

The growth–mortality tradeoff: evidence from anuran larvae and consequences for species distributions

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Received: 3 October 2005 / Accepted: 10 April 2006 / Published online: 10 May 2006
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Abstract A tradeoff affecting the ability to grow under high versus low resource levels has been commonly hypothesized to influence species distributions across resource gradients in a wide variety of taxa. This influence is dependent on individual growth being proportional to traits that affect demographic processes such as mortality. However, data on how individual growth scales with demographic performance are rare. We conducted a mesocosm experiment, and re-analyzed data from a similarly designed field experiment, to examine the relationship between growth and

mortality in two tadpole species that segregate across a resource gradient. Overall, environmental conditions leading to faster growth also lead to lower mortality rates. However, species differed in this relationship. Leopard frogs achieved faster growth than wood frogs, but their absolute mortality was greater and increased steeply as growth decreased. Conversely, absolute mortality of wood frogs was lower and less strongly dependent on growth. These interspecific differences suggest a second tradeoff, that between maximizing growth rates or minimizing mortality, with potentially important demographic consequences. Leopard frogs grow faster than wood frogs in productive ponds, but are excluded from unproductive ponds dominated by wood frogs due to accelerating mortality rates with declining realized growth. A review of the literature suggests that in diverse taxa, including plants, microcrustaceans and drosophilids, patterns in mortality are consistent with this tradeoff indicating that the mechanism we demonstrate could be a link between individual performance and demographic rates influencing species distributions in other systems.

Communicated by Steven Kohler

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Keywords Allocation · Resource gradients · Levels of biological organization · *Rana sylvatica* · *Rana pipiens*

Introduction

Evolutionary tradeoffs arising from constrained variation in individual traits have long been thought to contribute to patterns in species distributions and relative abundances in nature (Connell 1975; Grime 1979; Tilman 1990). For example, tradeoffs related to the ability to acquire, process and allocate resources to

growth often have been hypothesized to be responsible for differences in species distributions across resource gradients (Grime and Hunt 1975; Grime et al. 1997; Arendt 1997). Species that are capable of growing fast when resources are abundant often grow poorly when resources are rare. Conversely, species that are capable of growing, albeit slowly, when resources are rare exhibit comparatively little scope in responding to increases in resource abundance (Arendt 1997). There is ample evidence that such a tradeoff is general, as it is manifest among lineages of bacteria, higher plants, rotifers, microcrustaceans, mollusks, insects, amphibians and mammals (reviewed in Arendt 1997; see also Stemberger and Gilbert 1985; Grime et al. 1997; Tessier et al. 2000; Tessier and Woodruff 2002; Schiesari 2004).

However, such tradeoffs at the level of organismal physiology do not necessarily affect the demographic processes that determine species distributions in nature (Suding et al. 2003). In order for a tradeoff in the ability to grow at different resource levels to be responsible for patterns of species replacement across resource gradients, growth must be proportional to traits that affect demographic processes such as survivorship or fecundity. If this is the case, a species can exhibit a competitive advantage and be most abundant in regions where it grows the fastest relative to other species. A positive correlation among these traits seems intuitive and is often assumed, but is not necessarily the case because species may exhibit very different patterns of allocation of assimilated energy to body functions other than growth such as maintenance, defense, storage, and reproduction (Arendt 1997).

It is therefore critical to determine the relationships between sub-individual traits and individual performance, or those between individual performance and demographic processes that can ultimately be the causal basis of distributional patterns. For example, it is reasonable to expect that patterns of species replacement across resource gradients are at least partially determined by differential mortality rates; yet, it is often not clear how mortality rates scale with intra- and interspecific variation in growth rates. Intuitively, environmental conditions leading to faster growth are expected to lead to lower mortality, but there is also evidence that maximization of growth rate is in many cases related to increased probability of mortality (see below). Understanding the nature of the relationship between growth and mortality may therefore be instrumental in clarifying linkages between individual performance, demographic performance, and species distributions in nature. Most studies to date have focused on the relationship between growth and mortality as mediated by predation (through increased

foraging activity, decreased locomotory ability, or smaller energy allocation to hard structures; e.g., Werner and Anholt 1993; Lankford et al. 2001; Arendt et al. 2001), but there are also physiological costs to growth that might influence species distributions across resource gradients (e.g., allocation tradeoffs, decreased immunocompetence, accumulation of errors in DNA through increased transcription; Arendt 1997).

We present evidence in this paper that interspecific differences in the relationship between mortality and growth, and an underlying tradeoff, may influence the distribution of anuran species across a resource gradient. Re-analysis of data from a field experiment published previously (Werner and Glennemeier 1999) suggested that a slow-growing species of larval anuran exhibited low mortality over a broad range of realized growth rates, whereas mortality of a fast-growing species was steeply related to realized growth rates. Thus, maximizing performance in ponds where resource availability was high appeared to come at the cost of increased mortality in ponds yielding slow growth. To isolate the responses of these anuran larvae to resources from other covarying environmental variables in the field, we conducted a mesocosm experiment employing the same two closely related species manipulating a range of resource availabilities. This experiment directly tested, and corroborated, the hypothesis that maximization of intrinsic growth rate (i.e., maximum growth capacity) trades off with survivorship in these two species, especially under conditions of resource scarcity. We further conducted a literature survey that indicates that in diverse plant and animal taxa, patterns in mortality are consistent with this tradeoff indicating that the mechanism we demonstrate could be a link between individual performance and demographic rates influencing species distributions in other systems.

Background

We studied the two species of ranid anuran larvae, the wood frog (*Rana sylvatica* LeConte) and the leopard frog (*Rana pipiens* Schreber), that were employed in the field experiment of Werner and Glennemeier (1999). Both species breed in early spring and complete larval development in the summer. The two species differ in their distributions primarily in response to forest canopy cover over ponds (Skelly et al. 1999; E. E. Werner, unpublished work); leopard frogs are restricted to open-canopy ponds (i.e., <75% forest canopy cover), whereas wood frogs are found throughout the canopy cover gradient. In fact, of nine anuran species, the wood frog is the only species at our study site

in Southern Michigan capable of consistently using closed-canopy ponds and it often attains its highest densities in these ponds (Skelly et al. 1999; E. E. Werner, unpublished work). Although forest canopy cover influences abiotic conditions in ponds (Werner and Glennemeier 1999), its major effect on larval anuran performance is related to the marked reduction in primary productivity and nutritional quality of available resources (Werner and Glennemeier 1999; Skelly et al. 2002; Schiesari 2004, 2006).

Werner and Glennemeier (1999) transplanted wood and leopard frog larvae to enclosures free of predators in two open- and two closed-canopy ponds and measured performance responses as indicated by growth and mortality rates. Larvae of both species grew faster in open-canopy ponds, but leopard frogs grew more than 2 times faster than wood frogs. However, leopard frogs grew slower than wood frogs in closed-canopy ponds. Mortality responses also were different. Mortality rates for the leopard frog increased from 20–30% in open-canopy ponds to 75–99.5% in closed-canopy ponds. In strong contrast, mortality rates of wood frogs were low (~20%) and independent of canopy cover (ratios and percentages as reported in the original article).

The findings of Werner and Glennemeier suggest that species differ in the relationship between realized growth and mortality rates, a hypothesis that becomes explicit when data are re-analyzed and re-plotted (Fig. 1a; see Materials and methods). Mortality rates were higher overall in the fast-growing species, the leopard frog, and this mortality increased steeply as realized growth rates declined. In turn, mortality in the slow-growing wood frogs was low and essentially independent of realized growth rates. A second interesting result becomes apparent when we plot average mortality in closed-canopy (Fig. 2a) and in open-canopy ponds (Fig. 2c) as a function of species maximum growth rates (i.e., growth rates achieved in open-canopy ponds). Whereas the relationship between realized mortality and growth rates within species tended to be negative, when comparing across species it becomes clear that maximum growth rate was positively correlated with probability of mortality i.e., the fast-growing species suffered higher mortality than the slow-growing species under all resource conditions, even in the absence of predation. Re-analyzing growth and mortality within each pond type, mortality rates of leopard frogs were significantly higher than those of wood frogs not only in closed-canopy ponds (Fig. 2a, simple effects test $F_{1,19}=13.3$, $P=0.002$; see Materials and methods), but also in open-canopy ponds (Fig. 2c, $F_{1,19}=7.3$, $P=0.014$) where leopard frogs grew faster ($F_{1,17}=134.6$, $P<0.001$).

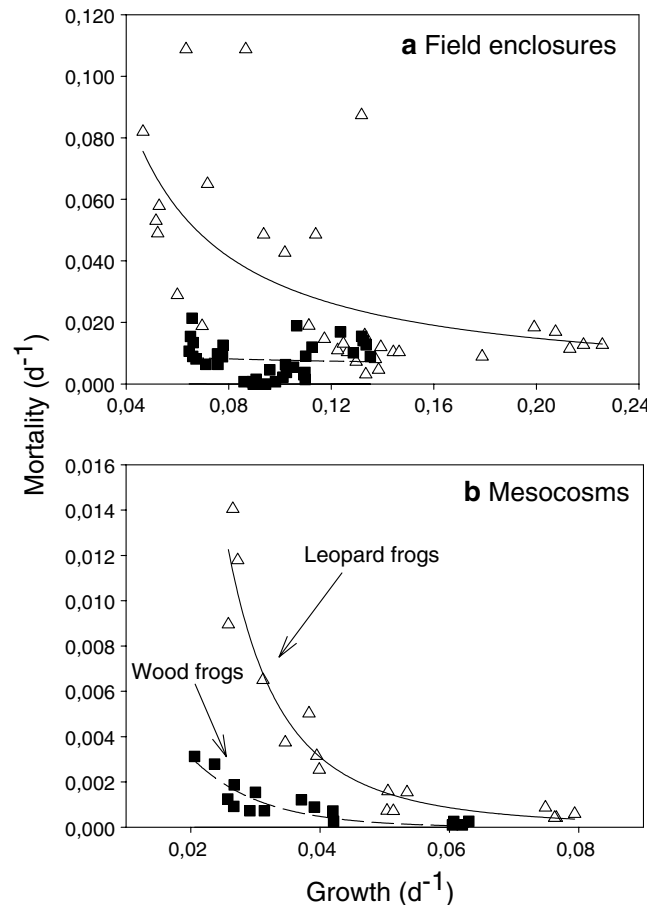


Fig. 1 Relationship between realized growth and mortality rates in wood frogs (*Rana sylvatica*; filled square) and leopard frogs (*Rana pipiens*; open triangle) in **a** the field enclosure experiments from Werner and Glennemeier (1999) (not including artificial food supplementation treatments) and **b** the mesocosm experiment. Each symbol represents means for one enclosure (45 individuals) or one tank (200 individuals), respectively. A power function in the form $u=ag^b$ provided best fit to the data overall, where u is mortality rate and g is specific growth rate. d^{-1} Day $^{-1}$

These observations are consistent with the hypothesis of a tradeoff between the maximization of intrinsic growth rates versus the minimization of mortality rates in these species, that is, being capable of growing fast when resources are abundant comes at the cost of higher background mortality overall, and steeply increasing mortality with decreasing realized growth rates. This tradeoff would be an important potential mechanism translating individual growth performance into demographic performance, because it suggests that a given absolute reduction in growth leads to a disproportional increase in mortality for some species, whereas for others, mortality and growth rates might be partially uncoupled traits. This tradeoff would account for several examples in the literature of fast-growing species continuing to grow faster than

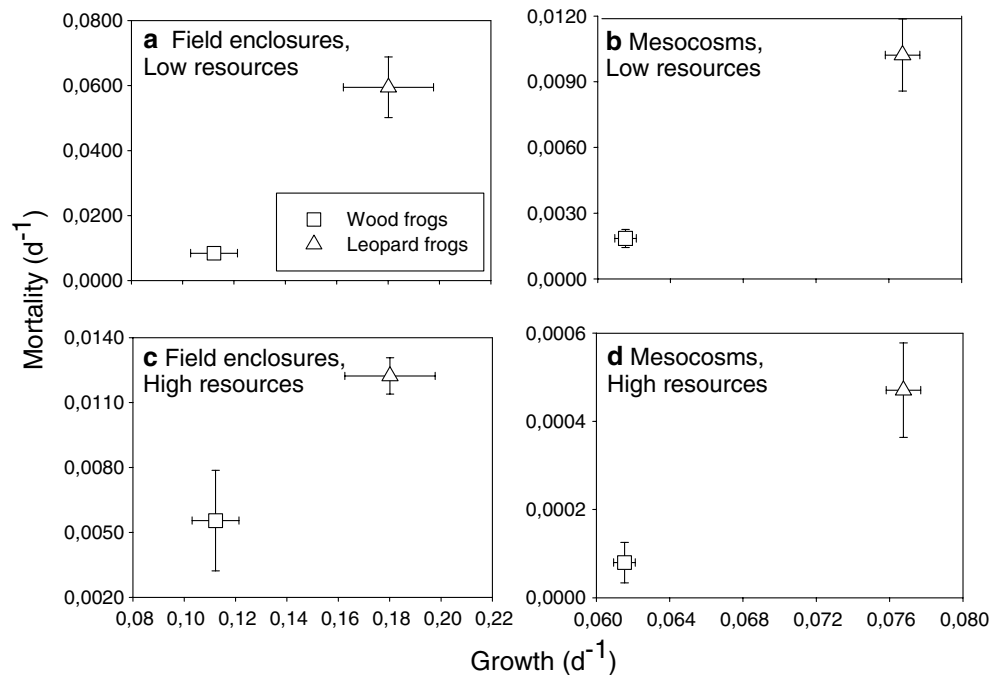


Fig. 2 Relationship between the intrinsic growth rate (growth at high resource levels), and the mortality rate of wood frogs (*open square*) and leopard frogs (*open triangle*) under **a, b** low and **c, d** high resource levels in field enclosures (*left*) and mesocosms

(*right*). Each symbol represents treatment means \pm SE of six replicated enclosures in the field experiment (45 individuals per enclosure) and four replicated tanks in the mesocosms experiment (200 individuals per tank)

slow-growing species when transplanted to resource-poor environments where they do not usually occur (Augsburger 1984a; Kitajima 1994; Ellison et al. 1993; this study); i.e., in the long run, the increased mortality may exclude fast-growing species from resource-poor environments.

It is important to note, however, that in the field experiment slow growth and high mortality rates of leopard frogs were associated with closed-canopy ponds and therefore could simply reflect habitat or food type differences rather than an intrinsic tradeoff. Therefore, we conducted a mesocosm experiment where we manipulated growth rates of both species using a gradient in artificial food supply rate to isolate the relationships between growth and mortality rates.

Materials and methods

Wood and leopard frog larvae were reared from multiple egg masses (>17 for each species) collected in ponds and marshes adjacent to Independence Lake, Webster, Michigan, and at the Michigan Department of Natural Resources’ Pond Facility at Saline, Michigan. All tadpoles were raised outdoors in 300-l wading pools and fed Purina rabbit chow until used in the experiments, which were performed at the University

of Michigan’s E. S. George Reserve near Pinckney, Michigan.

The experimental mesocosms were cylindrical cattle-watering tanks 1.9 m in diameter filled with 1,300 l well water; 350 g dry (predominantly *Quercus*) leaf litter was added to each tank to provide a source of natural food and nutrients, substrate for colonization of periphyton, and structural complexity. We inoculated each tank with phytoplankton, periphyton, and zooplankton from one closed- and one open-canopy pond. Tanks were covered with 60% shade cloth to prevent colonization by breeding anurans or insects with aquatic larvae.

We employed a factorial, randomized block design experiment manipulating the two species and four food levels. These food levels included a treatment with no artificial food added (i.e., resources were limited to detritus, phytoplankton and periphyton occurring in the tanks), and three artificial food addition treatments spanning a 12-fold range: 0.347, 1.042, and 4.167 g rabbit chow (~16% protein) added 3 times per week. Food levels were chosen based on previous experiments so as to provide a wide range of growth rates and allow greater resolution at slow growth. Each treatment combination was replicated 4 times, one per spatial block. To determine whether mortality occurred early in the experiment, we included three

additional replicates of the no-food addition treatment that were terminated 10 days after initiation of the experiment.

All tanks were filled with water on 9 May 2003, when we also added the leaf litter. On 10–12 May we added phytoplankton, periphyton and zooplankton. On 17 May we placed 200 tadpoles of either wood frogs or leopard frogs in each tank. We added 1 g ground rabbit chow to all tanks to provide an initial pulse of nutrients for the tadpoles and for the establishment of algae. Initial size of wood frogs was 78.0 ± 19.8 mg (mean \pm 1 SD), and that of leopard frogs 53.4 ± 16.4 mg.

We also estimated mortality due to handling by placing 20 individuals of each species separately in 10-l containers (three replicates each) in the laboratory. These tadpoles were handled the same way as the tadpoles stocked in the experiment, and the number of individuals surviving in the containers after 72 h was counted.

The experiment was terminated when at least a few larvae in any treatment reached Gosner stages 38–40 (Gosner 1960). The experiment was terminated over 3 days (17–19 June) and therefore lasted 31–33 days. All tadpoles were removed from each tank, counted and weighed.

Data analysis

We employed mean specific growth rates [$g = \ln(\text{final mass}) - \ln(\text{initial mass}) / \text{time elapsed}$] and mortality rates [$u = \ln(\text{initial number of individuals}) - \ln(\text{final number of individuals}) / \text{time elapsed}$] computed for each tank as response variables.

Our principal goal was to understand the relationship between growth and mortality rates. However, because both variables are expected to be influenced by the same set of factors, we first verified the plausibility of a model in which growth is used to predict mortality. We constructed a path analysis model including two regressions; one where food level (ln-transformed), species, and a food level-by-species interaction term were predictors of growth (ln-transformed); and another where the same variables were predictors of mortality ($u + 0.0001$, ln-transformed; see below). This model provided a good fit to the data, as indicated by the small values of a likelihood ratio χ^2 -test ($\chi^2 = 3.02$, $df = 1$, $P = 0.08$), and showed very close agreement between the observed correlation between u and g (-0.619) and the correlation between u and g as implied by the relationships of each of them with the predictor variables (-0.663). This strong agreement is consistent with the hypothesis that growth and mortality are influenced by the same factors, and does not

imply that growth causes mortality per se. Path analysis also indicated that there was a high correlation between food level and growth rates ($r = 0.93$). Path analysis was conducted employing the software AMOS version 5.0.

Because manipulated factors similarly influence both growth and mortality, and because food level and growth rates are highly correlated, we proceeded to understand the relationship between growth and mortality by using growth as a predictor of mortality in an analysis of covariance (ANCOVA) model. The data were strongly non-linear but could be adequately linearized employing the function $\ln(u) = \ln(a) + b \times \ln(g)$; a constant equaling 0.0001 was added to mortality rates because there were treatments with zero mortality. This value was chosen because it was smaller than the minimum observed non-zero value (0.000314) but of the same order of magnitude. For leopard frogs $b = -2.89$ ($SE = 0.25$, $R^2 = 0.91$) and for wood frogs $b = -2.59$ ($SE = 0.32$, $R^2 = 0.82$). The Kolmogorov–Smirnov (K–S) test for normality of residuals showed that the residuals did not deviate significantly from normality for either species (wood frogs K–S statistic = 0.17, $P = 0.2$; leopard frogs K–S statistic = 0.19, $P = 0.12$). The ANCOVA model included species as a factor, growth as a covariate, and mortality rate as the dependent variable. We also included the interaction between species and growth in the model. In the ANCOVA, the effect of species was analyzed at the average value of growth rate of all individuals of both species, although using the growth rate = 0 intercept yielded similar results. Block had no significant effects and was dropped from the analyses.

We also examined interspecific differences in performance within food levels. This was achieved by conducting a two-way ANOVA where species, food level and a species-by-food level interaction term were factors and growth was the response variable; and another where mortality was the response variable. We specified a model that had heterogeneous variances across the different food levels, which fit the data significantly better than a homogeneous variance model in both cases (Verbeke and Molenberghs 2002). We then carried out post hoc tests (i.e., simple effects tests), followed by Bonferroni adjustments. Similar analyses were conducted for interspecific differences in performance in the field experiment (results displayed in [Background](#)). We conducted a two-way ANOVA where species, canopy cover and a species-by-canopy cover interaction term were factors and growth was the response variable; and another where mortality was the response variable. In the case of mortality, but not of growth, a heterogeneous variances model provided better fit. We then performed

post-hoc tests (i.e., a simple effects tests) followed by Bonferroni adjustments. These analyses were carried out using Proc Mixed in SAS for Windows, release 9.1.3.

Finally, when comparing the partial mortality rates of wood frogs and leopard frogs (i.e., the mortality occurring within 10 days from the start of the experiment) we employed a one-way ANOVA where mortality was the dependent variable and species the factor. These analyses were conducted in SPSS 12.0.

Results

The shapes and relative magnitudes of the relationship between realized growth and mortality rates in the mesocosm experiment were generally qualitatively similar to those observed in the field experiment (Fig. 1b). Mortality rates decreased with increasing growth rates for both species (ANCOVA $F_{1,31}=133.5$, $P<0.001$). There was a significant effect of species (ANCOVA $F_{1,31}=8.74$, $P=0.006$), indicating that leopard frog mortality was higher than wood frog mortality at equivalent growth rates. In the figure of untransformed data (Fig. 1b) it is apparent that starting at equal growth rates, a decrease in growth rate is associated with a larger (absolute) increase in mortality rate for leopard frogs than wood frogs. When log-transforming both growth and mortality rates in the ANCOVA, the interaction term was not significant ($F_{1,31}=0.43$, $P=0.518$) indicating that this difference in species response is present, and equal in relative but not in absolute terms, across the range of growth rates measured.

Next consider interspecific differences in mortality rate and in growth rate within food level. At the highest food level, leopard frogs achieved higher growth rates than wood frogs (simple effects test $F_{1,24}=73.4$, $P<0.001$), but growth rates did not differ between species at the lowest food level ($F_{1,24}=1.2$, $P=0.29$). Mortality rates of leopard frogs were higher than those of wood frogs both at the lowest (Fig. 2b, $F_{1,24}=24.3$, $P<0.001$) and highest food levels (Fig. 2d, $F_{1,24}=11.3$, $P<0.001$). Thus, we found a positive relationship between intrinsic growth rate and mortality between species regardless of resource level.

It is important to determine whether mortality in the mesocosm experiment was due to the initial handling of the larvae, initial environmental conditions in the tanks, or occurred over the course of the experiment. Effects of handling on mortality in the first 72 h of the experiment were negligible for both species (0 day⁻¹ in wood frogs, 0.006±0.006 day⁻¹ in leopard frogs). In the

low-food treatments sacrificed after 10 days, mortality rates were identical for both species (0.003±0.002 day⁻¹ for wood frogs and 0.003±0.0004 day⁻¹ for leopard frogs; one-way ANOVA $F_{1,5}=0.01$, $P=0.927$). Mortality rates in the first 10 days did not differ from overall mortality rates in the low-food treatments calculated for the entire experiment for the wood frog (0.003±0.002 vs. 0.002±0.0004 day⁻¹; $F_{1,6}=0.33$, $P=0.59$), but were significantly lower for the leopard frog (0.003±0.001 vs. 0.01±0.002 day⁻¹; $F_{1,6}=14.3$, $P=0.01$). Therefore, mortality appears to have occurred over the course of the experiment.

Discussion

We found strong support for species-specific relationships between mortality and realized growth rates. Both in field and mesocosm experiments, mortality was a steep negative function of realized growth rate for the fast-growing species, the leopard frog. In contrast, for the slow-growing wood frog, mortality was independent of realized growth rate in the field and exhibited a weaker negative relationship to realized growth rate, in absolute terms, in the mesocosm experiment.

The overall relationship between mortality and realized growth rates is thus negative, supporting the expectation that environmental conditions yielding faster growth also yield lower mortality (also observed in plants; Augspurger 1984a; Kobe et al. 1995). This environmental correlation arises because higher resource availability allows more energy to be devoted to both growth and other body functions directly related to condition (storage, defense, maintenance) and therefore survivorship. However, growth and mortality appear to be at least partially decoupled judging from the stronger responsiveness of mortality to variation in resources than growth, the wide interspecific variation in the relationship between mortality and realized growth rates, and the weak relationship between these traits in wood frogs (Fig. 1a, b).

Whereas environmental conditions yielding fast growth also yield lower mortality within species, interspecific performance comparisons suggest that there is a tradeoff in the ability to maximize growth when resources are abundant versus the ability to minimize overall mortality, especially when resources are rare (Fig. 2a, b). Note that it is possible that this tradeoff might also be manifest within species, but our experimental design does not permit detection of such effects (i.e., requiring independent manipulation of genotypes; e.g., Blanckenhorn 1998). A tradeoff between mortality and growth capacity appears to arise because acquired

energy can be allocated to essential body functions other than growth that more strongly affect survivorship (storage, maintenance, defense). Rough estimates suggest that leopard frogs allocate nearly 90% of assimilated energy to growth as opposed to 50% in wood frogs (Schiesari 2004). This disproportional allocation to growth permits leopard frogs to exhibit greater scope of growth responses to increases in food quality or quantity, to achieve higher maximal growth rates, and to reach body masses at metamorphosis 2.5- to 3.5-fold greater than those of wood frogs in an only moderately longer larval period (Wright 1914; Collins 1975; Berven 1990; Schiesari 2004). However, investment in growth presumably comes at the expense of reduced investment in other essential physiological functions such as maintenance and immune defense, and could explain the high background mortality of leopard frogs in both favorable and unfavorable environmental conditions. Alternative but not mutually exclusive explanations for differences in mortality with growth capacity include increased DNA mistakes due to increased transcription rates (Arendt 1997), and accelerated tissue catabolism and depressed immunocompetence due to increased activation of the stress hormonal axis (Rollins-Smith and Cohen 1996; Glennemeier and Denver 2002; Denver et al. 2002).

This hypothesized tradeoff can potentially influence patterns of species distributions across resource gradients. Although unproductive habitats tend to be dominated by slow-growing species, and productive habitats tend to be dominated by fast-growing species, several experimental studies have demonstrated that species with higher intrinsic growth rates grew as fast or faster than species with lower intrinsic growth rates, even when resources were rare (e.g., this study for animals; and Augspurger 1984a; Kitajima 1994; Ellison et al. 1993; for plants). If growth rates were positively correlated with survivorship and/or fecundity, this would imply that species with a higher intrinsic growth rate would dominate across the entire gradient. However, increased mortality rates may prevent fast-growing species from colonizing unproductive habitats, and this effect may be further magnified under interspecific competition. Higher intrinsic growth rates may be advantageous when resources are abundant due to advantages in pre-emptive competitive ability (Grime 1979), or as a trait evolved in response to consistently higher predation rates (Dudycha 2001).

A mortality–growth tradeoff is likely important in influencing distributions of these anuran species. Because larval survival through metamorphosis is a strong predictor of adult population sizes and net replacement rates, and because adults exhibit limited

dispersal rates (e.g., wood frogs; Berven 1990), larval survival should greatly affect the probability of population persistence in a given pond where resources are low. In addition to displaying higher daily mortality rates, leopard frog larvae may also experience increased indirect mortality due to their slower development (Collins 1975; Schiesari 2004), which prolongs exposure to aquatic predators and increases the risk of desiccation in non-permanent ponds. Ultimately, the very high premetamorphic mortality of leopard frogs in resource-poor environments appears to lead to the strong pattern of habitat segregation across the canopy cover gradient. A corollary of the overall higher mortality rates of leopard frogs is that, all else being equal, wood frogs should dominate across the entire canopy cover gradient. One of us argues elsewhere (Schiesari 2006) that under typical conditions leopard frog populations may be maintained in open-canopy ponds despite the higher background mortality rates because open-canopy ponds tend to be more permanent, and permanent ponds may contain fish. Wood frogs are more vulnerable to fish predation because of higher palatability (Relyea 2001) and the species is virtually eliminated from ponds where fish are present.

Our results are based on a single pair of amphibian species, but synthesis of published information across organisms of widely different life histories and physiologies suggest that a tradeoff between intrinsic growth and mortality rates may be general. In seedlings and saplings of both temperate and tropical forest trees, species with highest intrinsic growth rates suffered higher mortality in the shade (Kitajima 1994; Kobe et al. 1995; Kobe and Coates 1997) but also in the sun (Brokaw 1980; Augspurger 1984a; Kitajima 1994). Analogous to our amphibian system, fast-growing sapling species allocate a high proportion of the assimilated energy into leaf surface, and thus further increase growth rate when resources (sunlight) are high. In turn, slow-growing sapling species allocate a high proportion of assimilated energy into structure (thicker leaves, higher wood density) and storage (Kitajima 1994; Kobe 1997). These traits are related to lower incidences of herbivory and disease (Augspurger 1984a, b) as well as to an ability to recover lost tissue which is a particularly useful trait when resources are rare (i.e., in the shade). Consequently, fast-growing sapling species display steep negative relationships between mortality and growth whereas slow-growing species tend to exhibit weakly negative, or no relationship at all, between these traits (Kobe et al. 1995; Kobe and Coates 1997; Kobe 1999). These species-specific mortality relationships, and the underlying tradeoff, have been implicated in mediating forest succession and

consequently temporal but also spatial plant distributions (Kobe et al. 1995; Hubbell 2001). Plants in tundra, arid grassland, and prairies also have been found to display positive correlations between intrinsic growth and mortality rates (Suding et al. 2003; K. N. Suding, personal communication).

Among animals, daphniid species with highest intrinsic growth rates have decreased survivorship even under satiating food levels and benign temperatures in the laboratory (Dudycha and Tessier 1999; see also Desmarais and Tessier 1999). In a diverse neotropical guild of frugivorous *Drosophila*, Sevenster and Van Alphen (1993) demonstrated that the larval developmental period was positively correlated with adult longevity both under starvation and in the presence of food ad libitum (the latter not significant). To test whether similar correlations would be observed if larval growth rates instead of developmental rates were employed, we estimated growth rates using Krijger et al.'s (2001) data on maximal body size and developmental time of seven *Drosophila* species from the same locality investigated by Sevenster and van Alphen (1993), assuming equal egg sizes among species. Larval growth rates were negatively correlated with longevity of adults both under starvation (Pearson's $r = -0.86$, $P = 0.01$) and abundant food conditions ($r = -0.81$, $P = 0.05$). This increased mortality is compensated for by earlier reproduction in daphniids (Dudycha and Tessier 1999), and earlier senescence by greater generalism in breeding site selection allowing early reproduction in drosophilids (Sevenster and van Alphen 1993). The results for juvenile trees and anuran larvae, however, clearly argue for a fundamental physiological tradeoff between maximum growth rate and survivorship, as no investment is made in reproduction in these stages.

We have provided direct experimental evidence that maximization of growth may come at the cost of increased mortality irrespective of resource availability, but especially under resource shortage. Such a tradeoff has the potential to bridge between individual performance and demographic rates, which ultimately may explain why individual growth rate is correlated with a species' position on resource gradients. Data from a variety of taxa suggest that this tradeoff may be general, and worthy of more extensive research.

Acknowledgements We thank Zack Schulman for field assistance, Faye Stoner of the Washtenaw County Parks and the Michigan DNR for egg collection permits, and the University of Michigan's Museum of Zoology for permission to work in the E. S. George Reserve. Insightful comments of Deborah Goldberg and Katie Nash-Suding, and statistical advice by Kathy Welch

and Laura Klem were particularly important for the development of this research. This research was funded by the Conselho Nacional de Desenvolvimento Científico e Tecnológico of the Brazilian Government (CNPq 200093/97–5), The University of Michigan (Rackham Predoctoral Fellowship), and the National Science Foundation (DEB-0089809). S. D. P. acknowledges support from the Michigan Agricultural Experimental Station. This is GLERL contribution 1384. The experiment reported here complies with all current laws of the USA.

References

- Arendt JD (1997) Adaptive intrinsic growth rates: an integration across taxa. *Q Rev Biol* 72:149–177
- Arendt JD, Wilson DS, Stark E (2001) Scale strength as a cost of rapid growth in sunfish. *Oikos* 93:95–100
- Augsburger CK (1984a) Light requirements of neotropical tree seedlings: a comparative study of growth and survival. *J Ecol* 72:777–795
- Augsburger CK (1984b) Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. *Ecology* 65:1705–1712
- Berven KA (1990) Factors affecting population fluctuations in larval and adult stages of the wood frog (*Rana sylvatica*). *Ecology* 71:1599–1608
- Blanckenhorn WU (1998) Adaptive phenotypic plasticity in growth, development, and body size in the yellow dung fly. *Evolution* 52:1394–1407
- Brokaw N (1980) Gap-phase regeneration in a neotropical forest. PhD dissertation, University of Chicago, Chicago, Ill.
- Collins JP (1975) A comparative study of the life history strategies in a community of frogs. PhD dissertation, University of Michigan, Mich.
- Connell JH (1975) Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In: Cody ML, Diamond JM (eds) *Ecology and evolution of communities*. Belknap Press of Harvard University Press, Cambridge, Mass., pp 460–490
- Denver RJ, Glennemeier KA, Boorse GC (2002) Endocrinology of complex life cycles: amphibians. In: Pfaff D, Arnold A, Etgen A, Fahrback S, Rubin R (eds) *Hormones, brain and behavior*, vol 2. Academic Press, San Diego, Calif., pp 469–513
- Desmarais KH, Tessier AJ (1999) Performance trade-off across a natural resource gradient. *Oecologia* 120:137–146
- Dudycha JL (2001) The senescence of *Daphnia* from risky and safe habitats. *Ecol Lett* 4:102–105
- Dudycha JL, Tessier AJ (1999) Natural genetic variation of life span, reproduction, and juvenile growth in *Daphnia*. *Evolution* 53:1744–1756
- Ellison AM, Denslow JS, Loiselle BA, Brenez MD (1993) Field and seedling ecology of neotropical Melastomataceae. *Ecology* 74:1733–1749
- Glennemeier KA, Denver RJ (2002) Role for corticoids in mediating the response of *Rana pipiens* tadpoles to intraspecific competition. *J Exp Zool* 292:32–42
- Gosner KL (1960) A simplified table for staging anuran embryos and larvae, with notes on identification. *Herpetologica* 16:183–190
- Grime JP (1979) *Plant strategies and vegetation processes*. Wiley, New York
- Grime JP, Hunt R (1975) Relative growth rate: its range and adaptive significance in a local flora. *J Ecol* 63:393–422

- Grime JP, Thompson K, Hunt R, Hodgson JG, Cornelissen JHC, Rorison IH, Hendry GAF, Ashenden TW, Askew AP, Band SR, Booth RE, Bossard CC, Campbell BD, Cooper JEL, Davison AW, Gupta PL, Hall W, Hand DW, Hannah MA, Hillier SH, Hodgkinson DJ, Jalili A, Liu Z, Mackey JML, Matthews N, Mowforth MA, Neal AM, Reader RJ, Reiling K, Ross-Fraser W, Spencer RE, Sutton F, Tasker DE, Thorpe PC, Whitehouse J (1997) Integrated screening validates primary axes of specialization in plants. *Oikos* 79:259–281
- Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, N.J.
- Kitajima K (1994) Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* 98:419–428
- Kobe RK (1997) Carbohydrate allocation to storage as a basis of interspecific variation in sapling survivorship and growth. *Oikos* 80:226–233
- Kobe RK (1999) Light gradient partitioning among tropical tree species through differential seedling mortality and growth. *Ecology* 80:187–201
- Kobe RK, Coates KD (1997) Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. *Can J For Res* 27:227–236
- Kobe RK, Pacala SW, Silander JA Jr (1995) Juvenile tree survivorship as a component of shade tolerance. *Ecol Appl* 5:517–532
- Krijger CL, Peters YC, Sevenster JG (2001) Competitive ability of neotropical *Drosophila* predicted from larval development times. *Oikos* 92:325–332
- Lankford TE Jr, Billerbeck JM, Conover DO (2001) Evolution of intrinsic growth and energy acquisition rates. II. Trade-offs with vulnerability to predation in *Menidia menidia*. *Evolution* 55:1873–1881
- Relyea RA (2001) The relationship between predation risk and antipredator responses in larval anurans. *Ecology* 82:541–554
- Rollins-Smith LA, Cohen N (1996) Metamorphosis: an immunologically unique period in the life of the frog. In: Gilbert LI, Tata JR, Atkinson BG (eds) *Metamorphosis: post embryonic reprogramming of gene expression in amphibian and insect cells*. Academic Press, San Diego, Calif., pp 626–646
- Schiesari L (2004) Performance tradeoffs across resource gradients in anuran larvae. PhD dissertation, University of Michigan, Mich.
- Schiesari L (2006) Pond canopy cover: a resource gradient for anuran larvae. *Freshwater Biol* 51:412–423
- Sevenster JG, van Alphen JJM (1993) A life history trade-off in *Drosophila* species and community structure in variable environments. *J Anim Ecol* 62:720–736
- Skelly DK, Werner EE, Cortwright SA (1999) Long-term distributional dynamics of a Michigan amphibian assemblage. *Ecology* 80:2326–2337
- Skelly DK, Freidenburg LK, Kiesecker JM (2002) Forest canopy and the performance of larval amphibians. *Ecology* 83:983–992
- Stemberger RS, Gilbert JJ (1985) Body size, food concentration, and population growth in planktonic rotifers. *Ecology* 66:1151–1159
- Suding KN, Goldberg DE, Hartman KM (2003) Relationships among species traits: separating levels of response and identifying linkages to abundance. *Ecology* 84:1–16
- Tessier A.J, Woodruff P (2002) Trading off the ability to exploit rich versus poor food quality. *Ecol Lett* 5:685–692
- Tessier AJ, Leibold MA, Tsao J (2000) A fundamental tradeoff in resource exploitation by *Daphnia* and consequences to plankton communities. *Ecology* 81:826–841
- Tilman D (1990) Constraints and tradeoffs: toward a predictive theory of competition and succession. *Oikos* 58:3–15
- Verbeke G, Molenberghs G (2002) Linear mixed models for longitudinal data. Springer, Berlin Heidelberg New York
- Werner EE, Anholt BR (1993) Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *Am Nat* 142:242–272
- Werner EE, Glennemeier K (1999) The influence of forest canopy cover on the breeding pond distributions of several amphibian species. *Copeia* 1:1–12
- Wright AH (1914) North American Anura—life histories of the Anura of Ithaca, New York. Carnegie Inst Wash Publ 197:1–98