing growth and development data taken at metamorphosis, we also analyzed data from the first two weeks of development because many *R. marina* died prior to metamorphosis (we refer to these data as "early" measures). Time to metamorphosis for *L. albilabris* was reciprocally transformed and early development for *R. marina* was squared so that the data conform to the assumption of normality. Other variables met the assumptions of parametric analysis. We used Pearson's correlation to compare the following dependent variables: Early mass, early total length, early body length, early development, early survival, mass at metamorphosis, total length at metamorphosis, body length at metamorphosis, time to metamorphosis, and percent matured. We identified groups of highly correlated variables (*Pearson's* $r \geq 0.6$) and retained one variable per group for further analysis. The retained variables were: Early mass, percent matured, mass at metamorphosis, and time to metamorphosis. For each species, we ran 2 × 3 full factorial General Linear Models (GLMs) to test for the effects of food availability, species composition, and their interaction on each of the response variables. When species composition was statistically significant, we ran post-hoc Ryan-Einot-Gabriel-Welsch Q (REGWQ) tests. All statistical analyses were conducted in SPSS (v. 17.0). Hypothesis tests used $\alpha = 0.05$.

RESULTS

Food calibration experiment.—There was a positive correlation between food availability and percent matured in both species (sigmoidal regression: *L. albilabris*, $r^2 = 0.488$, $F_{1,10} = 9.51$, $P = 0.012$; *R. marina*, $r^2 = 0.690$, $F_{1,10} = 22.30$, $P < 0.001$; Fig. 1). We used our sigmoidal regression models to estimate the amounts of food required for ~45% and ~75% survival to metamorphosis for use as "low food" and "high food" treatments, respectively. We selected 0.23 g of food as the low food treatment because it corresponded to predicted survival rates of 40.8% in *L. albilabris* and 47.6% in *R. marina*, which were very close to our original criterion of 45% survival. Our regression model predicted that only 54% of *L. albilabris* would survive under the 0.45 g treatment, which was too low for our high food treatment. Survival in both species was high at 0.90 g, but the water in some of the *R. marina* tanks showed signs of fouling. We therefore chose the intermediate value of 0.68 g for the high food treatment, which according to our models should result in 60.4% maturation for *L. albilabris* and 77.2% maturation for *R. marina*.

Competition experiment.—The response variables that we analyzed were statistically independent within species except for early mass and time to metamorphosis (reciprocally transformed) in *L. albilabris* (Pearson's correlation: $r = 0.717$, $N = 35$, $P < 0.001$). *Rhinella marina* suffered high mortality in the 6 L: 6 R aquaria,

TABLE 1. Results of GLM tests of the effects of food level and species composition on growth and development of *L. albilabris* larvae. Bold font denotes statistically significant results. Time to metamorphosis was reciprocally transformed prior to analysis to conform to the assumption of normality.

	Model			Food			Species Composition			Food * Species Interaction		
Dependent Variable	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*
Early mass	7.32	5,30	**< 0.001**	13.45	1,30	**0.001**	10.61	2,30	**< 0.001**	0.96	2,30	0.39
Percent matured	7.26	5,30	**< 0.001**	19.49	1,30	**< 0.001**	3.23	2,30	0.054	5.18	2,30	**0.012**
Mass at metamorphosis	0.88	5,29	0.51	0.99	1,29	0.33	1.62	2,29	0.22	0.027	2,29	0.97
Time to metamorphosis	17.13	5,29	**< 0.001**	45.54	1,29	**< 0.001**	12.07	2,29	**< 0.001**	6.92	2,29	**0.003**

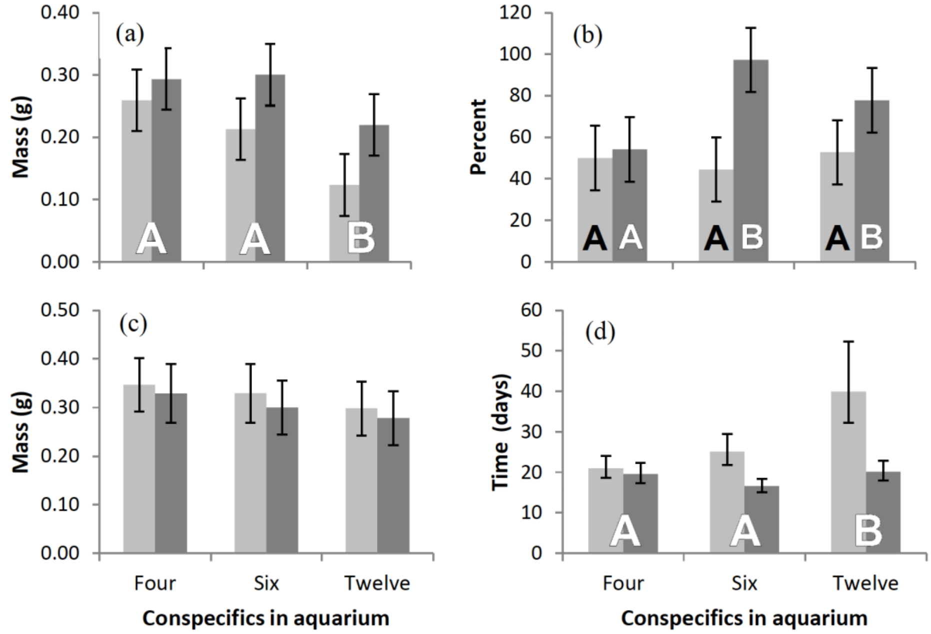

FIGURE 2. Bar graphs showing the development of *Leptodactylus albilabris* larvae as a function of food availability (light gray = low food; dark gray = high food) and species composition. Each aquarium held 12 individuals, comprising the number of *L. albilabris* indicated on the x-axis and 0−8 *Rhinella marina* larvae. The graphs show estimated marginal means and 95% confidence intervals of (a) mass measured at week two of the experiment, (b) percent of individuals that metamorphosed, (c) mass at metamorphosis, and (d) time to metamorphosis. We conducted post-hoc tests when omnibus tests were statistically significant. Letters indicate statistically distinct species composition treatments. Post-hoc tests on the percent of individuals that metamorphosed (b) were conducted separately for high food (open letters) and low food (solid letters) treatments.

so we did not analyze their time to metamorphosis or mass at metamorphosis for that treatment. On several occasions, we observed *L. albilabris* larvae eating dead *R. marina* larvae. Larval *L. albilabris* on the low food treatment exhibited lower early mass and percent matured, and a longer time to metamorphosis than those that received high food (Table 1; Fig. 2). When *R. marina* larvae were present, *L. albilabris* larvae achieved higher early mass and exhibited a shorter time to metamorphosis, although the latter effect was limited to the low food condition. For *L. albilabris*, the experimental manipulation did not affect mass at metamorphosis. Species composition had a marginally significant, non-monotonic effect on the percent of *L. albilabris* that matured. The interaction term was statistically significant. We were interested in better understanding how species composition affected the percent of *L. albilabris* that matured, so we ran separate GLM's on the high and low food treatments. Species composition did not affect the percent of *L. albilabris* that matured under low food conditions ($F_{2,15} = 0.32$, $P = 0.73$). Under high food conditions, however, it did have an effect ($F_{2,15} = 7.9$, $P = 0.005$) and post-hoc tests indicated that *L. abilabris* in the 4 L: 8 R high food treatment matured at a lower rate than those in the other *high* food treatments.

TABLE 2. Results of GLM tests of the effects of food level and species composition on growth and development of *R. marina* larvae. Bold font denotes statistically significant results. These analyses of the dependent variable (*) exclude data from the 6 L: 6 R aquaria because most of the *R. marina* in those treatments died prior to metamorphosis.

	Model			Food			Species Composition			Food * Species Interaction		
Dependent Variable	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*
Early mass	2.27	5,25	0.078	0.05	1,25	0.83	2.03	2,25	0.15	3.64	2,25	**0.041**
Percent matured	13.2	5,30	**< 0.001**	4.39	1,30	**0.045**	26.8	2,30	**< 0.001**	4.11	2,30	**0.026**
Mass at metamorphosis*	6.09	3,14	**0.007**	0.94	1,14	0.35	14.4	1,14	**0.002**	0.77	1,14	0.40
Time to metamorphosis*	5.02	3,14	**0.014**	1.22	1,14	0.29	11.3	1,14	**0.005**	0.048	1,14	0.83

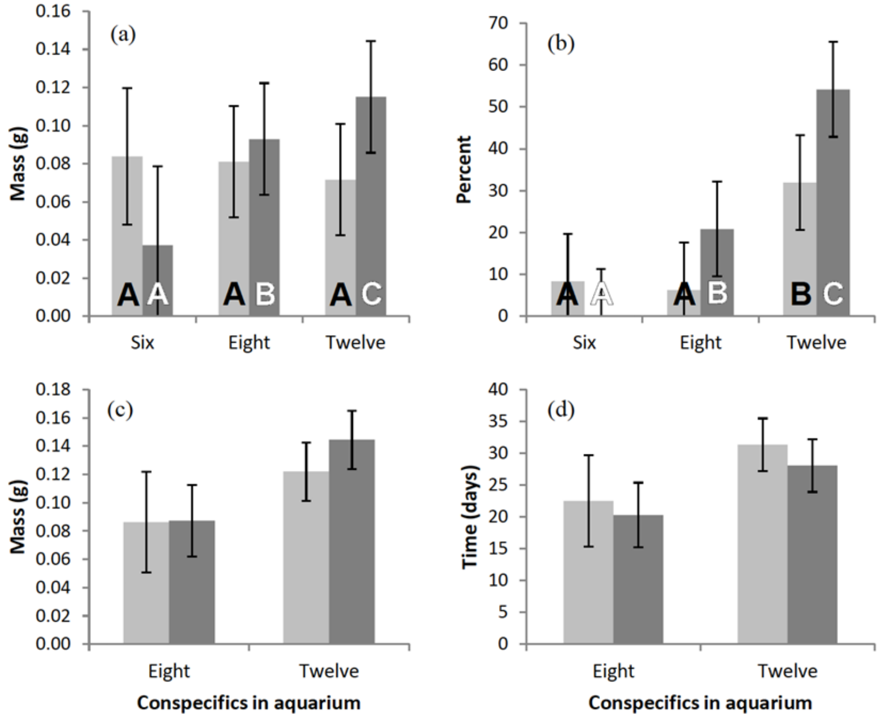

FIGURE 3. Bar graphs showing the development of *Rhinella marina* larvae as a function of food availability (light gray = low food; dark gray = high food) and species composition. Each aquarium held 12 individuals, comprising the number of *R. marina* indicated on the x-axis and 0−6 *Leptodactylus albilabris* larvae. The graphs show estimated marginal means and 95% confidence intervals of (a) mass measured at week two of the experiment, (b) percent of individuals that metamorphosed, (c) mass at metamorphosis, and (d) time to metamorphosis. We conducted post-hoc tests when omnibus tests were statistically significant. Letters indicate statistically distinct species composition treatments. Post-hoc tests on mass at week two and percent of individuals that metamorphosed (b) were conducted separately for high food (open letters) and low food (solid letters) treatments.

Significantly more *R. marina* larvae survived to maturity in the high food aquaria than in the low food aquaria, but the effect of food depended on species composition (i.e., a significant interaction; Table 2; Fig. 3). The presence of *L. albilabris* caused *R. marina* to metamorphose faster and at a lower mass. When we analyzed the two food treatments separately, species composition significantly affected survival in *R. marina* in both the low food ($F_{2,15}$ = 7.19, *P* = 0.006) and the high food ($F_{2,15}$ = 22.50, *P* < 0.001) treatments, and affected mass at two weeks in the high food treatment ($F_{2,15}$ = 11.19, *P* = 0.002) but not the low food treatment ($F_{2,15}$ = 0.17, *P* = 0.98). In all cases, the presence of *L. albilabris* had a negative effect on *R. marina*.

DISCUSSION

The purpose of the food calibration experiment was to identify a feeding regime that imposed strong nutritional stress, and another that imposed less nutritional stress. By that standard, we conclude that the experiment was successful because amount of food strongly affected survival in both species in the food calibration experiment. The high food and low food treatments that we selected based on the results of that experiment induced differential survival in both species during the competition experiment.

We tested the predictions that competition with the invasive toad *R. marina* would negatively affect the growth and development of the Puerto Rican native frog *L. albilabris*. Contrary to those predictions, we found that *L. albilabris* raised together with *R. marina* grew more in the first two weeks and metamorphosed more rapidly than those that were raised with only conspecifics. Under the low food regime, the presence of *R. marina* had no effect on the survival of *L. albilabris*. Under the high food regime, however, average *L. albilabris* survival was lowest when *R. marina* were more abundant. Our results indicate that *L. albilabris* larvae have a competitive advantage over *R. marina* when food is scarce, but *R. marina* larvae may negatively influence survival of *L. albilabris* when food is abundant and *R. marina* are more numerous.

We were surprised to find that *L. albilabris* negatively affected the growth and development of *R. marina* larvae. The presence of the native frog dramatically reduced the percentage of *R. marina* that survived to metamorphosis. The *R. marina* that did metamorphose in the presence of *L. albilabris* accelerated their development, resulting in a shorter larval period and a lower mass at metamorphosis compared to *R. marina* raised in monoculture. This finding is consistent with the hypothesis that development in *R. marina* is both plastic and subject to life history tradeoff (Warkentin 1995). According to this hypothesis, the presence of a superior competitor stimulates larvae to initiate metamorphosis at a smaller size (Wilbur and Collins 1973; Denver 1997). Reduced size at metamorphosis may negatively impact fitness by reducing juvenile survivorship and reproduction (Semlitsch et al. 1988; Denver 1997; Crossland et al. 2009). We did not observe a similar effect in *L. albilabris*. The largest average *L. albilabris* metamorphs came from the treatment with the most *R. marina*, and *L. albilabris* in the monospecific treatments took the longest time to metamorphose. Cabrera-Guzmán et al. (2011, 2013a) also reported that competition with native species negatively affected the growth and development of introduced *R. marina*. Further work by that team suggests that the mechanism of competition is best understood as exploitation, rather than chemically mediated interference (Cabrera-Guzmán et al. 2013b).

Comparing the effects of competition on the two species, it appears that *L. albilabris* has the competitive advantage. For example, in aquaria with equal numbers of each species (L 6: R 6), *L. albilabris* had high survival to metamorphosis (average ± SD; 70.8% ± 31.1%) while very few *R. marina* larvae survived (4.2% ± 10.4%; compare Figs. 2b and 3b). Therefore, where their numbers are equivalent, we expect *L. albilabris* to outcompete *R. marina*. Competition with equal numbers, however, may not be common in the wild because the 106 eggs per clutch average of *L. albilabris* (Joglar 2005) pales in comparison to the massive clutch size of *R. marina*, which can be up to 35,000 eggs (Rivero 1998). Thus, the outcomes of competitive interaction may be different under natural situations (Alford and Crump 1982; Pavignano 1990; Scott 1990; Wellborn et al. 1996; Williamson 1999). Caveats notwithstanding, our findings that competition with *R. marina* has limited effects on a native frog species and competing with a native species negatively impacts *R. marina* are consistent with other recent findings regarding competition between *R. marina* and native Australian frogs (Cabrera-Guzmán et al. 2013a, 2013b; Shine 2013).

The fact that *L. albilabris* tadpoles are larger than *R. marina* larvae may provide insights into their competitive interactions. Richter-Boix et al. (2007) studied intra- and interspecific effects in six anuran species, and showed that larger species were more affected by intra- rather than by interspecific competition. The results of several studies suggest that larger tadpoles are generally better competitors than smaller ones (Wilbur and Collins 1973; Griffiths 1991; Gollmann and Gollmann 1993). Species with larger larvae can suppress growth and reduce survival in smaller species by direct or indirect mechanisms (Wilbur and Collins 1973; Alford and Crump 1982; Laurila 2000; Katzmann et al. 2003; Richter-Boix et al. 2007). Although we did not quantify activity levels, we observed that *L. albilabris* tadpoles were more active than *R. marina*. Several studies have suggested that more active tadpoles are better competitors than less active tadpoles (Laurila 2000; Dayton and Fitzgerald 2001; Richter-Boix et al. 2007).

Other important factors that may explain the competitive advantage of *L. albilabris* are the adaptations that each species has for its typical habitat. *Leptodactylus albilabris* appears to be adapted to the ephemeral pools in which it is most often found (Heatwole et al. 1968; Rivero 1998; Joglar 2005). Tadpoles that develop in ephemeral water bodies need to grow quickly to escape the risk of death due to desiccation (Heatwole et al. 1968; Wellborn et al. 1996; Loman 1999; Richter-Boix et al. 2007). Time to acquire resources can be limited in ephemeral habitats, so tadpoles that develop in these systems tend to be more active feeders and grow faster (Wellborn et al. 1996; Loman 1999; Richter-Boix et al. 2007). Species adapted to life in permanent ponds, like *R. marina*, may be poor at exploitation competition (Richter-Boix et al. 2007). *Rhinella marina* tadpoles rely on their toxicity to escape predation, which is more important in permanent water bodies than in ephemeral ones (Heyer et al. 1975; Wellborn et al. 1996). In this study, *L. albilabris* scavenged dead *R. marina* tadpoles without apparent ill effect. *Leptodactylus albilabris* has had an evolutionary history of exposure to a bufonid (*Peltophryne lemur* [= *Bufo lemur*]) on the island of Puerto Rico, which may explain its ability to tolerate bufotoxins.

The use of native species to control invasive *R. marina* has been considered (Cabrera-Guzmán et al. 2011). Even if *L. albilabris* seems to be a superior competitor in a controlled setting during the larval phase, other aspects of natural history of the species need to be better understood before attempting to implement such a policy. For instance, larvae of *R. marina* can be found at higher densities than native species, and this could have a negative effect on native species development. Toxicity of *R. marina* can also have detrimental effects on native species (Crossland 2000; Crossland et al. 2008; Crossland and Shine 2010). Toxicity of *R. marina* varies during ontogeny, and eggs are known to be more toxic than larvae (Hayes et al. 2009). Finally, priority effects are known to alter interactions of species during the larval phase (Lawler and Morin 1993; Crossland et al. 2009).

In conclusion, we found that food competition between an introduced and native anuran does not negatively affect growth and development of the native species, and only affects the native species' survival when food is abundant. In contrast, the introduced species suffered high mortality and metamorphosed at lower mass when competing with the native species. These results are congruent with recent reports of native frogs outcompeting introduced *R. marina* in Australia (e.g., Cabrera-Guzmán 2011, 2013a, b; Shine 2013). Additional analyses of the ecology of these two species and their interactions would help to predict the long-term effects of the invasive *R. marina* on the native *L. albilabris*. Furthermore, how the introduced *R. marina* affects other frog species native to Puerto Rico (e.g., the Crested Toad, *Peltophryne lemur*) warrants future investigation, as does the potential effects of other introduced frog species such as the American Bullfrog (*Lithobates catesbeianus*), Pig Frog (*Rana grylio*), Cuban Treefrog (*Osteopilus septentrionalis*), and Green Treefrog (*Hyla cinerea*). Only through detailed studies of species interactions will we be able to gauge the effects of introduced species on native populations, communities, and ecosystems, and make informed decisions about where to focus conservation efforts.

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