POPULATION ECOLOGY

James R. Vonesh · Omar De la Cruz

Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines

Abstract In the last decade there has been increasing evidence of amphibian declines from relatively pristine areas. Some declines are hypothesized to be the result of egg mortality caused by factors such as elevated solar UV-B irradiation, chemical pollutants, pathogenic fungi, and climate change. However, the population-level consequences of egg mortality have not been examined explicitly, and may be complicated by density dependence in intervening life-history stages. Here we develop a demographic model for two amphibians with contrasting life-history strategies, *Bufo boreas* and *Ambystoma macrodactylum*. We then use the complementary approaches of elasticity and limitation to examine the relationships among stage-specific survival rates, larval-stage density dependence and amphibian population dynamics. Elasticity analyses showed that for a range of density dependence scenarios both species were more sensitive to changes in post-embryonic survival parameters, particularly juvenile survival, than to egg survival, suggesting that mortality of later stages may play an important role in driving declines. Limitation analyses revealed that larval density dependence can dramatically alter the consequences of early mortality, reducing or even reversing the expected population-level effects of egg mortality. Thus, greater focus on later life stages and density dependence is called for to accurately assess how stressors are likely to affect amphibian populations of conservation concern.

Keywords *Ambystoma* · *Bufo* · Elasticity · Population dynamics · Limitation

J.R. Vonesh (✉)
Department of Zoology, University of Florida, Gainesville, FL 32611, USA
e-mail: voneshjr@zoo.ufl.edu
Tel.: +1-352-392-9201, Fax: +1-352-3923704

O. De la Cruz
Department of Mathematics, Purdue University, Purdue, IN 47906, USA

Introduction

Since the early 1990s the scientific and conservation communities have been concerned with the apparent worldwide decline of amphibian populations (e.g., Wake 1991; Houlahan et al. 2000). The decline of species from what are thought to be relatively pristine habitats has been particularly disturbing (Drost and Fellers 1996; Laurance et al. 1996; Lips 1998). Efforts to explain these declines have focused in part on increased egg mortality caused by: exposure to elevated levels of solar UV-B radiation associated with atmospheric ozone depletion (Blaustein et al. 1994, 1995, 1997, 1998; Anzalone et al. 1998; Broomhall et al. 2000), pathogenic fungi (Kiesecker and Blaustein 1995; Kiesecker et al. 2001); acidification (Long et al. 1995), chemical pollutants (Ankley et al. 1998; Rowe et al. 2001), climate change (Davidson et al. 2001; Kiesecker et al. 2001) or a combination of these factors. However, while these stressors may reduce egg survival dramatically in some species, there has been little attempt to scale-up these egg-stage effects to the population-level.

The connection between life-stage-specific mortality and population-level phenomenon (e.g., amphibian decline) can be complicated if there is density dependence in one or more life-history stages (Wilbur 1996; Hellriegel 2000). For example, if larval survivorship is density-dependent, reducing egg-stage survival does not necessarily result in fewer emerging metamorphs. Decreased larval densities (through decreased egg survival) may reduce larval competition sufficiently to yield the same number of metamorphs as at higher larval densities. Density-dependent growth (reviewed in Skelly and Kiesecker 2001) and survival (e.g., Brockelman 1969; Wilbur 1976, 1977; Scott 1990; Van Buskirk and Smith 1991) in amphibian larvae has been documented (though not without exception) in field, artificial pond, and laboratory studies spanning more than three decades. While larval density dependence is well documented in amphibian systems, its importance when evaluating the implications of early mortality for amphibian populations has largely been overlooked.

Here we develop a stage-structured matrix model (Caswell 2000) that describes a generalized amphibian life cycle that explicitly incorporates larval-stage density dependence and then parameterize the model with data from published field studies. We focus on the Western toad, *Bufo boreas*, and the Long-toed salamander, *Ambystoma macrodactylum*. These species have very different reproductive strategies and may exhibit different relationships between egg mortality and density dependence. In addition, these species are known to be vulnerable during the egg stage to stressors such as UV-B irradiation, acidification, pathogenic fungi and climate change (Blaustein et al. 1994, 1997; Long et al. 1995; Kiesecker et al. 2001). We then examine the relationship among stage-specific survival rates, density dependence and adult equilibrium densities by two approaches: elasticity and limitation (Schmitt et al. 1999). Elasticity is a popular tool in conservation biology because it quantifies the relative importance of demographic transitions (e.g., stage-specific survival rates) to population dynamics. It is generally inferred that management efforts should be focused on the demographic parameters that have the largest elasticities (e.g., Crouse et al. 1987; Doak et al. 1994; de Kroon et al. 2000). We then use a limitation approach (Osenberg and Mittelbach 1996) to examine how large declines in egg-stage survival affect adult density. These are complementary approaches; both quantify how much a system is affected by particular processes but they differ in the scale of comparison. Elasticity addresses the population response to infinitesimal relative changes in model parameters, whereas limitation allows us to examine the population response to a large change in a specific stressor (Schmitt et al. 1999). Through this combined approach we will examine the role of larval-stage density dependence in determining; (1) which life-history stages contribute the greatest to adult dynamics, and (2) how egg mortality scales-up to the population-level.

Methods

General amphibian population model

Our model assumes a generalized amphibian life cycle (Fig. 1), where adults (A) emerge and breed synchronously in the spring. Eggs hatch into larvae that metamorphose by the end of that summer. Metamorphs over-winter and emerge as juveniles the following spring. Juveniles (J) then survive and mature into the breeding population. Using this scenario, we model per capita egg production as the mean clutch size (ϕ) adjusted by the adult sex ratio (ρ). Eggs survive to hatching with probability σ_e, and larvae survive to metamorphosis with probability σ_t, which is a function of larval density:

$$\sigma_t = \frac{\sigma_{tmax}}{(1+dT)^\gamma} \tag{1}$$

where σ_{tmax} is the maximal larval survival in the absence of density dependence, d is the density-dependence coefficient (m²/larvae), gamma (γ) is the density-dependence exponent (see below for an explanation of γ), and T is initial larval density:
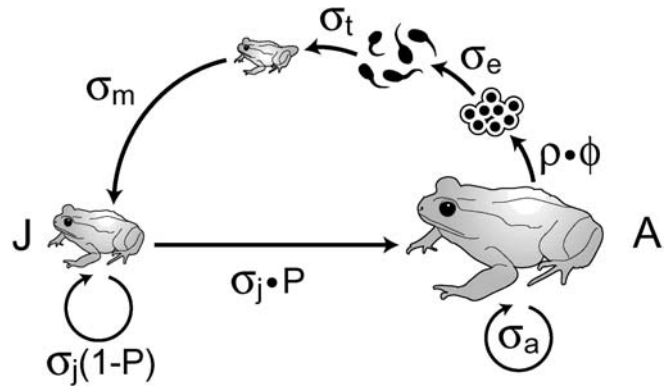
$$T = \rho\phi\sigma_e A \tag{2}$$

Fig. 1 Generalized amphibian life cycle. Oviposition occurs in the spring and egg production is determined by the sex ratio (ρ) multiplied by the average clutch size (ϕ). Eggs survive to become larvae with the probability σ_e. Larvae survive to metamorphosis with the probability σ_t, which is a function of initial larval density (Eq. 11), and metamorphs over-winter to emerge as juveniles (J) the following spring with the probability of σ_m. Annual juvenile survival is σ_j and the probability maturing is P. Adults (A) survive to the next year with the probability of σ_a

Metamorphs survive the first winter with the probability σ_m. Juveniles survive annually with the probability σ_j, and mature with probability P, and adults (A) survive from one year to the next with the probability σ_a. This yields the transition matrix,

$$\begin{bmatrix} J \\ A \end{bmatrix}_{t+1} = \begin{bmatrix} \sigma_j(1-P) & F(A) \\ \sigma_j P & \sigma_a \end{bmatrix} \begin{bmatrix} J \\ A \end{bmatrix}_t \tag{3}$$

which projects juvenile and adult densities (animals/m² shoreline habitat) forward in time steps of one year. The function F(A) represents the per adult annual production of new juveniles, which explicitly includes the expressions above for egg production and survival, density-dependent larval survival, and metamorph survival. All these processes occur within the first time step; thus,

$$F(A) = \rho\phi\sigma_e \frac{\sigma_{tmax}}{(1 + d\rho\phi\sigma_e A)^\gamma}\sigma_m \tag{4}$$

Equations 1 and 4 are related to the intraspecific competition model of Hassell (1975) and the simpler fisheries recruitment function of Beverton and Holt (1957). For the range of model parameter values used, the density-dependence exponent (γ) determines the form of larval density dependence (Eqs. 1, 4) and thus the relationship between the number of metamorphs (or juveniles) produced and the initial number of tadpoles in a cohort. When $\gamma=0$ this relationship is linear and juvenile recruitment is density independent. When $\gamma=1$ it is compensatory and juvenile recruitment approaches an asymptote as initial larval density increases (i.e., saturating function). When $0<\gamma<1$ weak density dependence occurs and the relationship is a decelerating curve in which juvenile production increases without limit as initial larval density increases. Finally, when $\gamma>1$, density dependence is strong and eventually produces over-compensation at high initial larval densities (i.e., hump-shaped function). The density-dependence coefficient (d) acts as a scaling parameter.

Equilibrium densities were calculated by setting $A_{t+1}=A_t\equiv\hat{A}$ in Eq. 3. The analytical expression for the nontrivial equilibrium, $\hat{A}$, is given by

$$\hat{A} = \frac{1}{d\rho\phi\sigma_e}\left[\left(\frac{\sigma_j P\rho\phi\sigma_e\sigma_{tmax}\sigma_m}{(1-\sigma_j(1-P))(1-\sigma_a)}\right)^{1/\gamma} - 1\right] \tag{5}$$

Sufficient conditions for the stability of $\hat{A}$ are given by the inequalities:

$$\frac{(1-\sigma_j(1-P))(1-\sigma_a)}{\sigma_j P \rho \phi \sigma_e \sigma_{tmax} \sigma_m} > \left[1 - \frac{2 - \sigma_a - \sigma_j(1-P)}{\gamma(1-\sigma_j(1-P))(1-\sigma_a)} \right]^\gamma \quad (6)$$

and

$$\frac{\sigma_j P \rho \phi \sigma_e \sigma_{tmax} \sigma_m}{(1-\sigma_j(1-P))(1-\sigma_a)} > 1 \quad (7)$$

as determined by the Jury criteria (Caswell 2000). When Eq. 6 fails, Eq. 5 provides a negative, unstable equilibrium, and the only stable population is 0. When Eq. 7 fails, the equilibrium in Eq. 5 is unstable, resulting in bifurcations and the onset of chaotic behavior. However, the parameter ranges considered here satisfy both equations.

Elasticity analysis – contribution of specific stages to population dynamics

We examined the effect of individual stage-specific survival parameters on equilibrium population density using elasticity analysis (Takada and Nakashizuka 1996; Grant 1997, 1998; Grant and Benton 2000). Elasticity analysis is similar to more classical sensitivity analysis, except that elasticity quantifies proportional rather than absolute changes, and is generally preferred for comparisons of demographic parameters (Caswell 2000). Here, elasticity, e, quantifies the proportionate change in adult equilibrium density ($\hat{A}$) that results from, and is expressed relative to, a small proportionate change in one of the model's demographic parameters (e.g., egg survival, $\sigma_e : e_{\sigma_e} = \partial \ln(\hat{A})/\partial \ln(\sigma_e)$). For example, $e_{\sigma_e} = 1$ indicates that a small change in egg survival (σ_e) yields an equivalent proportionate change in adult equilibrium density ($\hat{A}$); $e_{\sigma_e} > 1$ indicates that there is a greater than proportional change; and $e_{\sigma_e} < 1$ indicates that there is a less than proportional change. When $e_{\sigma_e} < 0$ (i.e., negative elasticities), a decrease in egg survival leads to an increase in equilibrium density. Because we were particularly interested in the relationship between larval-stage density dependence and the sensitivity of adult equilibrium density to changes in survival through different life-history stages, we calculated elasticities for egg survival, metamorph survival, density-independent larval survival, juvenile survival and adult survival for both focal species for a range of density dependence – ranging from weak to over-compensatory density dependence as controlled by the density-dependent exponent (γ).

Limitation analysis – scaling-up egg mortality

Elasticity analysis, which focuses on very small proportional changes, is unable to project responses to larger perturbations if responses are non-linear, as they are in this model. The limitation approach, on the other hand, allowed us to examine the effect of relatively large changes in a demographic parameter (e.g., egg survival in this case) on equilibrium adult density. We estimated the limitation imposed by increased egg mortality by comparing ambient adult density in the absence of added egg mortality ($\hat{A}_{Low}$) with adult density when egg mortality was elevated due to, for example, UV radiation ($\hat{A}_{High}$). We then expressed this as a relative change: i.e., $[(\hat{A}_{Low} - \hat{A}_{High})/\hat{A}_{Low}]$. For both focal species, we calculated the relative change in adult densities at three levels of elevated egg mortality (σ_e reduced by 25, 50, and 75%) for a range of larval density dependence scenarios (i.e., as γ was varied within empirically derived bounds: see below).

Amphibian parameter estimates

Following a general analysis of the model, we focused our analyses on the parameter space implicated by field studies of amphibians. Parameter values were obtained from published studies of the same species when available, or from studies of closely re-

lated species when the necessary data were not available for our focal taxa. While we have parameterized this model to describe the life histories of a number of amphibian species, here we focus on *B. boreas* and *A. macrodactylum* because of their different reproductive strategies (i.e., *B. boreas* has a clutch size >100 times larger than *A. macrodactylum*: see Table 2). In considering these two species, we hope to illustrate some of the potential variation among species in their population-level response to egg mortality.

Data on the functional form of larval density dependence for field populations are uncommon, and were unavailable for our focal species. For this reason throughout our analyses we consider a wide range of density dependence scenarios. However, we felt it would be informative to provide a rough estimate of density dependence based on field studies of amphibian systems. To accomplish this, we estimated the parameters that control the form of larval density dependence (σ_{tmax}, d, γ) by fitting Eq. 1 to data from field studies of congeneric amphibians with similar life histories using nonlinear least squares optimization (Table 3). Because multiple estimates of the density-dependence exponent (γ) were available, we used meta-analysis (Gurevitch and Hedges 1999; Osenberg et al. 1999) to (1) determine whether estimates for γ differed among studies or taxa, and (2) obtain estimates (and confidence intervals) for γ to guide our explorations of the population-level consequences of egg mortality. We used a mixed-model meta-analysis [using γ as the effect size and var(γ) in the weighting function], tested whether studies shared a common γ parameter, and obtained confidence limits from the bias-corrected bootstrap procedures in MetaWin v2.1 (Rosenberg et al. 2000).

Results and discussion

General results – elasticity analyses

Elasticities varied among the parameters and depended on the values of other parameters in the model (Table 1). We explored expressions for the elasticities to glean general patterns in the relative sensitivity of adult density to changes in parameter values. For example, elasticities for egg survival were guaranteed to be positive if $\gamma<1$, but could be negative if $\gamma>1$ (Table 1). Thus, there are some parameter value combinations under which adult densities can actually increase in response to additional egg mortality – increased egg mortality due to UV (or other mortality agents) can actually lead to higher adult densities. This occurs if the strength of density dependence in the larval stage is sufficiently strong to lead to over-compensation. As a result, more tadpoles can survive to metamorphosis if egg mortality is increased. Other life stages do not necessarily show this range of possible responses. Elasticities for juvenile and metamorph survival are always positive, demonstrating that increased mortality in these stages always decreases adult density.

Under some conditions, we can make more definitive comparisons. For example, if $\gamma=1$, then the it can be seen (by inspection of solutions in Table 1) that $0 < e_{\sigma_e} < e_{\sigma_{tmax}} = e_{\sigma_m} < e_{\sigma_j}$. Thus, increased mortality in immature stages always reduces adult density. However, under some conditions, this reduction can be vanishingly small (e.g., as $d \rho \phi \sigma_e A \rightarrow \infty$, $e_{\sigma_e} \rightarrow 0$). Of the parameters that govern the survival of immature stages, egg survival has the smallest influence on adult density.

Table 1 Equations for elasticity based on the adult equilibrium density function (Eq. 5) for stage-specific transition rates and parameters controlling density dependence

Model parameter	Elasticity based on Eq. 5
Egg survival $(\partial\ln\hat{A}/\partial\ln\sigma_e)$	$e_{\sigma_e} = \frac{1-\gamma}{\gamma} + \frac{1}{\gamma d\rho\phi\sigma_e\hat{A}}$
Maximum larval survival $(\partial\ln\hat{A}/\partial\ln\sigma_{tmax})$	$e_{\sigma_{tmax}} = \frac{1}{\gamma} \cdot \left(1 + \frac{1}{d\rho\phi\sigma_e\hat{A}}\right)$
Metamorph survival $(\partial\ln\hat{A}/\partial\ln\sigma_m)$	$e_{\sigma_m} = \frac{1}{\gamma} \cdot \left(1 + \frac{1}{d\rho\phi\sigma_e\hat{A}}\right)$
Juvenile survival $(\partial\ln\hat{A}/\partial\ln\sigma_j)$	$e_{\sigma_j} = \frac{1}{\gamma(1-\sigma_j)(1-P)} \cdot \left(1 + \frac{1}{d\rho\phi\sigma_e\hat{A}}\right)$
Adult survival $(\partial\ln\hat{A}/\partial\ln\sigma_e)$	$e_{\sigma_a} = \frac{1}{\gamma(1-\sigma_a)} \cdot \left(1 + \frac{1}{d\rho\phi\sigma_e\hat{A}}\right)$
Density dependence exponent $(\partial\ln\hat{A}/\partial\ln\gamma)$	$e_\gamma = \frac{-1}{\gamma} \cdot \log\left(\frac{\sigma_j P\rho\phi\sigma e\sigma_{tmax}\sigma_m}{(1-\sigma_j)(1-P)(1-\sigma_a)}\right)$
Density-dependence coefficient $(\partial\ln\hat{A}/\partial\ln d)$	$e_d = 1$

Table 2 Model parameters for *Bufo boreas* and *Ambystoma macrodactylum*

Parameter	Fixed	Range	Reference
Bufo boreas			
Clutch size (ϕ)	12000	5000–15,000	Nussbaum et al. 1983
Egg survival (σ_e)	0.6	0.55–0.84	Blaustein et al. 1994
Metamorph survival (σ_m)	0.2	0–1	Bayliss 1994[a]; Clarke 1977[b]
Juvenile survival (σ_j)	0.2	0–1	Bayliss 1994[a]; Clarke 1977[b]
Maturation probability (P)	0.25	0.20–0.25	Nussbaum et al. 1983
Adult survival (σ_a)	0.6	0.2–0.8	Olson 1988; Schmidt and Anholt 1999[c]
Density-dependent coeff. (d)	0.007	0.005–0.01	Brockelman 1969; Wilbur 1977[d]
Max. larval survival (σ_{tmax})	0.8	0–1.23	Brockelman 1969; Wilbur 1977[d]
Ambystoma macrodactylum			
Clutch size (ϕ)	90	41–140	Nussbaum et al. 1983
Egg survival (σ_e)	0.6	0.14–0.95	Blaustein et al. 1997
Metamorph survival (σ_m)	0.6	0.55–0.7	Russell et al. 1996
Juvenile survival (σ_j)	0.6	0.55–0.7	Russell et al. 1996
Maturation probability (P)	0.42	0.33–0.50	Russell et al. 1996
Adult survival (σ_a)	0.6	0.55–0.7	Russell et al. 1996
Density-dependent coeff. (d)	0.05	0.0004–0.1	Van Buskirk and Smith 1991; Petranka 1989[d]
Max. larval survival (σ_{tmax})	0.8	0–1.69	Van Buskirk and Smith 1991; Petranka 1989[d]

[a] Bufo marinus
[b] B. fowleri
[c] B. bufo
[d] See Table 3

Indeed, for this case with complete compensation in the tadpole stage, the effect of mortality on adult density decreases from egg to tadpole to metamorph to juvenile stage. Elasticity for adult survival is more complex and we are not able to make any general conclusions.

Case studies – using parameter estimates from amphibian studies

The above analyses highlight that knowledge of density dependence and other demographic parameters are critical for determining how stressors are likely to affect amphibian populations. A given increase in egg-stage mortality may increase, decrease, or have no effect on equilibrium densities, depending on strength of larval density dependence as determined by γ. However, the above general analyses do not address what the strength of density dependence is likely to be in natural systems, nor do

they constrain the insights to regions of parameter space that are appropriate for the species under study. Three pieces of information are required: (1) estimates of the effect of UV-mediated mortality (or other the effect of other mortality agents under study), (2) demographic data on basic life-history parameters, and (3) estimates of the strength of density dependence (γ). UV-mediated effects are required only for limitation analyses since elasticities focus on responses to infinitesimal effects. We therefore defer this portion of the analysis to a later section. Demographic data were gleaned from the literature (Table 2). The data currently available to estimate parameters controlling density dependence are limited and highly variable (e.g., see SE's in Table 3). However, by examining the data available from studies of other *Bufo* and *Ambystoma* species, we were able to develop hypotheses regarding the strength of larval density dependence in our focal taxa. A meta-analysis of γ for the four available studies (Table 3) revealed that there was not

Table 3 Parameter estimates for Eq. 1 fit to data from studies on larval density

Species	Parameter estimates (SE)		
	σ_{tmax}	d	γ
Bufo americanus[a]	0.8 (0.9)	0.007 (0.02)	0.96 (0.62)
B. americanus[b]	0.8 (1.23)	0.007 (0.03)	1.26 (1.45)
Ambystoma laterale[c]	0.91 (1.69)	0.05 (0.49)	0.76 (2.54)
A. opacum[d]	0.8 (0.33)	0.0004 (0.12)	84.37 (552.42)

[a] Brockelman (1969)
[b] Wilbur (1977)
[c] Van Buskirk and Smith (1991)
[d] Petranka (1989)

significant heterogeneity among studies (Q_{total}=0.068, P=0.995; i.e., we cannot reject the null hypothesis that all γ are equal) and that the average γ across all four studies was 0.995 (CI=0.76–1.26). We therefore focus on γ=1 and the surrounding parameter space (as suggested by the confidence interval).

Elasticity analyses

To facilitate comparisons of elasticity for different parameters, we used the best parameter estimates for each of the two species (fixed values, Table 2) but allowed γ to vary from 0.6 to 1.4 (slightly beyond the estimated confidence limits on γ). Both species were generally more sensitive (as assessed with elasticities) to changes in post-embryonic than embryonic (i.e., egg) survival (Fig. 2). Elasticities for the four post-embryonic parameters were positive for the entire parameter space considered, indicating that decreases in these parameters lead to decreases in equilibrium densities irrespective of the strength of larval density dependence. Again, both species were most sensitive to changes in juvenile survival. Elasticities for juvenile survival were ≥1 for most of the parameter space considered, indicating that decreases in this survival parameter usually results in an equivalent or greater proportional decrease in equilibrium densities. Similarly, both species were least sensitive to changes in egg survival, with large regions of parameter space exhibiting negative elasticities. Within these regions, small proportional decreases in egg survival *increase* equilibrium densities. For *B. boreas*, elasticities become negative for γ>1, indicating that compensatory larval density dependence is sufficient to ameliorate negative consequences that egg mortality might have on toad population densities. Thus for γ=1 and the other parameters held at the fixed estimates in Table 2 (dotted lines), the relative sensitivity of *B. boreas* to small changes in stage-specific survival parameters is: $0 \approx e_{\sigma_e} < 1 < e_{\sigma_{tmax}} \approx e_{\sigma_m} < e_{\sigma_j} < e_{\sigma_a}$ (Fig. 2). *A. macrodactylum* is generally more sensitive than *B. boreas* to changes in survival parameters, including egg survival. Egg survival elasticities for *A. macrodactylum* are negative only for regions of moderate to high egg survival and strong larval density dependence

(γ=1.2). The relative sensitivity of *A. macrodactylum* to small changes in stage-specific survival parameters when γ=1 is: $0 < e_{\sigma_e} < 1 < e_{\sigma_{tmax}} \approx e_{\sigma_m} < e_{\sigma_j} \approx e_{\sigma_a}$ (Fig. 2).
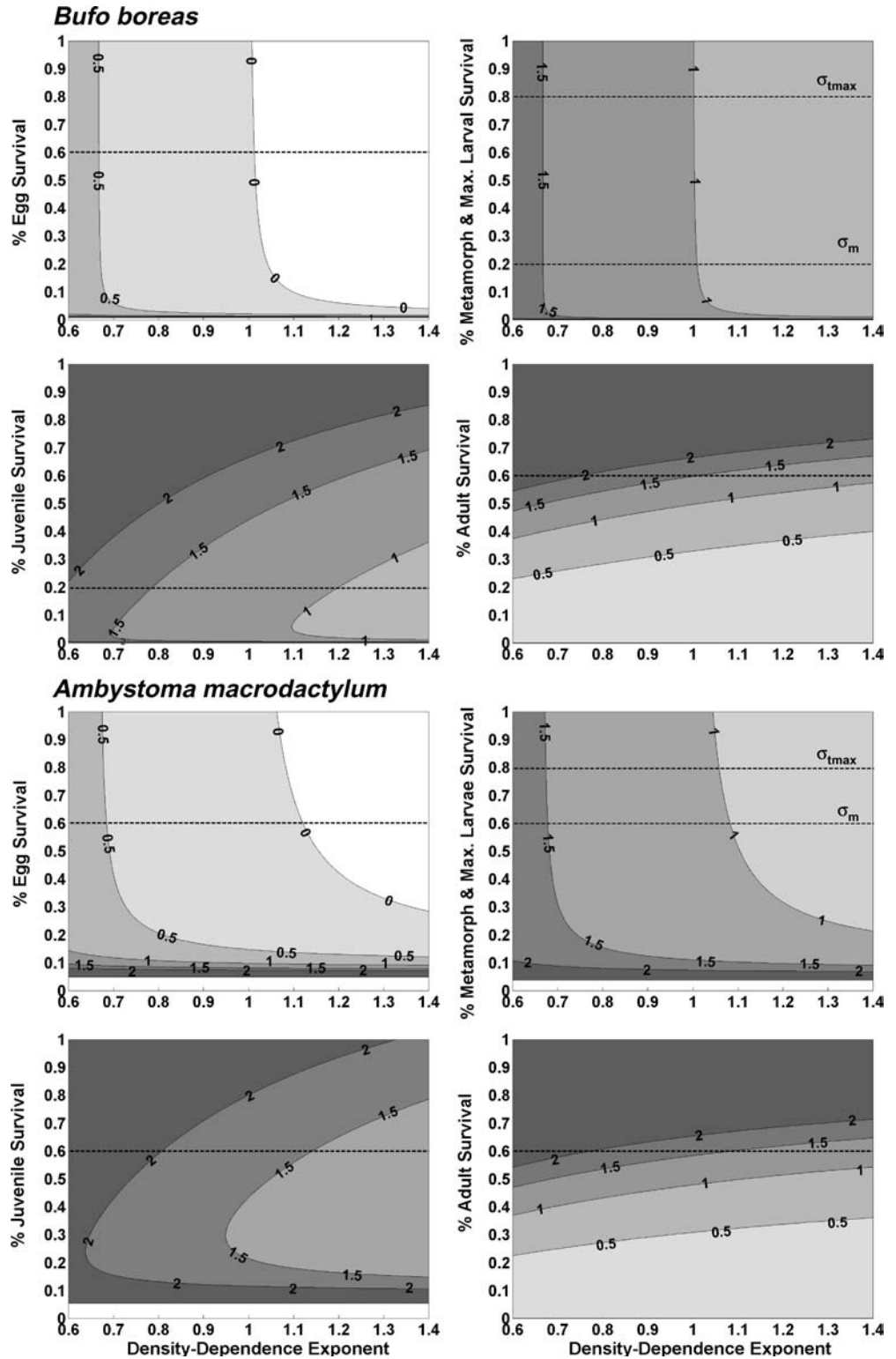
These results indicate that stressors that decrease survival in later life stages will have greater effects upon populations than those that affect the egg stage (see also Biek et al. 2002). However, perhaps due to the tractability of the egg stage, experimental studies of egg mortality are numerous relative to studies of mortality in later stages. For example, while studies examining the effect of UV-B on amphibians have focused on eggs and to lesser extent larvae, our model suggests that the negative effects of UV-B on these stages could be of less concern than effects of UV-B manifested in later stages (e.g., Belden et al. 2000). Thus, our empirical efforts need to be shifted – greater attention needs to be given to later life stages.

Limitation analyses

While elasticity analysis helps identify which life-history stages contribute the most to adult densities, elasticities are local estimates – they calculate the relative changes in population growth rates or equilibrium densities as the result of infinitesimal perturbations of the matrix elements (e.g., de Kroon et al. 2000). Thus, elasticities do not allow us to ask how large changes in a model's parameters directly affect equilibrium density – a question of obvious importance to conservation biologists. Limitation, in contrast, allows us to explore how large changes in model parameters are manifested at the population level. We specifically ask how possible decreases in egg survival should affect adult densities. Given the uncertainty in estimates of the strength of density dependence, we explored a range of values of γ as informed by the confidence intervals derived from the meta-analysis.

Density dependence has a large effect on how egg mortality is translated up to the population level. For both species, decreases in egg survival – even by 75% – can result in either declines, increases, or have no population-level effect, depending on the strength of larval-stage density dependence (Fig. 3). For *B. boreas*, large decreases in egg survival reduce equilibrium densities when density dependence is less than compensatory (γ<1) but increases densities when density dependence is over-compensatory. Egg mortality in *A. macrodactylum* causes decreases in equilibrium densities for a greater range of density-dependence scenarios than in *B. boreas* (decreases in Â for γ<1.2), but egg mortality can still lead to increases in density when larval density dependence is strong. The salamander, in general, is more sensitive to large decreases in egg survival than the toad. For example, when density dependence is moderately weak (γ=0.8) a 75% decrease in egg survival results in a 40% decrease in *Ambystoma* densities compared to a 30% decrease in *Bufo* densities (Fig. 3). Differences in the sensitivity of adult densities to equivalent reductions in egg-stage survival can be explained by differences in

life history that determine how early mortality is translated to the adult population. For example, a single *B. boreas* female is capable of producing as many as 15,000 eggs, while *A. macrodactylum* females produce only 140 eggs, per reproductive effort (Table 2). Thus, fewer adult female toads are needed to saturate the larval habitat.

We can make more accurate assessments of the response of populations by using observed effects of environmental stessors on egg mortality. Recent studies of *B. boreas* populations show that this species may experience decreases in egg survival of up to 50% due to the synergistic effects of UV-B irradiation, pathogenic fungi,
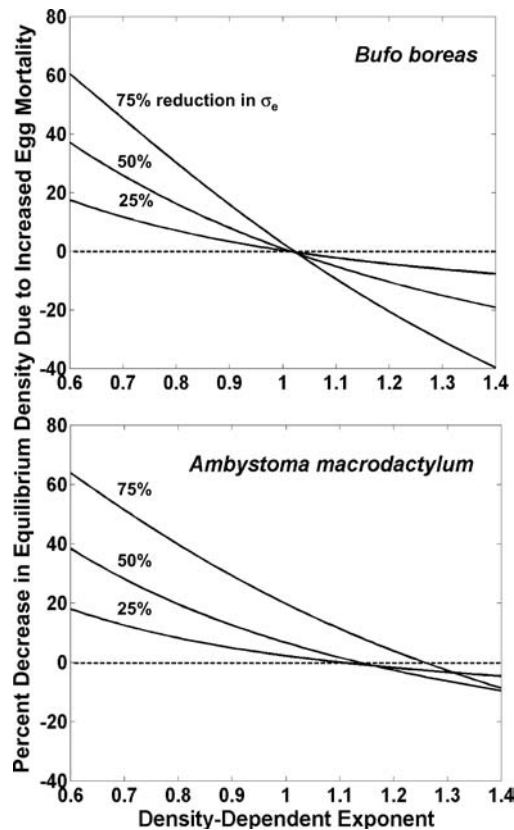
Fig. 3 Limitation analyses for *Bufo boreas* and *Ambystoma macrodactylum*. Panels show % decline in adult equilibrium densities over a range of the density dependent exponent (γ). Other parameters were held at the fixed value in Table 2. Isoclines for egg survival reduced by 75%, 50%, and 25% are presented. Percent declines of <0 indicate that reduced egg survival increases, rather than decreases, equilibrium adult density. The *dashed line* (0% change) indicates no net effect

Fig. 4 The effect of increased egg-stage mortality on *Bufo boreas* and *Ambystoma macrodactylum* adult equilibrium densities. *Dark solid isoclines* indicate adult equilibrium densities for the mean value of γ estimated from the studies in Table 3 by meta-analysis (*grey isoclines* represent the upper and lower bounds of the γ confidence interval): i.e., $\gamma=0.76$, 0.995, and 1.26. *Dotted vertical lines* indicate actual reductions in egg survival for these species due to UV-B irradiation (or combined UV, fungal, climate effects) as measured in published field studies. Parameters other than γ and σ_e were held at the fixed values estimated from field studies and reported in Table 2

and lower water levels associated with climate change (Kiesecker et al. 2001). However, due to the compensatory effects of larval density dependence, egg mortality of this magnitude may have little effect of adult equilibrium densities. When larval density dependence is compensatory ($\gamma=1.0$) a 50% reduction in egg survival (0.8 to 0.4) has no effect on equilibrium density (Fig. 4). Using the lower and upper confidence limits on γ, the population-level effect of a 50% reduction in egg survival ranges from an 18% decrease to a 10% increase in adult density. Note that this is a 'one-time' shift in equilibrium densities – not a rate of decline or increase. Thus, this preliminary analysis suggests that egg mortality alone, of the magnitude currently observed, may be insufficient to explain large declines in this species.

Studies of the effects of UV-B irradiation on *A. macrodactylum* suggest that the eggs of this species are more sensitive to UV than those of *B. boreas*. Exposure to ambient UV decreased *A. macrodactylum* egg survival 85% relative to controls (Blaustein et al. 1997). The expected effect of reduced egg survival of this magnitude ranges
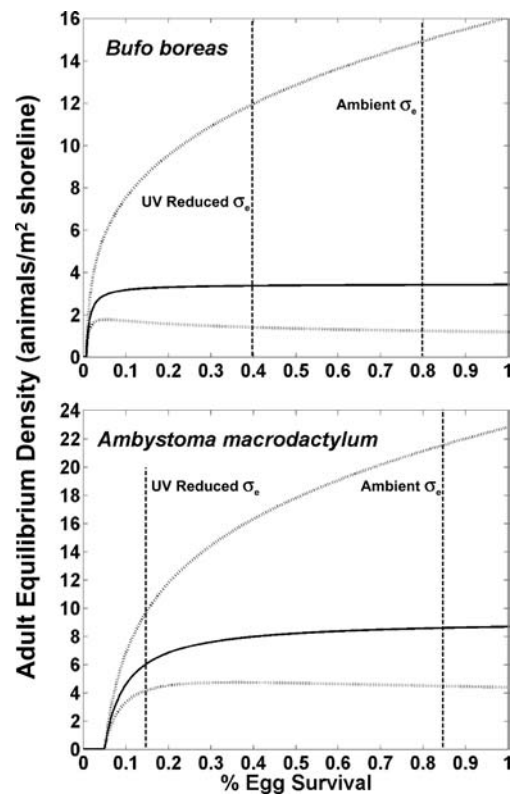
from a 10% to 60% decrease in adult equilibrium densities (Fig. 4). Thus, UV-induced egg mortality alone may be capable of causing large declines in this species, although the effect is damped due to density dependence in the larval stage. Furthermore, any additional egg-stage mortality beyond that caused by UV exposure may shift the system to a region where adult densities become increasingly sensitive to decreased egg mortality and the extinction of the population more likely (Fig. 4).

Conclusions and caveats

Population models parameterized from field studies provide a powerful approach for evaluating effects of environmental stressors. However, our application of this approach is not without limitations. We did not incorporate stochastic (Grant and Benton 2000) or spatial dynamics (Halley et al. 1996) in our analysis, and we assume density dependence operates in only a single life stage (Hellriegel 2000). It may be necessary to include such addi-

tional complexity to accurately predict the dynamics of specific populations. In addition, the reliability of these results depends upon the quality of the data used (and thus the accuracy of the parameter estimates). In several cases, we use parameters based upon closely related species, introducing an additional source of uncertainty. Also, the literature estimates used frequently lacked confidence intervals, and confidence intervals we estimated from available data were often very large (e.g., Table 3). We did not incorporate most of these sources of uncertainty into our analyses. These limitations highlight that accurate demographic data (e.g., Schmidt et al. 2002) and reliable estimates of density dependence will be invaluable to the future development of predictive models for specific amphibian populations.

Our goal was to produce a strategic model designed to help us explore the potentially important role of density dependence in these systems – a heuristic tool for focusing research efforts, developing hypotheses, and in making preliminary predictions. Our results demonstrate the importance of incorporating larval density dependence when assessing how stressors that act upon a particular life stage scale-up to the population level. Based upon the best field derived estimates we could obtain, our model suggests that amphibian abundance is more sensitive to changes in the survival of later stages than the egg stage and that larval density dependence dramatically alters the consequences of early mortality, reducing or even reversing the 'expected' population-level effects of egg mortality. Studies of later life stages and the functional form of larval density dependence are needed to assess accurately how stressors are likely to affect specific amphibian populations. Stage-specific effects should not be studied in isolation; instead, we need to explicitly consider the animal's entire life history in a dynamic context. Effective conservation strategies depend on such an approach.

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ERRATUM

James R. Vonesh · Omar De la Cruz

Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines

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The fifth sentence of the subsection entitled 'General amphibian population model' under Methods should read: 'Using this scenario, we model per capita egg production as the mean clutch size (ϕ) adjusted by the adult sex ratio (ρ; 0.5).'

J.R. Vonesh (✉)
Department of Zoology, University of Florida, Gainesville, FL 32611, USA
e-mail: voneshjr@zoo.ufl.edu
Tel.: +1-352-392-9201
Fax: +1-352-3923704

O. De la Cruz
Department of Mathematics, Purdue University, Purdue, IN 47906, USA