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COMPENSATORY LARVAL RESPONSES SHIFT TRADE-OFFS ASSOCIATED WITH PREDATOR-INDUCED HATCHING PLASTICITY

JAMES R. VONESH[1] AND BENJAMIN M. BOLKER

Department of Zoology, University of Florida, 223 Bartram Hall, Gainesville, Florida 32611 USA

Abstract. Many species with complex life histories can respond to risk by adaptively altering the timing of key life history switch points, including hatching. It is generally thought that such hatching plasticity involves a trade-off between embryonic and hatchling predation risk, e.g., hatching early to escape egg predation comes at the cost of increased vulnerability to hatchling predators. However, most empirical work has focused on simply detecting predator-induced hatching responses or on the short-term consequences of hatching plasticity. Short-term studies may not allow sufficient time for hatchlings to exhibit compensatory responses, which may extend to subsequent life stages and could alter the nature of the trade-offs associated with hatching plasticity. In this study, we examine the consequences of predator-induced hatching plasticity through the larval stage to metamorphosis in the East African reed frog, *Hyperolius spinigularis*. To do this we conducted an experiment in which we manipulated initial larval size and density (mimicking the effects of egg predators) and the presence of aquatic predators. We expected that predator-induced hatchlings (because they are less developed and smaller) would experience higher per capita predation rates and a longer larval period and thus would exhibit lower survival to metamorphosis in the presence of aquatic predators than larger, more developed, later hatched larvae. Surprisingly, we found that predator-induced hatchlings survived better, not worse, than hatchlings from undisturbed clutches. These results motivated us to develop a model parameterized from additional experiments to explore whether a combination of mechanisms, compensatory growth, and density- and size-specific predation, could give rise to this pattern. Predicted survival probabilities from the model with compensatory growth were consistent with those from the field experiment: early hatched larvae grew more rapidly through vulnerable size classes than later hatched larvae, resulting in higher survival at metamorphosis. Thus, in this system, there does not appear to be a trade-off in vulnerability between egg and larval predators. Instead, our results suggest that the cost that balances the survival benefit of hatching early to evade egg predators arises later in the life history, as a result of smaller size at metamorphosis.

Key words: *compensatory growth; density-mediated indirect interaction (DMII); functional response; hatching plasticity;* Hyperolius spinigularis; *multiple predators; phenotypic plasticity; size-selective predation; trait-mediated indirect interaction (TMII).*

INTRODUCTION

There is considerable evidence that prey can assess predation risk and respond to predators by changing their behavior, morphology, and life history (e.g., Lima and Dill 1990, Skelly 1992, Sih and Moore 1993, DeWitt 1998, Tollrian and Harvell 1999). Changes in the timing of habitat shifts, metamorphosis, and hatching are particularly compelling because they typically involve dramatic shifts in ecology, including changes in habitat, resources, and predators. Theory developed for organisms with complex life histories predicts that the timing of transitions between two life stages should evolve in response to variation in growth and mortality rates in the two stages (Werner and Gilliam 1984, Werner 1986). More recently, this theoretical framework has been applied to examine the timing of hatching, an event that separates embryonic and larval stages (Sih and Moore 1993).

A growing number of studies have detected hatching plasticity in response to predation risk. For example, the eggs of some salamanders (Sih and Moore 1993, Moore et al. 1996), anurans (Laurila et al. 2002, Schalk et al. 2002), crustaceans (Blaustein 1997), and fish (Jones et al. 2003) delay hatching in response to cues from post-hatching predators (review in Martin 1999). The postponement of hatching may allow hatchlings to reach a larger body size and more developed stage before encountering predators, potentially increasing their survival (Sih and Moore 1993). Similarly, the eggs of anurans (Warkentin 1995, 1999*a*, *b*, 2000, Vonesh 2000, Chivers et al. 2001, Warkentin et al. 2001), fish (Wedekind 2002), and arachnids (Li 2002) have been shown to hatch earlier in response to cues from

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[1] Present address: Tyson Research Center, Washington University at St. Louis, P.O. Box 258, Eureka, Missouri 63025 USA. E-mail: voneshjr@yahoo.com

egg-stage predators, potentially increasing egg-stage survival.

While predator-induced hatching plasticity has been documented in diverse taxa, empirical studies of the trade-offs associated with hatching early are few and focus on events near hatching. Sih and Moore (1993) observed delayed hatching in the salamander, *Ambystoma barbouri*, in response to cues from larval-stage predators. Delayed hatching resulted in increased size at hatching and larger larvae exhibited higher survival in the presence of larval predators. Similarly, Warkentin (1995, 1999*b*) observed that the arboreal embryos of the treefrog, *Agalychnis callidryas*, hatch early in response to cues from several egg-stage predators and that hatching early to avoid egg predators came at the cost of increased vulnerability to aquatic, larval predators. However, these studies only consider the first 24 h after hatching. Such short-term experiments ignore the potential for longer-term compensatory responses to hatching plasticity. Traits correlated with induced hatching expressed in later life stages (e.g., changes in larval behavior, morphology, physiology) could alter the ecological consequences of hatching plasticity.

In this study we evaluate the consequences of predator-induced hatching plasticity through to metamorphosis in the spiny-throated reed frog, *Hyperolius spinigularis*. To accomplish this, we conducted a field experiment in which we manipulated hatchling size and age, larval density, and aquatic predation and measured larval (e.g., duration, survival) and postmetamorphic (mass) responses. Hatching was manipulated to mimic predator-induced hatching plasticity. Initial larval densities were manipulated to mimic the numerical effects of two species of egg predators. Since embryos eaten by egg predators never become tadpoles, egg predators directly affect the larval environment by reducing larval density. Such density effects of egg-stage predation may alter the demographic consequences of predator-induced hatching, e.g., the consequences of hatching early and small may differ if larval competition is strong versus weak. Thus, we examine the effects of hatching plasticity at several densities reflecting the density effects of egg-stage predation.

We found, in contrast to previous studies (e.g., Warkentin 1995, 1999*b*), that small, early-hatched larvae survived better, not worse, than later hatched larvae. This surprising result motivated us to develop a mathematical model incorporating expressions for growth and size- and density-specific mortality to explore the role of these mechanisms in determining larval survival in our experiment. Through this combination of approaches we examine the following questions: What are the consequences of predator-induced early hatching at metamorphosis? What mechanisms give rise to the observed patterns of survival? Finally, what trade-offs might be associated with hatching early to escape egg predation in this system?

Materials and Methods

Site and system information

Site information.—This research was conducted at the Amani Nature Reserve (ANR) Conservation Headquarters in the East Usambara Mountains of northeastern Tanzania (5.06° S, 38.37° E; elevation 900 m) from October 2001 to August 2002. The ANR includes 8380 ha of transitional lowland–montane rainforest. The site receives approximately 2000 mm rainfall each year (Hamilton and Bensted-Smith 1989), which falls primarily in two distinct rainy seasons: October–November ("short rains") and March–June ("long rains"). ANR and the forests of the Usambara Mountains are among the threatened Eastern Arc Mountain biodiversity hotspots (Myers et al. 2000) noted for their high degree of diversity and endemism (Lovett and Wasser 1993). Field measurements of *H. spinigularis* clutch densities, egg predation, and aquatic predator densities were made at Amani Pond (~200 m North ANR field station) unless otherwise noted below. Amani Pond is an artificial (>50 yr old) permanent shallow pond (mean depth ~45 cm) bordered by submontane rainforest. Pond vegetation is dominated by floating mats of milfoil (*Myriophyllum spicatum*) and marginal patches of emergent cattails (*Typha* sp.; Appendix A, Fig. A1A).

System information.—*Hyperolius spinigularis* is endemic to a few submontane rainforest localities in Tanzania and Malawi (Schiøtz 1999). It breeds during both annual rainy seasons by attaching its eggs to vegetation overhanging permanent or semipermanent ponds or swamps. Upon hatching the tadpoles fall into the water (Appendix A, Fig. A2). Thus, hatching can be described as an ontogenetic niche shift: animals change habitats, become mobile, gain access to external resources, and are vulnerable to a new suite of predators. Arboreal and aerial predators attack eggs, but have limited access to tadpoles, while aquatic predators prey on larvae but have no access to eggs. Mortality rates may differ before and after hatching, creating the potential for trade-offs in risk between egg and larval stages. Surviving embryos from clutches attacked by the egg-eating reed frog *Afrixalus fornasini* (Appendix A, Fig. A3) and parasitoid flies of the genus *Typopsilopa* (Appendix A, Fig. A4) hatch approximately 30% earlier than embryos from undisturbed clutches (Vonesh 2003). As a result, hatchlings from clutches attacked by these predators initially drop into the pond at an earlier developmental stage (Gosner stage 20–21 vs. stage 23; Gosner 1960) and smaller size (~6 vs. 8 mm total length). Early-hatched larvae are smaller because they have not completely converted their yolk stores into tissue (i.e., they have more yolk at hatching than larvae from later hatched clutches) and possibly because exposure to embryonic predators alters how yolk stores are invested. While reed frogs and parasitoid flies have similar effects on the timing of hatching and initial

larval traits, these predators can differ considerably in their effect on initial larval density. For example, during the first month of the breeding season, egg-stage predation by *Afrixalus fornasini* can reduce the density of *H. spinigularis* tadpoles entering Amani Pond by more than 60%, while studies at several sites suggest that parasitoid flies attack many fewer clutches and have a much smaller effect on larval density (Vonesh 2000, 2003).

Hyperolius spinigularis larvae face a suite of potential aquatic predators (Appendix B). The most abundant and most effective aquatic predators of *H. spinigularis* larvae were larvae of the libellulid dragonfly *Trapezostigma basilaris* (Appendix B, Fig. B1, B2). For the experiments below we focus on this aquatic stage predator.

Consequences of egg-stage predator effects for growth and survival to metamorphosis

To evaluate the consequences of predator-induced hatching and egg predator effects on larval density, we conducted a 2 × 3 × 2 factorial experiment with a randomized block design in which we manipulated initial size/age, initial density, and presence of ambient densities of aquatic predators ($+P_{AQ}$ and $-P_{AQ}$; Appendix C, Table C1). Each of these 12 treatments was replicated four times. The two levels of the initial size factor represent larval hatching sizes in the presence and absence of egg-stage predation (S_{-EP}, S_{+EP}). The three levels of the initial density factor correspond to expected tadpole densities given no egg-stage predation (N_{-EP}) and densities reflecting the numerical effect of either of two egg predators, *Typopsilopa* sp. fly larvae (N_{+TY}) or the reed frog *A. fornasini* (N_{+AF}).

This experiment was performed in 48 white plastic water storage tanks (1.2 × 0.8 × 0.4 m; Chemi and Cotex Industries, Dar es Salaam, Tanzania) arranged in a 3 × 16 array in a partially shaded forest clearing. Pools were initially filled to a volume of 220 L with Amani Pond water filtered through a 0.3 mm mesh screen and were immediately covered with tight fitting lids of fiberglass window screening to prevent unwanted colonization by insects and frogs. Screened drain holes prevented overflow during heavy rains. Tanks were buried to a depth of 15 cm in shallow trenches to provide a more stable thermal regime. To each tank we added 200 g of washed and dried pond litter, 10 g of commercial fish food (Hikari brand, Kyorin Fish Industries, Himeji, Kyoro, Japan), 300 g (~25, 40 cm long stems) of washed freefloating macrophytes (*Myriophyllum spicatum*), and a 0.5 L inoculum of a stratified pond water sample collected from Amani Pond using a 80 μm plankton net. All components were assigned to pools randomly. Tanks were filled with water on 19 March, and litter and other components were added on 22 March. Tanks were allowed to equilibrate for approximately two weeks before the start of the experiment. Treatments were randomly assigned to tanks, and the experiment was initiated on 5 April with the addition of *H. spinigularis* and *T. basilaris* larvae. Growth and survivorship were estimated monthly by dipnetting out all larvae and taking digital photographs of the larvae from each tank. The total lengths (TL) of all larvae were measured using the open source digital image analysis software ImageJ (*available online*).[2] Measurements were calibrated for each image by referencing a ruler in each photograph. Damaged larvae or larvae hidden behind other larvae were not included in analyses. Metamorphosed dragonflies were replaced weekly to maintain predator density. After 16 weeks, tanks were emptied and any remaining larvae counted. Survival was estimated as the number of metamorphs (removed weekly) plus the number of surviving larvae [proportion of total survivors that completed metamorphosis (i.e., >Gosner stage 46): 0.75 ± 0.09, mean ± 95% CL]. We used general linear mixed effect models (Pinheiro and Bates 2000, Venables and Ripley 2002) to examine effects of initial larval density, initial size, and presence of aquatic predators on three response variables: (1) the proportion of larvae surviving to the end of the experiment; (2) the proportion of survivors at the end of the experiment to reach metamorphosis (Gosner stage 42); and (3) mass at metamorphosis (Gosner stage 46). Initial size, density, and predator presence–absence were considered fixed factors; block was modeled as a random factor. Proportional data were arcsine square-root transformed prior to analysis. All analyses were performed in R version 1.7.0, an open source language and environment for statistical computing and graphics (Ihaka and Gentleman 1996, R Development Core Team 2004).

Effects of predator-induced hatching plasticity: S_{-EP} and S_{+EP}.—In addition to the mortality caused by egg-stage predators, exposure to egg predators causes surviving embryos to hatch earlier and at a smaller initial size. To simulate this sublethal effect of egg-stage predation we collected fresh [<Gosner stage 10 (Gosner 1960); ~1–12 h old] *H. spinigularis* clutches from the field on two dates: 10 clutches each on 26 and 29 March (3 d age difference). These clutches of different known ages (10 and 7 d) were submerged in water and gently shaken to induce hatching (completed hatching occurred within minutes of induction) on 4 April, the day before the experiment began. Clutches within each date were pooled and larvae randomly assigned to density and predator treatments from respective pooled groups. To reduce the effect of initial handling on the experimental outcome, larvae were held overnight and dead larvae were replaced (<1% initial mortality). Larvae were then digitally photographed to establish initial size differences among treatments. Larvae from eggs collected on 26 March (~10 d old; $\bar{\chi}$ = 9.33 ± 0.08 mm total length, mean ± 95% CL) were used in S_{-EP} treatments and larvae from eggs collected on 29 March

[2] ⟨http://rsb.info.nih.gov/ij⟩

(~7 d old; $\bar{\chi}$ = 7.14 ± 0.06 mm total length) were used in S_{+EP} treatments.

These differences reflect a decrease in age and total length (TL) at hatching (Δ−3 d; −2.19 ± 0.11 mm TL; 23% decrease in TL) consistent with that induced by *A. fornasini* (Δ−2.6 ± 1.1 d; Δ−2.17 ± 0.77 mm; 27% decrease in TL) and ephydrid flies (Δ−4.0 ± 3.2 d; Δ−1.5 ± 1.1 mm TL; 19% decrease in TL) (Vonesh 2003). Within a given level of initial size there were no significant differences in total length among different levels of the density ($F_{2,36}$ = 1.1, P = 0.344) or predator ($F_{1,36}$ = 1.3, P = 0.255) factors.

Numerical effects of egg predators: N_{-EP} and N_{+AF}, N_{+TY}.—Initial tadpole densities in the experimental trials were based upon field estimates of mean clutch size, clutch density, the number of clutches attacked by each predator type, and the mean survivorship of undisturbed vs. attacked clutches. These parameters were estimated by monitoring reproductive effort and clutch survival along two randomly located 3 × 30 m transects in Amani Pond between October 2001 and the start of the experiment in April 2002. Clutch production along each transect was monitored at 2–3 d intervals, new clutches were marked and followed through to hatching, and clutch survivorship was determined by placing capture cups beneath clutches as they neared hatching (Hayes 1983, Warkentin 1995; Appendix A, Fig. A1B). A more detailed account of our clutch monitoring methodology is provided in Vonesh (2003).

The density of tadpoles in the absence of egg predators (N_{-EP}) was estimated from the mean clutch density (Φ; clutches/m^2), the mean clutch size (μ; eggs/clutch), and the mean proportional survival to hatching of embryos in clutches that are not attacked [σ_E; thus, $N_{-EP} = (\Phi)(\mu)(\sigma_E)$]. The density of tadpoles in the presence of egg predators (N_{+AF}, N_{+TY}) was estimated by including the proportion of the total clutches attacked by each predator (ψ_{+AF}, ψ_{+TY}) and the expected survival of embryos in clutches attacked by that predator (σ_{+AF}, σ_{+TY}). For example, initial density given the effects of *A. fornasini* (N_{+AF}) was the larval contribution of clutches that are not attacked [$(\Phi)(1 - \psi_{AF})(\mu)(\sigma_E)$], plus the contribution of clutches that are attacked [$(\Phi)(\psi_{AF})(\mu)(\sigma_{AF})$]. Standard deviations for initial densities were calculated from the standard deviations of each of the estimated parameters, using standard rules for error propagation (Lyons 1991). Tank densities reflecting larval densities in the absence of egg predation (N_{-EP}, treatments 1, 2, 7, and 8, Appendix C) were 38.8 larvae/m^2 (35 larvae/tank). Tank densities reflecting arboreal egg-stage predation by *A. fornasini* (i.e., *A. fornasini* density-mediated effect, N_{+AF}, treatments 3, 4, 9, and 10, Appendix C,) were 11.11 larvae/m^2 (10 larvae/tank). Tanks densities reflecting arboreal egg-stage predation by *Typopsilopa* fly larvae (i.e., *Typopsilopa* density-mediated effect, N_{+TY}, treatments 5, 6, 11, and 12, Appendix C) were 27.8 larvae/m^2 (25 larvae/tank). These densities fall within the confidence intervals estimated from the field data using the methods outlined above. A detailed account of how each density was estimated is given in Appendix A.

Integrating patterns of growth, and density and size-specific risk

To better understand the mechanisms that determined the survival of *H. spinigularis* larvae in the presence of predators, we developed a simulation model that incorporates differences in initial size and growth rates between early- and late-hatched larvae in the density × size manipulation experiment above, as well as size- and density-specific larval predation risk to dragonflies (as determined by two additional experiments for this paper). The goal of this model is evaluate whether an understanding of these mechanisms is sufficient to explain the patterns of survival observed in the field experiment.

Larval growth.—We focused on growth rates during the first 30 days, as this is the period when most growth and mortality occurs, and was prior to any metamorphosis. Alford and Jackson (1993) argued that the exponential growth model provides the most accurate description of growth prior to metamorphosis in amphibian larvae, so we modeled growth as

$$S_t = S_i e^{k_{ij}t} \quad (1)$$

where S_t is larval total length (mm) at age t days, S_i is total length at hatching, and k_{ij} is the exponential growth rate constant for the ith level of initial size and the jth level of the initial density factor (Appendix D, Table D1, growth). We estimated k_{ij} over the first 30 days via linear regression of log-transformed size data on time. Thus, we have modeled growth rates based on initial conditions and have not explicitly incorporated changes in growth due to the direct (e.g., depletion) or indirect (e.g., changes in larval foraging behavior) effects of larval-stage predation.

Effect of larval density on risk.—To estimate the shape of the functional response we conducted an experiment in which we varied larval density in the presence and absence (a control) of dragonfly larvae. This experiment was conducted in 32 300-L plastic tanks prepared in early November 2001 in the same manner as the density × size manipulation experiment. Treatments consisted of eight initial densities: 5, 10, 15, 20, 30, 50, 75, and 100 larvae/tank. Each treatment was replicated twice. *Hyperolius spinigularis* larvae used in the experiment came from 18 clutches collected upstream of Amani Pond that hatched naturally between 15 and 20 November. On 22 November, all hatchlings were pooled and randomly assigned treatments. To reduce the effect of initial handling on the experimental outcome, larvae were held overnight and dead larvae were replaced (<1% initial mortality). Larvae were then digitally photographed to establish initial size (9.69 ± 0.23 mm total length, mean ± SD). Three late-instar *T. basilaris* larvae (18.9 ± 2.26 mm total length)

were added to each tank. Tanks were checked every other day and metamorphosed dragonflies were replaced to maintain predator densities (none emerged, therefore none were replaced). Survivorship of frog larvae was estimated after 14 d by dipnetting out all *H. spinigularis* and dragonfly larvae from tanks. Mortality in the absence of predators was very low, and similar across densities (0.04 ± 0.03 larvae/tank).

We modeled predation risk with a type II functional response. However, the classic form of the type II functional response makes no allowance for prey depletion, and hence is only appropriate for studies of very short duration, experiments where prey are replaced as they are consumed, or in situations where predators search systematically so that they do not re-encounter previously exploited areas (Elliot 2003). Because our experimental design did not fit these criteria, we estimated values for the attack rate (α_D) and handling time (H_D) using the random predator equation of Rogers (1972; see also Juliano 1993). The random predator equation is equivalent to a type II functional response that incorporates the effects of prey depletion and is solved by integrating the foraging rate over time as prey density declines:

$$N_a = N[1 - e^{\alpha_D(N_a H_D - pt)}] \quad (2)$$

where N_a is the number of prey eaten in t days, N is the initial prey density, α_D is the attack rate (i.e., the instantaneous rate of discovering prey by one predator), p is the number of predators, and H_D is the handling time (Appendix D, Table D1, functional response). We assume that the actual number attacked, $\hat{N}_a$, for initial density N follows a binomial distribution, $\hat{N}_a \sim \text{Binom}(N, \sigma)$, where σ is the probability of an individual prey being killed during the course of the experiment ($\sigma = N_a/N$). We then obtained estimates for α_D and H_D that satisfy Eq. 2 and maximize the binomial likelihood. In our simulation model, where population densities are tracked daily and depletion therefore does not need to be modeled explicitly, we used these parameter estimates for α_D and H_D in a type II functional response (Holling 1959):

$$K = \frac{\alpha_D N}{1 + \alpha_D N H_D} \quad (3)$$

where K is the expected predation rate (i.e., number of prey eaten per predator per day). Ideally, this experiment would have been conducted for a fixed larval size. However, since larvae grew during the experiment, our estimated functional response is perhaps best viewed as an approximation of the functional response for larval size midway through the interval (~12.8 mm total length).

Effect of larval size on predation risk.—To quantify how size and age influence the vulnerability of *H. spinigularis* larvae, we exposed five larval size/age classes to dragonfly larvae and quantified survival. Each treatment was replicated three times. The experiment was conducted in 35-L plastic tubs (diameter = 0.32 cm^2) arrayed near the larger tanks above. Each tank was filled with 25-L filtered pond water and received four 40 cm stems of floating *M. spicatum*, 200 g of dried pond litter, and 20 g of commercial fish food (ad lib food). Tanks were covered with mosquito netting. *Hyperolius spinigularis* larvae were obtained from clutches collected on different dates, yielding five non-overlapping size/age classes (Appendix B, Fig. B2B). The smallest, youngest class was induced to hatch from three clutches collected from sites near Amani on 5 June (size/age class 1:0 d after hatching; 8.89 ± 0.04 mm total length, TL, mean ± SD). Larvae used in the remaining treatments were reared from 3 or 4 near-to-hatching clutches collected on different dates but reared under similar conditions: collected on 28 May (size/age class 2:7 d after hatching; 11.55 ± 0.28 mm TL), collected on 29 April (size class 3:5 wk after hatching; 20.42 ± 0.91 mm TL), collected on 21 April (size class 4:6 wk after hatching; 25.34 ± 0.75 mm TL), and collected on 29 March (size class 5:9 wk after hatching; 37.76 ± 1.18 mm TL). Late-instar *T. basilaris* nymphs (13.34 ± 1.23 mm TL), were collected from the field on 2 June, fed one *H. spinigularis* larvae, and then held without food until the beginning of the experiment. Dragonflies (two per tank) were randomly assigned to the predator treatment tanks on 4 June and the experiment began on 5 June with the addition of *H. spinigularis* larvae. Emerged dragonflies were replaced daily to maintain predator densities (only one was replaced). After 3 days all surviving larvae were counted.

We estimated the functional form of size specific mortality using a phenomenological (i.e., rather than mechanistic) model that allows for a peak in prey vulnerability at intermediate sizes:

$$\gamma_S = \frac{e^{[\varepsilon(\varphi - S)]}}{1 + e^{[\beta\varepsilon(\varphi - S)]}} \quad (4)$$

where γ_S is the size-specific predation rate, S is prey size, and ε, β, and φ are fitted constants (Appendix D, Table D1, size-specific attack rate). Note that this expression does not explicitly account for predator saturation with increasing prey density (i.e., as in Eq. 2). We assumed γ_S for size S follows a binomial distribution, $\gamma_S \sim \text{Binom}(N, \gamma_S)$ and obtained estimates for ε, β, and φ that maximized the binomial likelihood.

Combining size and density specific risk.—We next had to combine our estimate of the size-specific predation rate (which was measured at a single density) with our description of the functional response (which quantified the effect of prey density for a single prey size). We developed a model that predicted the attack rate for any combination of density and size by using the functional response to recover the attack rate without the effects of prey saturation from the predation rate we estimated from the size-manipulation experi-

ment, γ_S. We did this by setting K in Eq. 3 equal to $\gamma_S(N)$, setting prey density to N_S (i.e., the prey density used in the size-specific predation experiment) and then solving algebraically for the attack rate (now a function of size and density, so we now call it α_{SD}):

$$\alpha_{SD} = \frac{\gamma_S}{1 - \gamma_S N_S H_D}. \quad (5)$$

We assume that the handling time (H_D) estimated from the functional response holds across all larval sizes. The density and size-specific predation rate can then be estimated using Eq. 3 by replacing α_D with α_{SD}, providing us with a hypothesis regarding how the predation rate behaves across the range of relevant density and size parameter space.

Simulating larval growth and mortality.—We then simulated larval growth and survival in daily increments (i.e., ignoring effects of depletion and growth within a day) over the duration of the density × size manipulation experiment (112 d). Simulations were run for each experimental density and for two initial sizes (reflecting the mean size for either early or later hatched larvae). In each time step, larvae grew exponentially at rates specific to initial density and size, and were killed by predators according to size and density specific predation rates. Larvae that were killed were decremented from the density at the start of the next time step. We repeated this process until 112 d or all larvae reached 40 mm TL, at which point we assumed they are no longer vulnerable to predation. We calculated the total number killed over the experiment as the sum of the number killed in each time step.

Error estimates for model predictions were obtained via Monte Carlo uncertainty analysis (e.g., Caswell 2001). The distribution for total number killed at the end of the experiment for each density was generated according to the following steps: (1) we specified the joint probability distributions of the estimates of the parameter controlling growth (Eq. 1), and size- (Eq. 4) and density-specific mortality (Eq. 2) from the variance–covariance matrix of the maximum likelihood parameter estimates; (2) we drew random samples from the appropriate distribution for each parameter and calculated the total number killed; (3) we repeated this process (for a given set of parameter estimates) for 100 iterations of the simulation and estimated the mean of the Monte Carlo distribution of the total number killed; and (4) we repeated this process to obtain 100 estimates of the model's mean prediction (i.e., using 100 different parameter values, thus incorporating uncertainty in parameter estimation; sampling uncertainty for a set of parameters was greatly reduced via step 3).

RESULTS

Larval survival

Aquatic predators had a significant negative effect on larval survival (Table 1, Fig. 1A). Whereas survival in the predator free treatments was high (92%) and similar across density ($F_{2,18} = 0.09$, $P = 0.915$) and size factors ($F_{1,18} = 0.224$, $P = 0.642$), predators reduced mean survival proportionally by 44% (i.e., to 52%). Furthermore, the negative effect of predators on survival was greater for the initially larger/older larvae (i.e., initially smaller larvae survived better) and (marginally) for larvae at higher densities. Across density levels, dragonflies had a 50% greater effect on larger/older larvae compared with early-hatched, smaller larvae. Across initial size treatments, the average effect of dragonflies at initial densities of 25 and 35 larvae/tank was more than twice their effect at 10 larvae/tank; i.e., dragonflies reduced survival by ~53% on average at higher densities compared to only 23% at 10 larvae/tank. The effects of dragonflies at 25 and 35 larvae/tank were similar. Most mortality in the predator treatments for both larger/older (82%) and smaller/younger (88%) occurred during the first 30 days of the experiment.

TABLE 1. Results of analysis for effects of density, predator, and size treatments on *Hyperolius spinigularis* larval survival, proportion of survivors to metamorphose, and metamorph mass.

Factor	df	F	P
Survival			
Density	2, 33	3.73	0.035
Predator	1, 33	86.69	<0.001
Size	1, 33	2.64	0.11
Density × predator	2, 33	2.87	0.07
Density × size	2, 33	0.52	0.60
Predator × size	1, 33	4.91	0.03
Density × predator × size	2, 33	0.27	0.77
Proportion of survivors that metamorphosed			
Density	2, 33	10.99	<0.001
Predator	1, 33	1.97	0.17
Size	1, 33	1.50	0.23
Density × predator	2, 33	2.60	0.09
Density × size	2, 33	0.13	0.88
Predator × size	1, 33	0.74	0.40
Density × predator × size	2, 33	0.57	0.57
Mass at metamorphosis			
Density	2, 33	23.67	<0.001
Predator	1, 33	60.93	<0.001
Size	1, 33	4.32	0.046
Density × predator	2, 33	1.90	0.17
Density × size	2, 33	0.21	0.81
Predator × size	1, 33	0.53	0.47
Density × predator × size	2, 33	0.31	0.74

Reductions in larval density and hatchling size that mimicked egg predation by reed frogs increased larval survival to a similar degree (Vonesh and Osenberg 2003). Reductions in initial density due to predation by *A. fornasini* (we imposed a ~70% reduction mimicking estimates of predation in the field) resulted in a 110% increase in survival and reductions in hatchling size/age resulted in a 90% increase in mean larval survival. In contrast, size-mediated effects of *Typopsilopa* sp. predation had the greatest effect on larval survival. Reductions in initial density due to fly predation (we

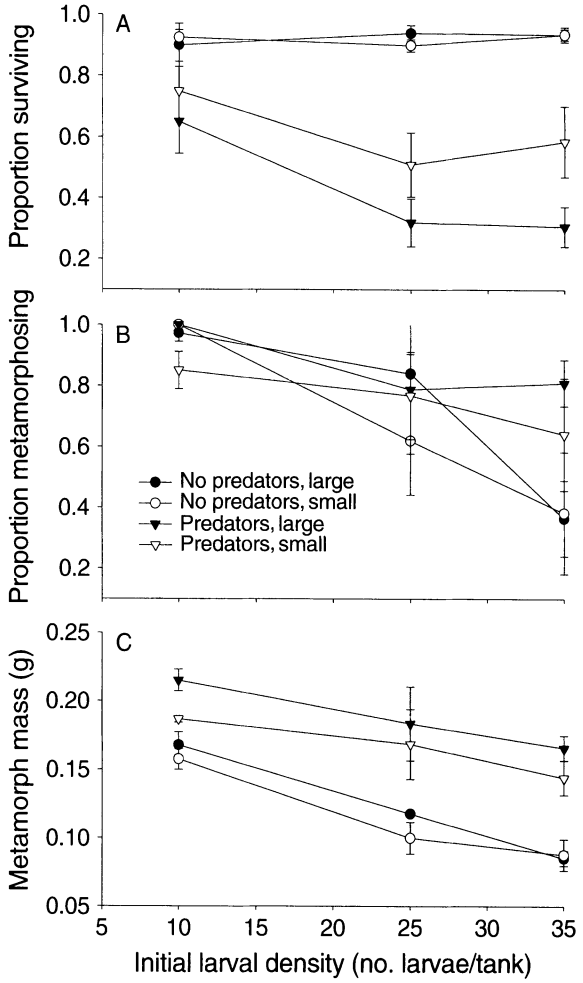

FIG. 1. Results from the tank experiment: (A) proportion of tadpoles surviving to metamorphosis or the end of the experiment; (B) proportion of surviving frogs (metamorphs and larvae) that reached metamorphosis; (C) mass at metamorphosis. All values shown are means ± SE. Our experimental design crossed three levels of initial larval density with two levels of initial larval size and the presence or absence of aquatic predators (Appendix B: Table B1).

imposed ~30% reduction) had almost no effect on larval survival (<3% increase), while the effect of reductions in hatchling size/age due to fly predation were the same as those for *A. fornasini* (i.e., a 90% increase in larval survival).

Proportion of surviving larvae that reach metamorphosis

Reductions in initial larval density (mimicking egg-stage predation) had a positive effect on larval development rate (Table 1, Fig. 1B). Across size and predator treatments, nearly all survivors metamorphosed from the lowest density tanks (96%), while only a little more than half (55%) metamorphosed from the highest density treatments, on average. However, this difference was reduced in the presence of aquatic predators. In the absence of predators, decreasing initial density from 35 to 10 larvae/tank increased the proportion of survivors to metamorphosis by 156%. In comparison, in the presence of predators the same decrease in density resulted in only a 31% increase in the proportion of metamorphs. There was no effect of initial hatchling size on larval development: the same proportion of small/early-hatched and large/late-hatched larvae had reached metamorphosis by the end of the experiment.

The density- and size-mediated effects of *A. fornasini* egg-stage predation on development were similar in magnitude but opposite in direction. Reductions in initial density due to reed frog predation resulted in a 23% increase in the proportion of survivors to reach metamorphosis in the predator treatments, while smaller size/age at hatching reduced the proportion of metamorphs by 20% (although this difference was not statistically significant, $P = 0.23$). Reductions in initial density due to fly predation had no effect on the proportion of metamorphs in the predator treatments (<3% increase), while the effect of reductions in hatchling size/age due to fly predation was the same as the effect due to reductions due to frog predation.

Mass at metamorphosis

Larval density, aquatic predators, and initial size all affected mass at metamorphosis (Table 1, Fig. 1C). Metamorphs from the lowest density treatments had 50% greater mass on average than metamorphs from the highest density treatments. Metamorphs from predator treatments averaged 48% greater mass than metamorphs from no predator treatments. In addition, metamorphs that were initially larger/older at hatching had 13% greater mass compared to initially smaller (and younger) hatchlings. As a result there was a considerable range—from 0.08 to 0.22 g—in mean mass at metamorphosis among treatments.

The density- and size-mediated effects of *A. fornasini* egg-stage predation on metamorph mass were asymmetrical in size and direction. Reductions in density mimicking frog predation increased metamorph mass by 30%, while reductions in size decreased mass by 13%. Thus, we expect a net gain in mass of ~17% (0.028 g) for density and size effects combined (assuming they are independent). Metamorph size from the treatment with both the density and size effects of frog predation were 13% larger on average than metamorphs from the predator treatments with no effect of egg-stage predators (Fig. 1C). In comparison, density- and size-mediated effects of fly egg-stage predation on metamorph mass also acted in opposite directions but were similar in magnitude. Reductions in initial density due to fly predation increased mean mass 11%, while the effect of reductions in hatchling size/age reduced mean mass by 13%.

Growth rates

Over the first 30 days of larval development, early-hatched smaller larvae (mimicking predator-induced

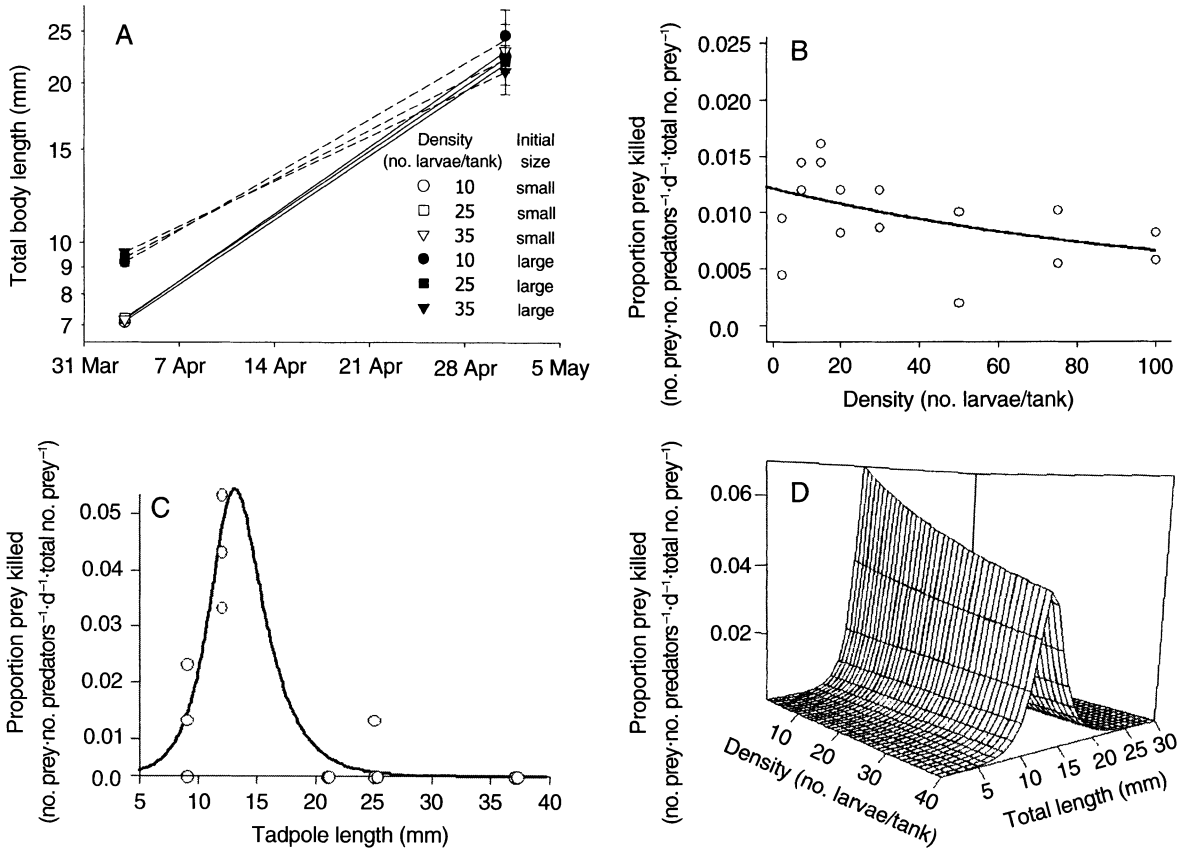

FIG. 2. Parameterization of the model. (A) Larval growth over the first 30 d for each density and initial size combination (means ± SE). The slopes from these regression were used to parameterize larval growth in the model. Dates shown are during 2002. (B) The proportion of larval *H. spinigularis* (~12 mm total length) killed by *T. basilaris* (Eq. 2). (C) The functional form of *H. spinigularis* size-specific predation risk by *T. basilaris* (Eq. 4). (D) The hypothesized relationship among predation rate and tadpole size and density used in the simulation model (Eq. 3 using α_{SD}). Parameter estimates and confidence intervals are presented in Appendix D (Table D1).

effects on hatching traits) exhibited higher growth rates ($\bar{\chi}$ = 0.0393 ± 0.005 mm/d, mean ± SD) than late-hatched larvae ($\bar{\chi}$ = 0.0296 ± 0.003 mm/d; Appendix D, Fig. 2A). Furthermore, the difference between the growth rates of these two initial size classes increased as initial density increased. At low densities (10 larvae/tank) growth rates for early-hatched larvae were 18% higher than late-hatched larvae, while at highest densities (35 larvae/tank) early-hatched growth rates were 48% higher, on average.

Density and size-specific risk

Due to the combined effects of encounter rates and handling time, predation risk from the dragonfly larvae, *T. basilaris*, decreased with density and was a hump-shaped function of size (Appendix D, Fig. 2B–D). Vulnerability to dragonflies was initially low, increased until ~13 mm TL, and then declined to zero as larvae approached 25 mm TL (Fig. 2C). We combined the expressions for size- and density-specific risk to generate a predation risk surface that described predation rates as a function of both larval size and density (Fig. 2D).

Comparison of observed vs. simulated larval survival

We examined the contribution of the compensatory growth we observed in early-hatched larvae to survival by implementing a simulation with two growth responses; (1) we averaged small and large growth rates for a given initial density (i.e., removed the compensatory response), and (2) we used size- and density-specific estimates for growth (i.e., included compensatory response). If compensatory growth was responsible for the reduced risk of small larvae, then only the second simulation should produce patterns similar to those observed.

Under both of these conditions the simulation predicted similar survival across densities as we observed in our experiment (Fig. 3A–C, proportional survival ($\bar{\chi}$ ± SD) in experiment, 0.52 ± 0.18; in no compensatory response model, 0.49 ± 0.022; in compensatory response model, 0.49 ± 0.05). In the absence of the

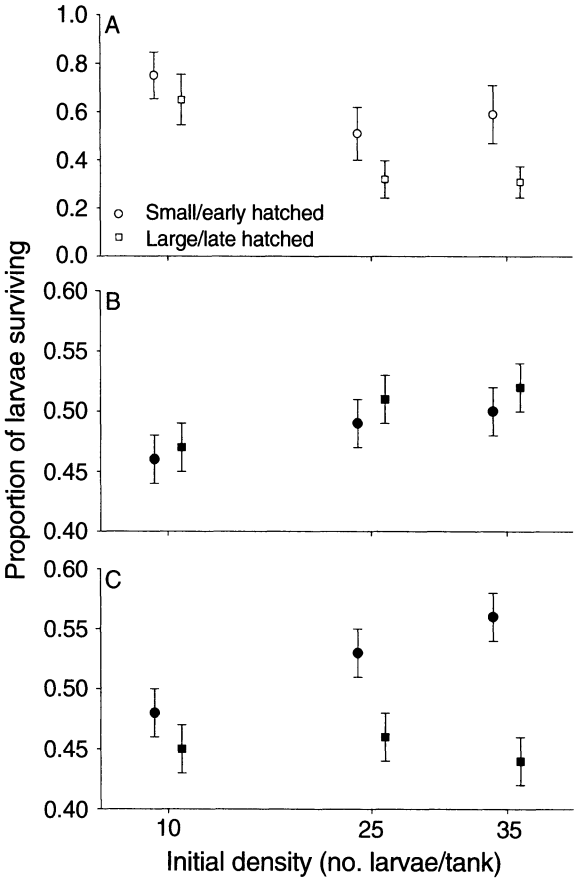

FIG. 3. Larval survival: comparison of experimental and simulation results. (A) Experimental results: proportional survival (means ± SE) to the end of the experiment in the presence of predators at each initial density. (B and C) Simulations results (note change in scale). (B) Equal growth rates: proportional survival (means ± SD) through the experiment as predicted by the simulation with equal growth rates for small/early-hatched and large/late-hatched larvae. (C) Compensatory response: proportional survival (means ± SD) through experiment as predicted by the simulation with initial size and density specific growth rates (Appendix D, Fig. 2).

compensatory growth response, the simulation predicted similar survival for early- and late-hatched tadpoles (late-hatched larvae survived ~3% better, Fig. 3B). When the compensatory growth response of early-hatched larvae was included in the simulation this pattern reversed itself: early-hatched larvae survived better than late hatchers. This survival difference increased with increasing density: early-hatched larvae survived 7%, 15%, and 30% better than late-hatched larvae as initial densities increased from our low to medium to high, respectively (Appendix D, Fig. 3C). While this qualitatively matches the pattern observed in the experimental results (i.e., small larvae survived better, particularly at high densities), in the experimental results the difference in survival between these initial size classes was considerably larger. In addition, the model also appears to underestimate the mean survival of both initial size classes at low densities.

DISCUSSION

Previous empirical work on predator-induced hatching found that early hatching increased mortality during the larval stage (Warkentin 1995). Theoretical studies support this result: predator-specific defenses (e.g., predator-induced early hatching to avoid egg-stage predators) should result in increased vulnerability to other predators (e.g., aquatic stage predators) (Matsuda et al. 1993, 1994, 1996). This trade-off maintains the complex life history; in the absence of the trade-off, larvae should hatch earlier and earlier, eventually eliminating the egg stage from the life history. Interestingly, we found no evidence of a predation risk trade-off across egg and larval stages in our system. While early-hatched/smaller and late-hatched/larger larvae survived equally well in the absence of predators, early hatchlings survived better in the presence of aquatic predators (Fig. 1A). If hatching early is a successful strategy for evading egg-stage predators and there is no trade-off in embryonic vs. larval predation risk (or even a survival benefit) why don't larvae hatch early all the time? Other costs of early hatching may arise later in the life history. For example, hatching early could delay larval development and lead to longer exposure to larval predators. However, there was no significant effect of early hatching on larval development rate, as measured by the proportion of survivors that reached metamorphosis (Fig. 1B). There was, however, a significant effect of size at hatching on size at metamorphosis (Fig. 1C). Metamorphs from early-hatched larvae were 13% smaller than those from late-hatched larvae. Smaller size at metamorphosis can reduce post-metamorphic survival and growth and lead to smaller size at sexual maturity, and hence lower reproductive success (e.g., Smith 1987, Berven 1990, Altwegg and Reyer 2003). In addition to these potential fitness consequences associated with relatively smaller size at metamorphosis, Vonesh (2003) explored an immediate cost of smaller size at metamorphosis by looking at size-specific predation on metamorphs by common fishing spiders. This study shows that smaller metamorphs were more vulnerable fishing spider predation. Thus, a trade-off between egg survival and the costs and benefits associated with metamorph size may help maintain a balance between early and late hatching.

The fact that small/early-hatched larvae survived better than large/late-hatched larvae was a surprise to us. We expected late-hatched larvae, by virtue of their greater size, would escape relatively more larval mortality. A number of previous studies indicate that larval anuran risk to odonate predators decreases with increased tadpole size (summarized in Table 10 of Alford 1999). However, in our system, risk to libellulid predation was greatest at intermediate size classes with size refugia for small and large tadpoles. This pattern

may reflect the combination of predator-induced effects on hatching size and developmental traits in our study. The initial increase in vulnerability with size/age is likely driven by changes in activity associated with the shift from reliance upon yolk stores to active foraging (i.e., a developmental effect), which increases predator encounter rates, while the subsequent decline in risk is likely driven by the size effects observed in previous studies. Indeed, greatest risk at intermediate size classes is expected when encounter rates increase and capture probabilities decrease with increasing size (Osenberg and Mittelbach 1989).

However, a hump-shaped risk function alone is insufficient to explain the better survival of early-hatched tadpoles. Both early- and late-hatched larvae drop into the aquatic environment at small sizes before risk to dragonfly predation peaks. Thus, both early and late hatchers must grow through the vulnerable size classes. If they grow at the same rate, small/early-hatched larvae should still suffer higher mortality because large/late-hatched larvae will maintain their head start and spend less time in vulnerable size classes. This result is confirmed in simulation results: when early- and late-hatched larvae have equal growth rates, late-hatched larvae survived slightly better (Fig. 3B). However, early-hatched larvae in the tank experiment exhibited compensatory growth (i.e., increased growth independent of egg and/or larval predator effects on density, etc.), growing more rapidly during the first thirty days of the larval stage than later hatched larvae. This difference in growth tended to be greater at higher densities (Appendix D, Fig. 2A). If increased growth rates of early-hatched larvae enabled them to grow more quickly than late-hatched larvae through the sizes vulnerable to libellulid predation, the survival benefit of compensatory growth may swamp the negative consequences of hatching early. As a result, smaller/early-hatched larvae would survive better than late-hatched larvae. The simulation results suggest that these mechanisms could generate the pattern of survival we observed in the tank experiment. When we include the compensatory growth response of early-hatched larvae in the model, we find that early-hatched larvae exhibit higher survival than late-hatched larvae and that the survival difference between these size classes increases with increasing density (Fig. 3C).

Recent theoretical studies have highlighted that the strength of trait-mediated indirect effects of predators is sensitive to the timing of experimental manipulations and the length of observation (Luttbeg et al. 2003). Differences in the time scale of experimental manipulations may explain the discrepancy between our results and previous studies. For example, Warkentin (1995) found that hatching early increased vulnerability to aquatic predators, while we observed that early-hatched larvae survive better in the presence of predators. However, Warkentin's (1995) predation trials focused on the first 24-h post-hatching. In our system it appears that early-hatched larvae survive better because they grow faster than late-hatched larvae through vulnerable size classes. This type of a response to predators was not possible in Warkentin's (1995) short-term studies. However, in a longer study without predators, Warkentin (1999*a*) observed faster growth rates as well as more rapid onset of feeding and development of feeding structures in predator-induced early- vs. unexposed, late-hatched red-eyed treefrog larvae, and noted that this could yield an advantage to early hatchers. Thus, the longer term survival consequences of early hatching may swamp the early survival costs Warkentin (1995) observed for small larvae, yielding no net difference (or even a reversal) in the larval survival of early- and late-hatched larvae. As a result, it is not clear if there is a trade-off between early hatching and larval survival. In our study system there were no short-term costs (because of the hump-shaped survival function), and thus hatching early only had beneficial effects on larval survival.

Compensatory growth in larval anurans has been reported in response to poor conditions or stress early in ontogeny associated with low resources (Alford and Harris 1988) and decreased pH (Räsänen et al. 2002) and predator-induced early hatching (Warkentin 1999*a*; this study). Given that delayed larval development or reduced metamorph size can have potential long-term fitness consequences, selection is expected to favor compensatory strategies, provided that compensation in and of itself is not too costly. However, a growing body of studies, from diverse taxa, show that such compensatory responses are costly, and that these costs are frequently manifested much later in ontogeny (reviewed in Metcalfe and Monaghan 2001). For larval anurans potential costs of compensatory growth include elevated predation rates (due to increased foraging activity; Anholt and Werner 1998) and delayed timing of metamorphosis (Downie and Weir 1997). In our study, reduced mass at metamorphosis may represent a cost of compensatory growth for early-hatched tadpoles. While small/early-hatched larvae grew more rapidly than larger/late-hatched larvae through the first month (when they were vulnerable to predation) this trend gradually reversed itself later in larval ontogeny. Thus, while early-hatched larvae gained a survival benefit from rapid compensatory growth early in larval ontogeny it may have come at the cost of later growth/mass at metamorphosis.

While the simulation results confirm that the combination of size-selective predation and compensatory growth mechanisms can generate survival patterns consistent with the experimental data, there are other mechanisms that could explain or contribute to greater survival in early-hatched tadpoles that we were unable to evaluate. For example, morphological or behavioral differences between early- vs. late-hatched tadpoles have been documented in other systems (e.g., Warkentin 1999*a*, *b*, Laurila et al. 2001), and may result in

differences in their relative vulnerability to aquatic predation. In addition, the simulation was relatively poor at predicting the proportion of larvae that survived at low densities. Data from the predator-present treatments show that larvae at low densities tended to survive better than larvae from higher density treatments, while the simulation results indicate that the proportion surviving is similar or slightly increasing with increasing density.

Our study highlights that the consequences of predator-induced hatching plasticity need to be examined within the context of the numerical effects of predators. For example, in our study both the numerical and size/age effects of egg-stage predators acted to enhance larval survival; thus, considering only the predator effects on hatchling traits would have led us to underestimate the consequences of egg predation on survival. Furthermore, our study highlights the importance of considering the potential for compensatory responses in the prey when evaluating life history trade-offs arising from predator effects on prey traits. In our system, prey compensatory responses reversed any initial negative effects of egg predators on hatchling size/age. For prey with complex life cycles, ignoring prey compensatory responses could lead to misidentifying the trade-offs that maintain the timing of key life history transitions.

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APPENDIX A

Estimates of the effect of egg predation on larval densities with photographs of the field site, of *Hyperolius spinigularis*, and of egg-stage predators are available in ESA's Electronic Data Archive: *Ecological Archives* E086-086-A1.

APPENDIX B

Methods and results associated with aquatic predator abundance and efficacy are available in ESA's Electronic Data Archive: *Ecological Archives* E086-086-A2.

APPENDIX C

A description of the design of the sequential multiple predator experiment is available in ESA's Electronic Data Archive: *Ecological Archives* E086-086-A3.

APPENDIX D

A table showing parameter estimates for simulation is available in ESA's Electronic Data Archive: *Ecological Archives* E086-086-A4.