

Effects of nonindigenous tadpoles on native tadpoles in Florida: evidence of competition

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Abstract

The impacts of nonindigenous species on native ecosystems can be severe, sometimes leading to the extinction of native taxa. Interspecific competition is a potential mechanism of negative impact of invasive species, but few studies have conclusively demonstrated competition between native and nonindigenous taxa. In this study I used experimental manipulations to examine the competitive effects of the larvae of two widely introduced anurans, the cane toad, *Bufo marinus*, and the Cuban treefrog, *Osteopilus septentrionalis*, on the growth and development of the larvae of two native anurans (the southern toad, *Bufo terrestris*, and the green treefrog, *Hyla cinerea*). The presence of *O. septentrionalis* larvae consistently impacted growth and development of native larvae, resulting in reduced growth rates and delayed metamorphosis of both native species and smaller mass at metamorphosis of *B. terrestris*. *Hyla cinerea* larvae transformed at greater body masses when reared with the rapidly transforming nonindigenous species as a result of competitive release. The negative effects of *O. septentrionalis* on native larvae were generally significant whether native tadpoles were exposed to *O. septentrionalis* alone or in combination with *B. marinus*. In contrast, *B. marinus* tadpoles did not significantly impact the growth or development of either native species. Neither nonindigenous species significantly decreased the survivorship of native larvae, although a trend toward decreased survivorship was evident for *H. cinerea*. These results suggest that nonindigenous larval anurans may adversely impact native tadpole communities as a result of interspecific competition.

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1. Introduction

Invasive species are widely considered to be a significant threat to native biodiversity (Wilcove et al., 1998; Mack et al., 2000). Consequently, the biology of invasive and nonindigenous species has become a focus of conservation biology (e.g., Mooney and Drake, 1986; Simberloff et al., 1997). Despite this focus, evidence of the ecological impacts of nonindigenous species on native species is frequently absent or is strictly anecdotal (Vitousek et al., 1987; Simberloff, 1995, 1997). As a re-

sult, biologists often lack the information necessary to prioritize conservation and management recommendations when faced with the presence of many nonindigenous species. Furthermore, not all nonindigenous species become invasive or injurious to native communities. Research that contributes to the correct identification of potentially injurious nonindigenous species is therefore essential, as is evidenced by the sometimes ecologically or economically severe impacts of such species (Diamond, 1984; Savidge, 1987; Wilcove et al., 1998; Pimentel et al., 2000).

Nonindigenous species may impact native taxa through several mechanisms, one of which is interspecific competition. Though frequently studied in native

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communities (reviewed in Schoener, 1983), interspecific competition is relatively difficult to demonstrate unequivocally in invaded communities (Vitousek et al., 1987; Simberloff, 1997). As a result, studies assessing the role of interspecific competition as a mechanism of impact of nonindigenous species are few, especially among vertebrates (but see Petren et al., 1993; Petren and Case, 1996; Kupferberg, 1997; Kiesecker and Blaustein, 1998; Gurnell et al., 2004). A better understanding of the significance of competition to the impacts of invasive species is needed.

Larval anuran (tadpole) communities are ideal model communities for the study of competition between native and nonindigenous taxa. Such communities may be particularly vulnerable to competition with exotic species because they are frequently characterized by high population densities in temporally and spatially restricted aquatic habitats. As a result, competition is an important ecological factor in tadpole communities (reviewed in Wilbur, 1980 and Alford, 1999). Despite the importance of competition in tadpole communities and the potential for competition between nonindigenous and native species, there has been little research on the impacts of nonindigenous tadpoles on native tadpoles due to competition per se (but see Kupferberg, 1997; Kiesecker and Blaustein, 1998).

In this study, I designed laboratory microcosm experiments to address the possibility of competition among native and exotic anuran larvae. I combined larvae of two nonindigenous anurans, the Cuban treefrog, *Osteopilus septentrionalis*, and the cane toad, *Bufo marinus*, with larvae of one of two anurans native to Florida, USA (southern toad, *Bufo terrestris*, and green treefrog, *Hyla cinerea*). The goal of this study was to determine whether *B. marinus* and *O. septentrionalis* larvae affect the growth, development, and survivorship of larval *B. terrestris* and *H. cinerea*.

2. Study system

Both *B. marinus* and *O. septentrionalis* have occurred in Florida for more than 50 years. *Bufo marinus* is native to South and Central America (Zug and Zug, 1979) but became established in Florida prior to 1957 as the result of several intentional and accidental introductions beginning around 1936 (Easteal, 1981; Wilson and Porras, 1983). Since its initial establishment in the Miami-Dade Co. area, *B. marinus* has expanded its range throughout much of southern peninsular Florida (Lever, 2001). *Osteopilus septentrionalis* is native to Cuba and adjacent islands (Duellman and Crombie, 1970) and was established in mainland Florida by 1951 (Schwartz, 1952). *Osteopilus septentrionalis* now occurs in much of peninsular Florida (Meshaka, 2001) and both species

are syntopic with several native anurans, including *B. terrestris* and *H. cinerea*.

Bufo terrestris and *H. cinerea* are both locally abundant, widespread species that occur throughout Florida and the southeastern coastal plain of the United States. Although populations of both native species are apparently stable throughout most of their range (Bartlett and Bartlett, 1999), several ecologists have expressed concern regarding the impacts of *B. marinus* and *O. septentrionalis* on native anurans in south Florida and suggest that declines of native species have occurred (Bartlett, 1967; Rossi, 1981; Bartlett and Bartlett, 1999). The role of larval interactions in these putative declines has been almost entirely ignored, however (but see Rossi, 1981).

Several characteristics of larval *B. marinus* and *O. septentrionalis* suggest that these species may impact native tadpole communities. Both *B. marinus* and *O. septentrionalis* larvae occur in temporary or ephemeral bodies of water and develop rapidly in these habitats, which may suggest the potential for competition with native temporary pond species such as *B. terrestris* and *H. cinerea*. Additionally, carnivory and cannibalism are traits of some ephemeral pond species (Hoff et al., 1999) and *O. septentrionalis* is known to be cannibalistic when reared in high densities (Crump, 1986) and will prey on heterospecific anuran larvae under certain conditions (low food, high density; Smith, in press). Larvae of *B. marinus* are not carnivorous but are toxic to many vertebrate and invertebrate predators (Crossland, 1998, 1999; Crossland and Alford, 1998), including some anuran larvae (Crossland, 2000). Although few native anuran larvae in Florida are carnivorous, most species will scavenge dead tadpoles, so dead *B. marinus* larvae may be a toxic food source for native tadpoles.

3. Materials and methods

3.1. Tadpole collection

I collected freshly laid clutches of *B. terrestris* and *H. cinerea* from wild-caught colonies held in vinyl tanks at the U.S. Geological Survey Florida Integrated Science Center in Alachua Co., Florida (hereafter, FISC) on 24 May 2003. Freshly laid clutches of *B. marinus* and *O. septentrionalis* were collected from a flooded field in Dade Co., Florida on the morning of 25 May. When available, multiple egg clutches were used for each species to reduce genetic effects on competitive ability (Traavis, 1980). Limited availability of eggs and time constraints precluded the use of multiple clutches for all species, however (*B. terrestris* and *B. marinus*, one clutch each). All eggs were hatched in captivity and hatchlings were fed tadpole chow ad libitum until the experiments began on 30 May. Tadpole chow was a 3:1 ratio by mass of finely ground rabbit chow pellets

(primary ingredient = alfalfa) and TetraFin™ goldfish food and was similar to that used in similar research (e.g., Alford, 1994).

3.2. Experimental design

I simultaneously conducted two randomized block experiments to assess the competitive effects of *B. marinus* and *O. septentrionalis* tadpoles on a single native species; one experiment measured effects on *B. terrestris* and one measured effects on *H. cinerea*. Native and non-indigenous tadpoles were randomly assigned to one of four experimental treatments: native control (36 native larvae with no nonindigenous larvae), *B. marinus* treatment (18 native larvae with 18 *B. marinus* larvae), *O. septentrionalis* treatment (18 native larvae with 18 *O. septentrionalis* larvae), and *B. marinus* + *O. septentrionalis* treatment (12 native larvae with 12 *B. marinus* larvae and 12 *O. septentrionalis* larvae). Initial density of all treatments was 36 tadpoles per aquarium (two tadpoles/L) and is within the highly variable range of naturally occurring densities of these species. All four treatments were included in one of four spatial blocks (four treatments per block X four replicates = 16 aquaria per experiment) and the location of each treatment within a block was randomly assigned with the restriction that no treatment would be adjacent to the same treatment in another block.

All experimental microcosms were housed in the North Wet Lab of FISC. Microcosms were 10 gal (37.85 L; 25.5 cm × 50 cm) glass aquaria fitted with standpipe drains and filled with aerated well water to a depth of 14.5 cm (approximately 18 L). All aquaria were flushed with fresh well water for 15 min every 1–3 days to prevent the accumulation of lethal levels of metabolic products without completely removing potentially allelopathic substances from the microcosms. Ten grams of oven-dried oak leaves were added to each aquarium prior to the start of each experiment to provide microhabitat complexity. Aquaria were arranged on a pallet rack shelving system with an entire experiment (16 aquaria) on one shelf. Artificial light was provided on a 12:12 h light:dark cycle from a fluorescent light source directly above the rack system. Food was added to all aquaria at a ration of 2.7 g tadpole chow per aquarium every three days throughout the experimental period.

3.3. Response variables, data collection and statistical analysis

At the onset of the experiments, a haphazard sample of larvae of each native species ($n = 30$) was collected for developmental stage determination (Gosner stage; Gosner, 1960), body length measurement (to nearest 0.1 mm; as described in Altig and McDiarmid, 1999), and wet body mass measurement (to nearest 0.1 mg; as

Table 1
Range of Gosner stage and mean (± 1 S.D.) of mass and body length of tadpoles at day 0 of this study

Species	Gosner stage	Mass (mg)	Body length (mm)
<i>Bufo terrestris</i>	25–27	7.18 \pm 0.728	3.6 \pm 0.15
<i>Hyla cinerea</i>	25	7.05 \pm 2.651	2.9 \pm 0.34
<i>Bufo marinus</i>	24–27	3.34 \pm 0.968	2.9 \pm 0.29
<i>Osteopilus septentrionalis</i>	25–26	13.74 \pm 3.653	4.0 \pm 0.44

For all species $n = 30$.

described in Alford, 1994). Differences in size and developmental stage of tadpoles at the start of the experiments were the result of natural differences in hatching and developmental rates (Table 1).

Because both nonindigenous species develop and reach metamorphosis rapidly, data on growth and development of focal species (*B. terrestris* and *H. cinerea*) were collected twice during the experimental period. All native tadpoles were weighed when the first tadpole in an experiment reached metamorphosis (experiment days 15–16; “early larval period”), which reflected the effects of the initial densities of each treatment. Each tadpole was weighed again individually at metamorphosis, which reflected the effects of decreasing densities during the experiment as competitors transformed. Metamorphosis was defined as the emergence of the second forelimb (Gosner stage 42) at which time the individual was permanently removed from the aquarium. Data collected from transforming individuals were date of transformation and wet mass to nearest 0.1 mg. These data allowed for comparison of relative larval growth and developmental rates, which are positively correlated with adult anuran survival and fitness (Berven and Gill, 1983; Smith, 1987). These data also allowed for the calculation of time to metamorphosis and proportion surviving to metamorphosis for focal species in each treatment group.

I used multivariate analysis of variance (MANOVA) to detect the effects of independent factors (presence of nonindigenous tadpoles) on the growth and development of native anuran larvae. Data from both the early larval period and metamorphosis were combined in a single MANOVA for each native species to test for the overall effects of the presence of nonindigenous tadpoles. Response variables used for the early larval period were body mass and Gosner stage and those used for metamorphosis were body mass and time to metamorphosis. Proportion surviving to metamorphosis (arcsine transformed) was analyzed in a separate ANOVA. I used treatment means in all statistical analyses to avoid pseudoreplication. Data from one microcosm in the *B. terrestris* experiment were eliminated from analysis due to contamination and failure. If MANOVA results indicated a significant treatment effect I then used individual univariate ANOVAs to determine the response variables

in which significant effects occurred. The use of a multivariate test such as MANOVA prior to multiple ANOVAs avoids problems associated with experimentwise error rate inflation and replaces the use of more subjective error control methods such as Bonferroni corrections (Cabin and Mitchell, 2000; Moran, 2003). If MANOVA and ANOVA results showed significant differences among groups, I then used post hoc contrasts (Tukey–Kramer Multiple Comparison Tests) to detect the presence of significant differences among specific treatment groups within significant response variables as determined by ANOVA. In all analyses, “replicate” was used as a random effects blocking factor. I used NCSS (Hintze, 2001) and a significance level of $\alpha = 0.05$ for all statistical analyses.

4. Results

4.1. Effects of nonindigenous tadpoles on larval *Bufo terrestris*

The presence of nonindigenous larvae significantly reduced the growth and developmental rates of *B. terrestris* tadpoles over the entire larval period (MANOVA, treatment effect $F_{12,14} = 11.87$, $P < 0.001$; block effect $F_{12,14} = 1.33$, $P = 0.307$). Specifically, larvae of *O. septentrionalis* alone or in combination with *B. marinus* inhibited the growth of *B. terrestris* tadpoles as measured by body mass during both the early larval period (ANOVA, $F_{3,11} = 15.76$, $P < 0.01$) and at metamorphosis (ANOVA, $F_{3,11} = 81.43$, $P < 0.001$; Fig. 1). In contrast, body mass of *B. terrestris* was not significantly affected by the presence of *B. marinus* and did not differ between the *O. septentrionalis* treatment and the *B. marinus* + *O. septentrionalis* treatment (Tukey–Kramer test; Fig. 1), suggesting that the main effect on *B. terrestris* was driven by the presence of *O. septentrionalis*.

Only the presence of *O. septentrionalis* larvae affected the developmental rate of *B. terrestris* during the early larval period. After 15 days, *B. terrestris* larvae reared with *O. septentrionalis* larvae were significantly less developed as measured by Gosner stage when compared to the control group (ANOVA, $F_{3,11} = 28.96$, $P < 0.001$; Table 2). This depressed developmental rate persisted to metamorphosis, as *B. terrestris* tadpoles also transformed later when reared with *O. septentrionalis* larvae (ANOVA, $F_{3,11} = 11.68$, $P < 0.01$). The magnitude of this effect was the addition of 1.9 days (12.1%) to the larval period of *B. terrestris* (Table 2).

Low mortality of *B. terrestris* in all treatments resulted in no significant difference in survivorship of *B. terrestris* among treatments (ANOVA, $F_{3,11} = 2.04$, $P = 0.1874$). The mean proportion surviving to metamorphosis across all treatments was 0.9756 ± 0.02 for this species.

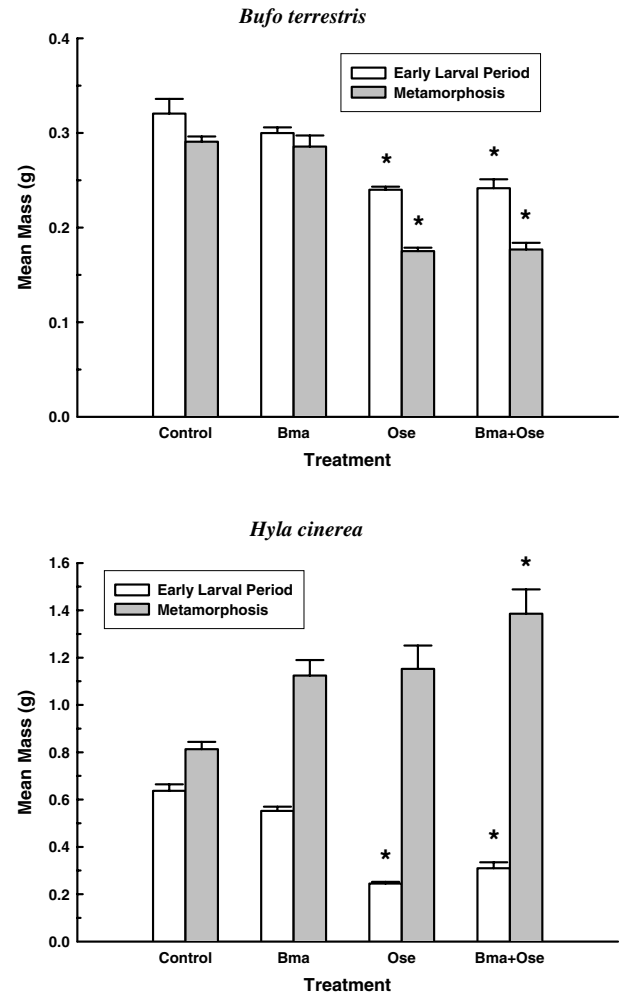


Fig. 1. Effects of the presence of nonindigenous tadpoles (Bma, *Bufo marinus*; Ose, *Osteopilus septentrionalis*) on body mass of larval *Bufo terrestris* and *Hyla cinerea* after early larval development and at metamorphosis. “Early larval period” data were collected on days 15 and 16 for *B. terrestris* and *H. cinerea*, respectively. Error bars show +1 S.E. Asterisks (*) indicate a significant difference from the control group (Tukey–Kramer Multiple Comparison Test, $\alpha = 0.05$).

4.2. Effects of nonindigenous tadpoles on larval *Hyla cinerea*

The presence of nonindigenous tadpoles also affected the growth and developmental rates of *H. cinerea* tadpoles during the entire larval period in this study (MANOVA, treatment effect $F_{12,16} = 10.31$, $P < 0.001$; block effect $F_{12,16} = 1.28$, $P = 0.317$). After 16 days, *H. cinerea* tadpoles exposed to *O. septentrionalis* larvae were significantly smaller than *H. cinerea* tadpoles in the control group as measured by body mass (ANOVA, $F_{3,12} = 79.03$, $P < 0.001$; Fig. 1). The effects of *O. septentrionalis* larvae alone were not significantly different from the effects of *B. marinus* + *O. septentrionalis* larvae and *B. marinus* tadpoles had no significant effect on body mass of *H. cinerea* (Tukey–Kramer Test; Fig. 1).

Table 2

Measures of development (Gosner stage or time to metamorphosis) of *Bufo terrestris* and *Hyla cinerea* tadpoles when reared in the presence and absence of nonindigenous tadpoles

Treatment	Gosner stage	
	<i>B. terrestris</i>	<i>H. cinerea</i>
<i>Early larval period</i>		
Control	41.6 ± 0.22	34.6 ± 0.20
<i>B. marinus</i>	41.6 ± 0.10	33.9 ± 0.25
<i>O. septentrionalis</i>	40.2 ± 0.16	30.8 ± 0.27
<i>B. marinus</i> + <i>O. septentrionalis</i>	41.0 ± 0.03	31.6 ± 0.38
<i>Time to metamorphosis (days)</i>		
<i>Metamorphosis</i>		
Control	15.7 ± 0.43	36.7 ± 0.51
<i>B. marinus</i>	15.5 ± 0.14	35.5 ± 0.46
<i>O. septentrionalis</i>	17.6 ± 0.21	40.8 ± 0.71
<i>B. marinus</i> + <i>O. septentrionalis</i>	16.9 ± 0.26	38.1 ± 0.92

“Early larval period” data were collected on days 15 and 16 for *B. terrestris* and *H. cinerea*, respectively. Values are means ± 1 S.E. and boldface type indicates a significant difference between that value and the control group ($\alpha = 0.05$).

The presence of nonindigenous anuran larvae also affected body mass of *H. cinerea* at metamorphosis. However, in contrast to the early larval period, *H. cinerea* tadpoles reared with both nonindigenous species transformed at larger body mass than in the control group (ANOVA, $F_{3,12} = 7.49$, $P < 0.01$; Fig. 1). This result suggests that *H. cinerea* larvae benefited from the presence of nonindigenous tadpoles during late larval development. However, in this experiment both nonindigenous species reached metamorphosis more rapidly than did the native *H. cinerea*. The mean time to metamorphosis (± 1 S.E.) of *H. cinerea* in this study was 37.5 (± 0.37) days, compared to 17.4 (± 0.32) days and 17.4 (± 0.21) days for the nonindigenous *B. marinus* and *O. septentrionalis*, respectively. Consequently, *H. cinerea* tadpoles reared with nonindigenous tadpoles experienced lower densities during the latter part of the study period (12 or 18 *H. cinerea* per aquarium) than did those in the control group (36 *H. cinerea* per aquarium), due to the metamorphosis of nonindigenous larvae. Individuals in the control group were therefore exposed to higher tadpole densities – and greater intraspecific competition – for a longer period of time.

If these results were caused by lower levels of density-dependent intraspecific competition, then change in mass during the late larval period of *H. cinerea* should be inversely correlated with the number of *H. cinerea* tadpoles in each treatment. This prediction is confirmed; a strong negative relationship exists between increase in body mass during the late larval period and number of *H. cinerea* tadpoles per treatment group (Spearman rank correlation, $r_s = -0.8245$, $n = 16$, $P < 0.001$). This result suggests that differences in mean metamorphic body mass of *H. cinerea* were related to larval density rather than to the presence of nonindigenous tadpoles.

The developmental rate of *H. cinerea* was also significantly affected by the presence of *O. septentrionalis* throughout the larval period (Table 2). *Hyla cinerea* tadpoles exposed to either the *O. septentrionalis* or the *B. marinus* + *O. septentrionalis* treatment were less developed after 16 days than were *H. cinerea* tadpoles in the control group (ANOVA, $F_{3,12} = 50.80$, $P < 0.001$). Despite experiencing decreased competition during the late larval period, *H. cinerea* tadpoles took significantly longer to reach metamorphosis when reared with *O. septentrionalis* larvae (ANOVA, $F_{3,12} = 13.18$, $P < 0.01$). The magnitude of this effect was the addition of 4.1 days (11.2%) to the larval period of *H. cinerea*. The presence of *B. marinus* tadpoles alone had no effect on the developmental rate of *H. cinerea* tadpoles, suggesting that the main effect on the development of *H. cinerea* was due to the presence of *O. septentrionalis*.

A trend toward decreased survivorship in *H. cinerea* reared with *O. septentrionalis* larvae was detected, but this result was not statistically significant (ANOVA, $F_{3,12} = 3.03$, $P = 0.086$). Mean proportion surviving to metamorphosis across all treatments was 0.8775 ± 0.03 for this species.

4.3. Metamorphosis and survivorship of nonindigenous species

Neither *B. marinus* nor *O. septentrionalis* exhibited significant variation in time to metamorphosis or proportion surviving across treatments in either experiment in this study (Table 3).

Table 3

ANOVA results and proportion survivorship and time to metamorphosis of *Bufo marinus* and *Osteopilus septentrionalis* in the two experiments in this study

	<i>B. terrestris</i> experiment		<i>H. cinerea</i> experiment	
	Survivorship	Time to metamorphosis (days)	Survivorship	Time to metamorphosis (days)
<i>B. marinus</i>	$F_{1,6} = 0.02$, $P = 0.9075$ 0.981 ± 0.013	$F_{1,6} = 2.58$, $P = 0.2067$ 18.3 ± 0.41	$F_{1,6} = 0.40$, $P = 0.5712$ 0.955 ± 0.024	$F_{1,6} = 0.88$, $P = 0.4178$ 17.4 ± 0.32
<i>O. septentrionalis</i>	$F_{1,6} = 0.36$, $P = 0.5931$ 0.945 ± 0.017	$F_{1,6} = 0.25$, $P = 0.6498$ 18.2 ± 0.25	$F_{1,6} = 3.56$, $P = 0.1555$ 0.936 ± 0.019	$F_{1,6} = 1.07$, $P = 0.3771$ 17.4 ± 0.21

F and P values are from an ANOVA across treatments for each species within an experiment. Values are pooled means (\pm S.E.) of all treatments and replicates.

5. Discussion

Ecological interactions among anuran larvae can lead to several outcomes that may negatively affect the fitness of competing tadpoles. Interactions may result in mortality, resulting in decreased recruitment to the breeding population. Interspecific predation among tadpoles (e.g., Heyer et al., 1975), toxicity of tadpoles (e.g., Crossland, 2000), or interspecific competition (e.g., Wilbur and Fauth, 1990) are three mechanisms that may result in decreased survivorship of tadpoles. Alternatively, interactions among tadpoles may also have sublethal – but still deleterious – effects on the growth and developmental rates community members. In such cases, survivorship to metamorphosis may not be significantly affected, but the subsequent fitness of juveniles or adults may be compromised as a result of interactions among tadpoles (Smith, 1987).

5.1. Survivorship of native tadpoles

In this study, the proportion of native tadpoles surviving to metamorphosis was not significantly affected by the presence of nonindigenous tadpoles, although a trend toward reduced survival was seen in *H. cinerea*. This result allows for the elimination of several potential mechanisms of impacts of *B. marinus* and *O. septentrionalis* on *B. terrestris* and *H. cinerea*. Although *O. septentrionalis* tadpoles will prey on heterospecific larvae when reared in high densities (approx. 60 tadpoles/L) and held without other food (Smith, in press), significant predation of native tadpoles by *O. septentrionalis* did not occur in this study, perhaps because densities in this study were moderate (two tadpoles/L) and food was readily available. The conditions of high tadpole densities and low food availability may exist during the drying of natural ephemeral pools, however, so predation by *O. septentrionalis* on native tadpoles may yet be a significant impact in natural settings.

The toxicity of *B. marinus* also did not affect survivorship of either native species, despite evidence that both *B. terrestris* and *H. cinerea* are susceptible to *B. marinus* toxin (Punzo and Lindstrom, 2001). Since survivorship of *B. marinus* was high in this study (Table 3), few potentially toxic carcasses of this species were available for scavenging by *B. terrestris* or *H. cinerea*.

A trend toward decreased survivorship of *H. cinerea* was evident in this study; marginally fewer *H. cinerea* tadpoles survived to metamorphosis when reared with *O. septentrionalis* or both *B. marinus* and *O. septentrionalis*. This trend suggests that were *B. marinus* and *O. septentrionalis* larvae present for the entire larval period of *H. cinerea*, survival to metamorphosis of *H. cinerea* may have been significantly compromised. Additional experiments in which transforming nonindigenous tad-

poles are replaced would have greater realism to natural systems and can be used to evaluate the trend reported here.

5.2. Delayed metamorphosis of native tadpoles

Both *B. terrestris* and *H. cinerea* use a variety of breeding habitats including temporary bodies of water with short hydroperiods, which are the preferred breeding habitat of *O. septentrionalis*. In these habitats, the addition of two to four days to the larval period (the increase in the larval period for *B. terrestris* and *H. cinerea*, respectively, as a result of the presence of *O. septentrionalis* larvae) may significantly decrease larval survivorship to metamorphosis due to desiccation or increased predation. Desiccation due to pond drying is a significant source of mortality in some tadpoles (Seale, 1982; Newman, 1987) and in habitats in which desiccation is not a factor, longer larval periods can also decrease survival by increasing the duration of exposure to aquatic predators (Pritchard, 1965; Heyer et al., 1975; Caldwell et al., 1980; Wilbur, 1980). Risk of desiccation or predation were not factors in this microcosm study, so survivorship of *B. terrestris* and *H. cinerea* was not adversely affected by delayed metamorphosis. One or both of these factors are expected to be present in natural tadpole communities, however, where an increase in the duration of the larval period of *B. terrestris* and *H. cinerea* as a result of the presence of *O. septentrionalis* may lead to reduced recruitment of the native species. Additional experiments that include predators or implement a drying regime can more rigorously evaluate the importance of delayed metamorphosis to larval survivorship.

5.3. Body size at metamorphosis

In addition to experiencing delayed metamorphosis, larvae of *B. terrestris* also transformed at significantly smaller sizes when reared with *O. septentrionalis* larvae. Tadpoles that transform at small body mass are generally less likely to survive to reproduction and those that do survive grow to smaller adult body sizes (Berven and Gill, 1983; Smith, 1987; Berven, 1990). Furthermore, mating success and clutch size are positively correlated with adult body size in some anurans (e.g., Howard, 1978; Berven, 1981; Woolbright, 1983), so even small decreases in growth or developmental rates of larval anurans may affect fitness if such decreases result in smaller reproductive body size. If the results from this study are representative of the impacts of *O. septentrionalis* on native anuran larvae in natural settings, the fitness and survival of adult native anurans such as *B. terrestris* may be affected by the presence of this nonindigenous species, even if larval survival per se is not affected.

In contrast to *B. terrestris*, the size of larval *H. cinerea* at metamorphosis was not negatively affected by the presence of nonindigenous larvae. However, *H. cinerea* larvae experienced decreased growth and developmental rates during the early larval period as a result of exposure to larval *O. septentrionalis*. These results suggest that *H. cinerea* larvae may be able to recover from the competitive effects of the presence of nonindigenous tadpoles if they are released from competition by the transformation of more rapidly developing *B. marinus* and *O. septentrionalis* larvae. This type of competitive release has been documented for related species (e.g., as a result of predation on competitors, Morin, 1983), but because the length of the larval period may be determined during early growth and development (Travis, 1984), delayed metamorphosis may still result as it did in this study. Additionally, ecological release and compensatory growth may not occur in natural populations of *H. cinerea* where adult *O. septentrionalis* reproduce continuously throughout the breeding season and repeatedly re-establish their larvae as potential competitors. Finally, these results may also suggest that native species with shorter larval periods will be more sensitive to the competitive effects of nonindigenous tadpoles, as there will be greater temporal overlap between the competing species.

6. Conservation implications

The results of this study strongly suggest that nonindigenous anuran larvae, in this case those of *O. septentrionalis*, may impact native anuran larvae through interspecific competition. Although the presence of *B. marinus* did not significantly affect the native tadpoles in this study, the potential toxicity of the eggs and larvae of *B. marinus* to aquatic predators warrants further examination of the impacts of this species on native aquatic taxa.

Although the results of this study are striking, the impacts of the presence of *O. septentrionalis* in natural tadpole communities remain unknown. Declines of some native anurans in south Florida have been reported and are anecdotally correlated with the arrival of *O. septentrionalis* (Bartlett, 1967). These declines have been attributed to predation by adult nonindigenous anurans on native species (Bartlett, 1967) and, perhaps more probably, to concurrent effects of habitat destruction (Krakauer, 1968; Wilson and Porras, 1983). Whatever the cause of past declines, the ability of *O. septentrionalis* to disperse (Meshaka, 1996) and to penetrate relatively undisturbed, protected habitats such as Everglades National Park (Butterfield et al., 1997; Meshaka, 2001) suggests that future impacts are possible since most habitats in peninsular Florida will eventually

be invaded by *O. septentrionalis*. Additional research, including that conducted in more natural settings, will help determine the importance of larval competition with *O. septentrionalis* to the population status of native anurans in Florida.

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