

Interactions Between Competition and Predation Shape Early Growth and Survival of Two Neotropical Hylid Tadpoles

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ABSTRACT

Experimental studies in temperate regions have revealed that competition and predation interact to shape aquatic communities. Predators typically reduce the effect of competition on growth and competitors provide alternative prey subjects, which may also alter predation. Here, we examine the independent and combined effects of competition and predation on the survival and growth of hatchling tadpoles of two widespread co-occurring Neotropical hylid frogs (*Agalychnis callidryas* and *Dendropsophus ebraccatus*). Using 400 L mesocosms, we used a 2 × 3 factorial substitutive design, which crossed tadpole species composition with the presence or absence of a free-roaming predator (*Anax amazili* dragonfly larva). Dragonflies were effective predators of both species, but had larger effects on *A. callidryas* survival. Both species had similar growth rates when alone, whereas *A. callidryas* grew 30 percent faster than *D. ebraccatus* when they co-occurred, suggesting interspecific rather than intraspecific competition had relatively stronger effects on *D. ebraccatus* growth, while the opposite was true for *A. callidryas*. Predator presence dramatically reduced growth rates of both species and erased this asymmetry. Results suggest that the effects of predator induction (*i.e.*, nonconsumptive effects) on growth were larger than both consumptive and competitive effects. Our study demonstrates that predators have strong effects on both survival and growth of prey, highlighting the potential importance of predators in shaping prey populations and tropical aquatic food web interactions.

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Key words: Anura; *Hyla ebraccata*; Panama; phenotypic plasticity; treefrog.

UNDERSTANDING THE INDEPENDENT AND COMBINED EFFECTS OF COMPETITION AND PREDATION in shaping prey communities has been a major focus in ecology (Sih *et al.* 1985, Gurevitch *et al.* 2000). Competition for limited resources can reduce growth, fecundity and survival (Connell 1983, Schoener 1983). Predators can affect prey populations and communities by consuming prey and by inducing shifts in prey traits that alter growth and development (Van Buskirk & Yurewicz 1998, Relyea 2002a). Competition typically has stronger effects on growth than the presence of predators, while predator presence has larger effects on survival (Gurevitch *et al.* 2000). Further, the presence of predators frequently alters the strength of competition among prey (Werner & McPeek 1994, Relyea 2000), typically lessening competitive effects on growth (Gurevitch *et al.* 2000). Similarly, the presence of alternative prey may indirectly alter the effects of predators on focal taxa (*e.g.*, apparent competition; Holt 1977, Bonsall & Hassell 1997). Thus the interactive effects of predation and competition can have important consequences for population dynamics and community structure (Paine 1969, Morin 1983).

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The importance of predation and competition has been particularly well examined in freshwater food webs comprised of larval amphibians and their predators (*e.g.*, see reviews in Duellman & Treub 1986, McDiarmid & Altig 1999, Wells 2007). Competition among different species of tadpoles can take different forms, most often seen as effects on growth rates and changes in gut morphology (Skelly 1995, Relyea & Auld 2004). Most field studies reveal competitive effects within and among species, although the strength of these effects varies with taxa and venue (reviewed in Skelly & Kiesecker 2001, Wells 2007). For example, some co-occurring species exhibit weak interspecific competition, where conspecific and heterospecific competitors have similar effects on growth (Alford 1989, Skelly 1995, Bardsley & Beebee 1998), whereas others display strong asymmetrical competition, in which one species has a strong effect on a competitor but the reciprocal effect is weak (Morin & Johnson 1988, Werner & McPeek 1994, Alford 1999). This variation in the strength of competition might reflect differences in trophic overlap among species competing through exploitative mechanisms (*i.e.*, through depletion of a shared limiting resource). Few studies, however, examine overlap in resource use and most tadpoles are assumed to be generalist periphyton grazers (Altig *et al.* 2007, Wells 2007). Alternatively, variation in

competition might reflect species specific differences in interference mechanisms (Faragher & Jaeger 1998, Bardsley & Beebee 2001). Thus, although competition is thought to be relatively common in tadpole assemblages because of high population densities and relatively low niche differentiation, little is known about how tadpoles may actually be competing (Alford 1999).

Predation can also play an important role in shaping amphibian populations and communities (Wellborn *et al.* 1996, Werner *et al.* 2007). Predators reduce tadpole abundance by eating them and may influence community level patterns by preferentially consuming some species over others (Werner & McPeek 1994). Further, many larval anurans are sensitive to chemical cues from predators and exhibit phenotypic plasticity in response to predation risk (*e.g.*, Werner & Anholt 1996). Induced responses to predators include altering life history trajectories (Warkentin 1995, Vonesh & Warkentin 2006), morphology and coloration (Touchon & Warkentin 2008a), and foraging behaviors (Werner & Anholt 1996, Van Buskirk & Yurewicz 1998), all of which can reduce risk to predators but may incur some other fitness cost (Werner & Anholt 1996, Relyea 2002b). For example, reducing foraging activity in response to predator cues can reduce predator encounters but may come at the cost of reduced growth (Werner & Anholt 1996). Predators may also drive indirect effects in aquatic food webs, both through consumptive and nonconsumptive mechanisms. For example, predator cues alone can change the nature of competitive interactions among larval anurans, most often reducing the strength of competition (Werner & McPeek 1994, Relyea 2000). By consuming some individuals, predators can also release survivors from competition (*e.g.*, thinning). In addition, phenotypic responses to predators can alter the competitive ability of prey. Thus, predators can shape prey populations and communities directly through their effects on prey (both consumptive and nonconsumptive) and indirectly by altering the strength of competitive interactions among prey (Van Buskirk & Yurewicz 1998, Relyea 2000).

While larval anurans and their predators have been a model system for understanding the role of predation and competition in aquatic communities, this work has been almost entirely limited to the temperate region. We know very little about how these factors shape tropical tadpole communities, which can be more complex and include a greater range of trophic adaptations than those in temperate regions (Wells 2007). Furthermore, many species have prolonged breeding activity, which increases the opportunity for temporal overlap of cohorts of different species and ages in larval habitats. Studies of competition among tropical anurans are rare; of the 35 species used in experimental competition studies reviewed by Skelly and Kiesecker (2001), only three species (8%) from a single study (Gascon 1992a) had tropical distributions (see also Twomey *et al.* 2008). Historically, authors have suggested that predation might play a more important role in shaping tropical vs. temperate communities (Paine 1969), and correlative studies of factors shaping assemblages of larval anurans provide some support for this hypothesis (*e.g.*, contrast: Azevedo-Ramos *et al.* 1999, Hero *et al.* 2001 vs. Werner *et al.* 2007). Few experimental studies, however, have examined the role of predators in shaping tropical anuran

assemblages (Gascon 1991, 1992b; Caldwell 1993; Gascon 1995); none, to the best of our knowledge, have examined the interaction of competition and predation. Here we examine of the effects of competition and predation on the tadpoles of two commonly co-occurring Neotropical hylid frogs, the red-eyed treefrog (*Agalychnis callidryas*) and the pantless tree frog (*Dendropsophus ebraccatus*). Specifically, we examine: (1) the relative importance of inter- and intraspecific competition; (2) the relative vulnerability to a common predator. We also test (3) whether the presence of predators alters the strength of competitive interactions; and (4) whether the presence of the heterospecific tadpoles alters predation.

METHODS

STUDY SYSTEM.—This study was conducted at the Smithsonian Tropical Research Institute field station in Gamboa, Panama ($9^{\circ}7'17''$ N, $79^{\circ}42'11''$ W) between 19 July and 4 August 2009. *Dendropsophus ebraccatus* and *A. callidryas* are locally abundant treefrogs with prolonged reproduction throughout the rainy season (about May–December). *Agalychnis callidryas* is a leaf breeding frog (Warkentin 2000, Savage 2002) with 35 ± 16.7 eggs per clutch (mean \pm SD, here and throughout; Hite 2009), while *D. ebraccatus* is a facultative leaf or aquatic breeder with 64 ± 27.4 eggs per clutch (Touchon & Warkentin 2008b, 2009). Eggs, tadpoles and adults of both species commonly co-occur throughout the rainy season in all six Gamboa area ponds we have worked in. Both species prefer fishless ponds where aquatic invertebrates might be important predators. Aeshnid dragonfly larvae, including those of the Amazon darner *Anax amazili* (Odonata: Aeshnidae), are often found in the breeding ponds shared by *D. ebraccatus* and *A. callidryas* (four of six Gamboa area ponds; J. C. Touchon & J. R. Vonesh, unpubl. data).

EXPERIMENTAL DESIGN.—On 19 July, we collected 21 *D. ebraccatus* and 25 *A. callidryas* newly laid clutches from vegetation around Experimental Pond, an artificial pond on the edge of secondary forest. Clutches were maintained in an ambient temperature laboratory with frequent misting, and allowed to develop and hatch. Eggs from each species were allowed to hatch into a single container, allowing families to mix in the water. Although eggs from both taxa were of the same age, *D. ebraccatus* tadpoles hatched earlier because they are smaller and develop more rapidly (Touchon & Warkentin 2010). As a result, *D. ebraccatus* were 4 d post-hatching and *A. callidryas* tadpoles were one to two days post-hatching at the beginning of the experiment. Tadpoles were haphazardly sampled and assigned to treatments randomly.

To examine the interaction between predation and competition on growth and survival of *D. ebraccatus* and *A. callidryas*, we conducted a 2×3 factorial experiment where we crossed predator presence or absence with tadpole species composition (50 *A. callidryas*, 50 *D. ebraccatus*, or 25 *A. callidryas* and 25 *D. ebraccatus* together). Each treatment was replicated six times. This substitutive design allows us to measure the relative intensity of inter- and intraspecific competition, although not the absolute strength of competition (Gurevitch & Scheiner 2001, Gotelli & Ellison 2004), in

the presence and absence of predators at a common total prey density. Predator treatments included one free-roaming late instar *A. amazili* larva ($\bar{x} \pm SD$ total length [TL]: 22.23 ± 2.7 mm) collected from Quarry Pond in Gamboa. Initial tadpole (0.125 tadpole/L) and predator (0.0025 dragonfly/L) densities were within the natural range as observed during field estimates of tadpole densities across five breeding ponds in the Gamboa area in 2004 (J. C. Touchon & J. R. Vonesh, unpubl. data). Treatments were randomly assigned to 400 L mesocosms (0.75 m diameter \times 0.8 m high, with screened drain holes at 0.75 m height) arranged in one 6×6 block in an open field next to secondary forest. Tanks were filled with a mix of aged tap and rain water, 50 g of dried leaf litter and covered with insect screen to prevent unwanted colonization. Tadpole food was supplemented at the start of the experiment and on day five by providing 0.75 g of Sera Micron® and 0.75 g of powdered rabbit chow (primarily alfalfa) pellets in suspension. The former remains in suspension for aquatic filter feeders and the latter quickly precipitates onto the bottom and surfaces where it can be grazed. Tadpoles were dorsally photographed in a white tray with a Nikon D40x digital camera and added to mesocosms on 27 July. The experiment ended on 4 August, at which point all tadpoles and predators were dip-netted from tanks, counted, and re-photographed. All photographs included a ruler for scale calibration. We used ImageJ (<http://rsbweb.nih.gov/ij/>) to obtain measurements of TL from images.

All analyses were conducted on tank means using R version 2.11.1 (R Development Core Team 2010). We first tested for main and interactive effects of predator, species composition and species identity on tadpole mortality and growth rate, followed by analysis of predator and species composition effects for each species. Tadpole mortality was analyzed using general linear models with underlying quasi-binomial error distribution and logit link functions. Using the quasi-binomial error distribution allowed us to account for overdispersion in our data and adjusted *P*-values accordingly (Pinheiro & Bates 2000). Because *A. callidryas* is a larger species than *D. ebraccatus*, our analysis focused on relative growth rate, measured as log (final TL/initial TL) analyzed with normal errors without further transformation using standard linear models. Final models were obtained through a stepwise model simplification approach and model fit and influence of specific data were evaluated using standard regression diagnostics (Crawley 2007).

RESULTS

Predators (GLM likelihood ratio $\chi^2_{1,44} = 224.9$, $P < 0.001$), species composition ($\chi^2_{1,44} = 15.59$, $P < 0.001$) and the interaction between species identity and predators ($\chi^2_{1,44} = 10.87$, $P < 0.001$) all affected tadpole mortality (deviance explained: 90%). When species were examined separately, predator presence was the only significant predictor of *A. callidryas* mortality ($\chi^2_{1,20} = 117.3$, $P < 0.001$, deviance explained: 84%; Fig. 1A), while *D. ebraccatus* mortality was dependent on both predator presence ($\chi^2_{1,20} = 202.5$, $P < 0.001$) and species composition ($\chi^2_{1,20} = 11.5$, $P < 0.001$; deviance explained: 91%; Fig. 1B). In the absence of predators and the

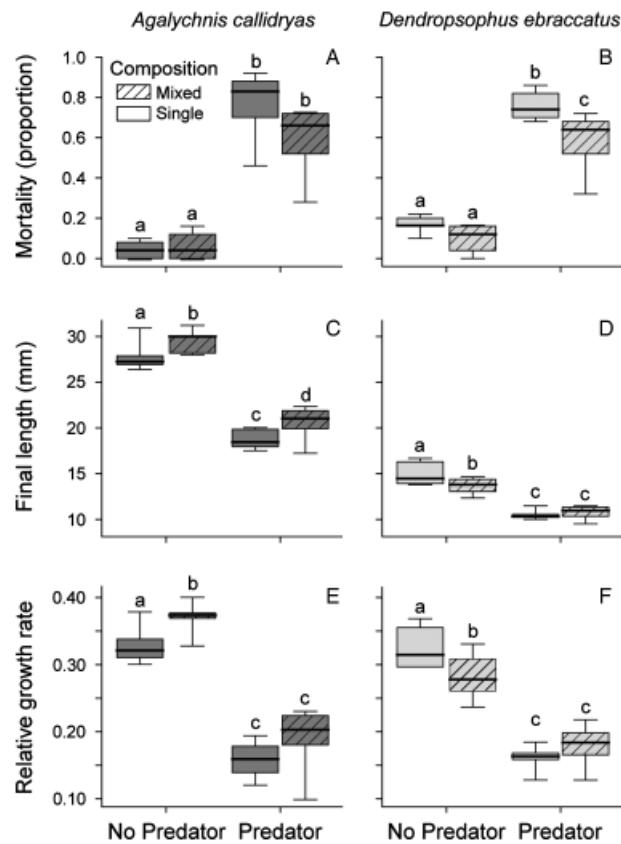


FIGURE 1. Proportional mortality (A, B), final total length (C, D) and relative growth rates (E, F) of *Agalychnis callidryas* and *Dendropsophus ebraccatus* tadpoles in a factorial experiment in which we manipulated species composition (each species alone and mixed) crossed with the presence and absence of predatory *Anax amazili* dragonfly nymphs. Box plots show the median, quartiles and data minimum and maximum for each treatment ($N=6$). Letters indicate statistically different treatments for each species based on unadjusted pair-wise planned comparisons.

other taxa, background mortality was higher for *D. ebraccatus* ($\text{mean} \pm \text{SD}$: 0.17 ± 0.04) than *A. callidryas* (0.04 ± 0.04). Adding predators increased mortality for both species, but more so for *A. callidryas* (~17 fold increase to 0.77 ± 0.17) than *D. ebraccatus* (~3.5 fold increase to 0.76 ± 0.07). The presence of the other frog species reduced mortality, which was around 25 percent higher in single species (0.42 ± 0.35) compared with mixed species treatments (0.34 ± 0.29).

At the start of the experiment, *A. callidryas* tadpoles were 12.97 mm (Range: 11.85–14.0) and *D. ebraccatus* were 7.12 mm (Range: 6.72–7.47) in TL. There were no differences in initial size within species across treatments (*A. callidryas*: $F_{3,20} = 2.45$, $P = 0.1$; *D. ebraccatus*: $F_{3,20} = 0.28$, $P = 0.84$). Predators ($F_{1,39} = 301.9$, $P < 0.001$), species identity ($F_{1,39} = 1139.8$, $P < 0.001$) and the interactions between species identity and predators ($F_{1,39} = 4.89$, $P = 0.03$) and species identity and species composition ($F_{1,39} = 8.01$, $P = 0.007$) were all significant predictors of tadpole final TL (model $F_{7,39} = 204.8$, $P < 0.001$, $R^2 = 0.97$). When *A.*

callidryas was examined alone, predator presence ($F_{1,20} = 207.0, P < 0.001$) and species composition ($F_{1,20} = 8.73, P = 0.007$) were significant predictors of final TL (model $F_{3,20} = 72.0, P < 0.001, R^2: 0.90$; Fig. 1C). *Dendropsophus ebraccatus* final TL was dependent on predator presence ($F_{1,20} = 207.0, P < 0.001$) and the final model also retained the predator by species composition interaction term ($F_{1,20} = 3.9, P = 0.05$; model $F_{3,19} = 37.2, P < 0.001, R^2 = 0.83$; Fig. 1D). At the end of the experiment, *A. callidryas* (27.8 ± 1.6) were nearly twice as large as *D. ebraccatus* (14.9 ± 1.3) when species occurred alone in the absence of predators. Adding predators decreased TL for both species by approximately 30 percent (*A. callidryas*: to 18.7 ± 1.0 ; *D. ebraccatus*: to 10.5 ± 0.5). In the absence of predators, *A. callidryas* was 7 percent larger (29.6 ± 1.2 mm) and *D. ebraccatus* 8 percent smaller (13.7 ± 0.86) when the species co-occurred. When *Anax* was present, *A. callidryas* still attained larger sizes in mixed vs. single species treatment (mixed: 20.6 ± 1.8 ; single: 18.7 ± 1.0). *D. ebraccatus* were smaller when they co-occurred with *A. callidryas* in the absence of predators; in the presence of predators, however, tadpoles from mixed and single species treatments were similar (mixed: 10.7 ± 0.7 ; single: 10.5 ± 0.5).

Treatment effects on tadpole relative growth rates generally mirror those of TL, but focusing on growth rate facilitates comparison between these species that are naturally different in absolute size. Predators ($F_{1,39} = 94.5, P < 0.001$), species composition ($F_{1,38} = 5.0, P = 0.03$), species identity ($F_{1,38} = 22.4, P < 0.001$) and the interactions between species identity and predators ($F_{1,39} = 8.8, P = 0.005$) and species identity and species composition ($F_{1,39} = 10.2, P = 0.002$) were all significant predictors of tadpole growth rate. The final model also retained coefficients for the predator by composition interaction ($F_{1,39} = 0.15, P = 0.70$) and the three-way interaction ($F_{1,39} = 3.64, P = 0.06$; model $F_{7,39} = 427.2, P < 0.001, R^2 = 0.86$). When species were examined separately, *A. callidryas* growth rate was dependent on predators ($F_{1,20} = 84.40, P < 0.001$) and species composition ($F_{1,20} = 4.7, P = 0.047$; model $F_{3,20} = 55.43, P < 0.001, R^2 = 0.88$; Fig. 1E), while *D. ebraccatus* growth was dependent on predators ($F_{1,20} = 34.95, P < 0.001$), species composition ($F_{1,20} = 5.98, P = 0.02$) and their interaction ($F_{1,20} = 5.96, P = 0.02$; model $F_{3,19} = 39.49, P < 0.001, R^2 = 0.84$; Fig. 1F). In the absence of predators and the other taxa, both species had nearly identical growth rates (*A. callidryas*: 0.33 ± 0.03 ; *D. ebraccatus*: 0.32 ± 0.03). Adding predators to single species treatments had similar and dramatic effects on both species, reducing growth rates by ~50 percent (*A. callidryas*: 0.16 ± 0.03 ; *D. ebraccatus*: 0.16 ± 0.02). Although both species responded similarly to predators, they responded differently to the presence of each other. In the absence of predators, *A. callidryas* grew about 12 percent faster with *D. ebraccatus* (0.37 ± 0.01) while *D. ebraccatus* grew 13 percent slower with *A. callidryas* (0.28 ± 0.03). Thus, while both species grew similarly when alone, *A. callidryas* grew ~30 percent faster than *D. ebraccatus* when they co-occurred. This interaction between species identity and species composition was, however, erased by predators. In the presence of predators, growth rates were similar across taxa and species composition (*A. callidryas* single:

0.16 ± 0.03 , mixed: 0.19 ± 0.05 ; *D. ebraccatus* single: 0.16 ± 0.02 , mixed: 0.17 ± 0.03).

DISCUSSION

Competition and predation both play an important role in structuring larval anuran assemblages. In this study, we found that while both focal species had similar growth rates in single species treatments without predators, *A. callidryas* tadpoles grew 30 percent faster than *D. ebraccatus* when the two species co-occurred, suggesting that intraspecific competition is relatively stronger for *A. callidryas* than interspecific competition, while interspecific competition was stronger for *D. ebraccatus*. Although our design does not allow us to separate the absolute strength of inter- and intraspecific interactions between these species, this pattern is consistent with asymmetrical competitive interactions. We initially had the expectation that these two species might utilize resources differently. *Agalychnis callidryas* tadpoles are suspension-rasper feeders that primarily filter-feed while suspended in the water column, but also have the ability to graze periphyton (Duellman & Treub 1986, McDiarmid & Altig 1999, Savage 2002, Wells 2007). Tadpoles of *D. ebraccatus* are macrophagous herbivores thought to feed on filamentous algae and graze periphyton (Duellman & Treub 1986, McDiarmid & Altig 1999, Savage 2002, Wells 2007). If these species were using different resources (e.g., phyto- vs. periphyton), we might still expect to see *A. callidryas* to perform better in mixed treatments due to reduced intraspecific competition. We would also have expected *D. ebraccatus* to have similar or higher growth in mixed treatments for the same reason. Instead, we saw that *D. ebraccatus* grew more slowly. This suggests that both species were competing for similar resources, likely periphyton and supplemented food that settled on surfaces. Because we did not directly measure consumer effects on food resources or directly observe tadpole interactions, we cannot be certain of the mechanisms giving rise to this pattern. Furthermore, differences in the relative strength of inter- and intraspecific competition between these species may be driven by differences in body size. *Agalychnis callidryas* is nearly twice the size of *D. ebraccatus*. If resource use increases with total tadpole biomass, we might expect both species to be more affected by changes in the density of the larger species. Thus, *A. callidryas* are more sensitive to intraspecific competition and experience increased growth in mixed tanks relative to single species tanks where large conspecifics have been replaced with an equal number of small *D. ebraccatus*. For *D. ebraccatus* the reverse may be true.

Anax amazili nymphs were extremely effective predators consuming > 60 percent of both species in single species treatments over the experiment. Furthermore, species differed in their vulnerability. After accounting for background mortality, dragonflies consumed 22 percent more *A. callidryas* (4.5 tadpoles/d) than *D. ebraccatus* (3.7 tadpoles/d). Higher predation on *Agalychnis* was not dependent on species composition (i.e., *A. callidryas* tadpoles were eaten equally well when alone or in mixed species groups), so it does not appear that dragonfly nymphs behaviorally selected this species. Rather, *Anax* may be inherently better at consuming *Agalychnis*

tadpoles. This was somewhat surprising to us, as we expected that *A. callidryas* might have a spatial refuge from this predator, as they often hang in the water column while filter feeding. Studies at smaller sites show that when *Anax* are present most hatchling *A. callidryas* are found hanging from the water surface or in the water column (B. Willink, pers. comm.). Aeshnid dragonfly larvae are visually oriented sit-and-pursue predators that generally hunt from a substrate. They wait for prey to approach before striking, and then propel themselves rapidly through the water using a jet-propulsion system (e.g., Michel & Adams 2009). It is possible that *Agalychnis* tadpoles were consumed more frequently because their larger size and increased time moving in the water column made them more conspicuous.

By consuming prey and thinning their numbers, predators can positively affect the growth of survivors. Relyea (2002a) showed that the thinning effect of *Anax longipes* predation on *Hyla versicolor* tadpoles increased tadpole growth by ~60 percent. Given the effectiveness of *A. amazili* at consuming tadpoles of both species, we expected *per capita* resource availability to increase and perhaps tadpole growth rates as well. We did not, however, observe an increase in growth after thinning. Instead, tadpoles of both species grew 50 percent slower when exposed to lethal predators. This result could have arisen through predator selection (*i.e.*, *Anax* consumed the largest tadpoles reducing mean size), predator-induced effects on tadpole growth (e.g., trade-offs associated with phenotypic responses to perceived predation risk), or a combination of these factors. Predator selection alone seems unlikely, as the distribution of final TL in the presence and absence of predators was completely nonoverlapping for both species, *i.e.*, the distribution in the presence of predators is not simply a truncated predator free distribution (Figs. 1C and D). This suggests predator induction played a large role.

Predator-induced reductions in growth are commonly found in anuran larvae (e.g., Werner & Anholt 1996, Relyea 2002b, Van Buskirk 2002; but see Peacor 2002). These effects on prey growth can arise through reduced foraging activity in the presence of predator cues (Werner & Anholt 1996) or from increased metabolic and physiological costs (Steiner 2007). Reductions in prey growth because of perceived predation risk are often outweighed by predator thinning (e.g., Van Buskirk & Yurewicz 1998, Relyea 2002a). Our results are thus interesting in that the total effect of *Anax* in our study was a large net reduction in growth despite considerable thinning of tadpoles. It is possible that an energetic trade-off associated with altering the expression of phenotypically plastic traits may have been partly responsible for the observed reduction in growth of tadpoles in our predator treatments. Touchon and Warkentin (2008a) observed a reduction in overall growth in *D. ebraccatus* tadpoles associated with enlargement and reddening of the tail in response to an odonate predator. Vonesh and Warkentin (2006) found that *A. callidryas* tadpoles exposed to a nonlethal (caged) aquatic predator were smaller at metamorphosis than those in control treatments despite no significant difference in timing at metamorphosis—an effect that was not attributable to changes in behavior.

The consumption of prey and degree to which perceived predation risk induces lower growth in prey may be positively corre-

lated in some circumstances. Predators that consume more prey may increase the concentration of cue in the environment, which can increase the magnitude of the nonlethal response of surviving prey (Mirza *et al.* 2006, Kesavaraju *et al.* 2007). *Anax amazili* is one of the most effective predators we have studied based on short-term predation trials ($N=13$ predator species, J. C. Touchon & J. R. Vonesh, unpubl. data). Several other species of predators we have worked with are relatively less effective (e.g., *Belostoma* water bugs, libellulid dragonflies) and do not appear to elicit such strong growth responses. This suggests that either tadpoles have taxa specific responses to these predators, or that of the predators studied thus far, only the predation rates of *Anax* have been high enough cross a threshold cue level needed to induce a response. We are currently conducting studies in this system to elucidate how tadpole response to predators is dependent on cue concentration and prey size.

The magnitude of the predator effect on growth was larger than the effects of changes in species composition in our experiment. For example, the presence of *Agalychnis* reduced *Dendropsophus* growth by 13 percent while predators reduced growth by 50 percent. Thus, while previous studies that experimentally manipulate competition and predation typically show that competitors most strongly affect growth responses while predators affect survival (Gurevitch *et al.* 2000), we find that under these experimental conditions the presence of larval *Anax* dominates growth and survival for both frog species. Furthermore, the presence of predators erased the effects of competition. This may have resulted from the combined effects of thinning and reduced foraging; predation reduced tadpole densities, leaving more resources *per capita* and thus reducing competition. Previous research has revealed that predators often ameliorate the effect of competition (Gurevitch *et al.* 2000). Our results provide further evidence that predators are important in shaping competitive interactions among tadpoles. Although our study examines a single density, and focuses on early larval development, it is important to appreciate that the relative importance of predation and competition may shift through ontogeny and over the range of naturally occurring competitor and predator densities.

This is the first experiment we are aware of to examine competition and predation simultaneously in a tropical anuran community. As many similar studies have been conducted in temperate communities, this stimulates us to question the possible differences in how top-down and bottom-up forces shape communities across latitudes, and whether or not such broad ecological generalities actually exist across a variety of communities in different ecosystems. It also prompts us to question what the potential role of predator-induced phenotypic plasticity among prey species plays in shaping community interactions. Correlative studies from tropical regions point to an important role for predators in shaping larval anuran communities (Hero *et al.* 1998, Azevedo-Ramos *et al.* 1999). In this experimental study, with a simple aquatic community, we demonstrate that predators dramatically reduced survival, growth and the relative importance of inter- and intraspecific competition. Additional studies in tropical anuran communities are necessary to further illuminate if differences exist between temperate and tropical groups.

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