Evolution of juvenile growth rates in female guppies (*Poecilia reticulata*): predator regime or resource level?

Jeffrey D. Arendt* and David N. Reznick

Department of Biology, University of California at Riverside, Riverside, CA 92521, USA

Recent theoretical and empirical work argues that growth rate can evolve and be optimized, rather than always being maximized. Chronically low resource availability is predicted to favour the evolution of slow growth, whereas attaining a size-refuge from mortality risk is predicted to favour the evolution of rapid growth. Guppies (*Poecilia reticulata*) evolve differences in behaviour, morphology and life-history traits in response to predation, thus demonstrating that predators are potent agents of selection. Predators in low-predation environments prey preferentially on small guppies, but those in high-predation environments appear to be non-selective. Because guppies can outgrow their main predator in low- but not high-predation localities, we predict that predation will select for higher growth rates in the low-predation environments. However, low-predation localities also tend to have lower productivity than high-predation localities, yielding the prediction that guppies from these sites should have slower growth rates. Here we compare the growth rates of the second laboratory-born generation of guppies from paired high- and low-predation localities from four different drainages. In two out of four comparisons, guppies from high-predation sites grew significantly faster than their low-predation counterparts. We also compare laboratory born descendants from a field introduction experiment and show that guppies introduced to a low-predation environment evolved slower growth rates after 13 years, although this was evident only at the high food level. The weight of the evidence suggests that resource availability plays a more important role than predation in shaping the evolution of growth rates.

Keywords: guppy; growth rate; size-selective predation; resource availability

1. INTRODUCTION

Ecological and life-history studies often assume that growth rates are maximized so that variation among populations is a passive consequence of environmental factors such as resources or temperature. Recent theoretical and empirical work shows that growth rates are optimized rather than maximized, and population variation often reflects local adaptation (reviewed in Arendt 1997). So far, only a few studies have documented adaptive variation in growth rate within species (e.g. Berven *et al.* 1979; Conover & Present 1990; Gotthard *et al.* 1994; Arendt & Wilson 1997; Laugen *et al.* 2002). We evaluate competing hypotheses for the evolution of growth rate using the guppy (*Poecilia reticulata*), a model system for studying adaptation in the wild. In addition to population comparisons, two introduction experiments represent the first direct test for the evolution of growth rate under natural conditions.

Theory predicts the evolution of slow growth in response to chronically low resource conditions, such as low light or low nutrient levels (e.g. Poorter 1989; Iwasa 1991; Niewiarowski & Roosenburg 1993; Sinervo & Adolph 1994) to minimize costs of growth. Rapid growth is predicted when exceeding some critical size reduces the risk of mortality. For example, a short growing season coupled with a minimum size for over-winter survival often results in the evolution of rapid growth to obtain a critical size in a limited amount of time (Berven 1987; Conover & Present 1990; Gotthard *et al.* 1994; Ayres & Scriber 1994; Brown *et al.*

1998). Arendt & Wilson (1997, 1999) show that a size-refuge from competition also favours the evolution of rapid growth. Similarly, theory predicts that a size-refuge from predation will favour rapid growth (Abrams *et al.* 1996). The evolution of rapid growth to avoid predation should be especially common in aquatic organisms because predatory fishes are often gape-limited (Hambright 1991; Persson *et al.* 1996; Magnhagen & Heibo 2001) and invertebrate predators are also unable to handle prey above a certain size (Reist 1980; Werner & McPeck 1994; McPeck 1995).

Two of these theories, predation and resources, apply to guppies and yield opposite predictions. Guppies have been most intensively studied in the Northern Range Mountains of Trinidad. In streams on the southern slopes of these mountains the dominant guppy predator is the pike cichlid (*Crenicichla alta*), a piscivore capable of eating guppies of any size (e.g. Mattingly & Butler 1994; Reznick *et al.* 1996). Upstream localities are separated from *Crenicichla* locals by barrier waterfalls that prevent the migration of most fishes. Upstream locals are characterized by the killifish (*Rivulus hartii*), a generalist predator that occasionally eats guppies and, when it does, feeds predominantly on small guppies (Mattingly & Butler 1994). A parallel pattern occurs in rivers on the northern slope, except that high-predation sites contain numerous gobies (most notably *Eleotris pisonis*, *Gobiomorus dormitor* and *Dormitator maculatus*) and low-predation sites contain *Rivulus* and prawns, including *Macrobrachium crenulatum*. Although the specific identity of predators is different between north and south slopes, similar life-history patterns have evolved under these predation regimes. Guppies from high-predation localities

* Author for correspondence (jarendt@citrus.ucr.edu).

Table 1. Populations sampled for each experiment analysed.

study	drainage	population	predation	life-history study
(a) south slope	Oropuche	Oropuche	high	Reznick (1982)
		Quare	low	
	Caroni	El Cedro	high	
		Aripo	low	
(b) north slope	Yarra	Yarra	high	Reznick & Bryga (1996)
		Yarra-Trib	low	
	Madamas	Madamas	high	
		Madamas-Trib	low	
(c) El Cedro introduction				Reznick & Bryga (1987)
				Reznick <i>et al.</i> (1997)
Aripo introduction				Reznick <i>et al.</i> (1990)

mature earlier, produce more but smaller young, reproduce more frequently, and have greater reproductive effort per pregnancy than do guppies from low-predation localities (summarized in Reznick *et al.* 1996b). In addition, this shift in life-history pattern can occur very quickly. High-predation guppies transplanted to low-predation sites evolve some features of the low-predation life history in as few as 4 years (Reznick & Bryga 1987; Reznick *et al.* 1997). Guppies co-occur with gape-limited predators in low-predation localities, so selection should favour the evolution of rapid growth to reach a size-refuge as rapidly as possible. In high-predation localities, predators are capable of taking guppies of any size, so there is no size-refuge and no advantage to rapid growth (as predicted in Arendt (1997)).

Resource availability covaries with predator community and is also a potential factor in the evolution of growth rates. Low-predation localities are usually upstream, headwater sites with closed canopies. Productivity is usually low at these sites (Grether *et al.* 2001) with high population densities, resulting in slow realized growth rates in the field (Reznick *et al.* 2001). High-predation localities are downstream sites with open canopies, greater productivity, lower population densities and higher growth rates. Lower resource availability in low-predation sites is thus caused by a combination of a confounding environmental factor (canopy cover) and an indirect effect of predation (population density).

The two most important ecological factors in guppy life-history evolution predict opposite outcomes; predation regime favours rapid growth but resource availability favours slow growth in upstream habitats relative to downstream habitats. We test for population differences in growth rate under common laboratory conditions collected over the past two decades and use these results to infer whether predation pressure or resource availability is more important in driving the evolution of growth rate. Although predation has served as an *ad hoc* explanation for variation in growth rate (Seed & Brown 1978; Johannesson *et al.* 1997), this is the first test of predation based on an *a priori* prediction (Arendt 1997). In addition to population comparisons, two transplant experiments serve as a direct test for selection on growth rate in the wild.

2. MATERIAL AND METHODS

Growth rates were analysed from six comparisons of a high-predation site to a nearby low-predation site. By assay these were:

(i) two high- and low-predation sites on south slope streams. These include the El Cedro River (high-predation) and Aripo Tributary (low-predation) in the Caroni River Drainage and the Oropuche River (high-predation) and a tributary to the Quare River (low-predation) from the Oropuche Drainage; (ii) paired high- and low-predation sites on north slope streams along the Yarra and Madamas Rivers; and (iii) two transplant experiments with guppies moved from a high-predation site to a previously guppy-free low-predation site compared with their original high-predation population. One transplant was on the Aripo River assayed 11 years after the introduction. A transplant on the El Cedro River was assayed 4, 7 and 13 years after the introduction. Multiple assays are important to determine how quickly differences in growth evolve because different life-history traits evolve at different rates. Transplant populations differ from those on the same river used in the south slope comparisons. References detailing life-history differences among populations are given in table 1 (see also fig. 1 in Reznick *et al.* (1996b) for a map of these locations).

Because growth rate is strongly influenced by environmental and maternal effects and commonly shows counter-gradient variation, studies of the evolution of growth rate are best conducted using either reciprocal crosses or common garden conditions (Conover & Schultz 1995). Guppies used for growth rate analyses are the second (F_2) generation raised in the laboratory, a common garden design that also minimizes maternal effects. We analysed growth rates in females because male guppies show determinate growth, stopping soon after maturation. Females have indeterminate growth so the evolution of growth rate is less likely to be correlated with selection on size or age at maturation. In addition, females mature late enough after the initiation of controlled food availability for several size measures to be available before maturation and the shift of some resource allocation to reproduction. Guppies were typically raised on two food levels but the specific amount of food varied among studies, so we refer to these as high and low rations (further details of rearing conditions can be found in Reznick (1982)). All food was eaten between feedings (i.e. no guppy was ever fed *ad libitum*). Guppies from the El Cedro introduction were raised at two food levels in years 4 and 13. However, a single, low food level was used during the El Cedro 7 year assay and the Aripo assay. An individual guppy was placed on the experimental food level at between three and four weeks of age, when it could first be sexed. Each female was housed individually in a 81 aquarium and was mated once per week until she gave birth to her first litter, then again after the birth of each litter. Aquaria were arrayed in a stratified, randomized block

Figure 1. Mean growth rates and standard deviations for (a) south slope and (b) north slope populations. Growth rates are the slope estimated by regression of $\ln(\text{mass})$ on age. Symbols represent a given drainage within each comparison. Open symbols are the upstream (low predation) populations, filled symbols are the downstream (high predation) populations. There was an average of seven females in each treatment in the south slope study and 15 females in each treatment in the north slope study.

design so there was no confounding between locality, food availability and uncontrolled environmental variation in the laboratory. Size was estimated in two ways; mass was estimated to the nearest milligram on an electronic balance, and standard length was estimated to the nearest 0.5 mm using digital callipers. Initially, only mass was measured, but both measures were taken every two weeks thereafter.

All size measures were natural log ($\ln$)-transformed before analysis to remove heteroscedasticity and linearize the growth trajectory. We estimated growth rate in different ways depending upon the number of size estimates that were taken for each guppy. Nearly all guppies showed linear growth trajectories over the sizes measured. We therefore used the slope of the linear regression of $\ln(\text{size})$ on age as our estimate of growth rate. We also analysed instantaneous growth rate ($= [\ln(\text{size}_2) - \ln(\text{size}_1)]/\text{time}$) for all guppies using the initial and final size measure before first parturition. The two estimates yield similar results so only growth rates based on slope are reported.

Because the precise amount of food used at the high and low food levels varied among studies, we analysed each study separately. Differences in growth rate were analysed using a mixed nested analysis of variance design (see Neter *et al.* 1996). Predator effect (low-predation upstream versus high-predation downstream) was nested within drainage, and the nested factors were

crossed with food level. There is no drainage effect for the introduction experiments so these results were analysed with a two-factor analysis of variance (ANOVA) (food level $\times$ population) for the year 4 and year 13 samples from the El Cedro River and a one-way ANOVA for the year 7 El Cedro sample and year 11 Aripo sample, where only one food level was used.

3. RESULTS

Food level had a significant effect on growth rate in the first two studies (south slope mass $F_{1,2} = 242$, $p < 0.01$; length $F_{1,2} = 54$, $p = 0.02$; north slope mass $F_{1,2} = 356$, $p < 0.01$; length $F_{1,2} = 3613$, $p < 0.01$), with fish on the high food level growing faster than those on the low food level (figure 1). Drainage effects were not significant either among south slope populations (study A) or among north slope populations (study B). North slope populations had a significant food $\times$ drainage interaction for growth in length ($F_{1,2} = 35$, $p < 0.03$) because both populations from the Madamas drainage showed a slightly greater response to food level than do populations of the Yarra drainage. Both studies also showed a significant effect of predation regime for both estimates of growth rate (south slope mass $F_{2,40} = 9.39$, $p < 0.01$; length $F_{2,44} = 6.86$, $p < 0.01$; north slope mass $F_{2,118} = 15.9$, $p < 0.01$; length $F_{2,118} = 5.12$, $p < 0.01$). Paired comparisons within each study revealed that in each case one of the two replicates had higher growth rates in high-predation guppies (Oropuche and Yarra) but that predation did not influence growth rate in the other replicate (Caroni and Madamas).

There was also a highly significant food effect in years 4 ($F_{1,56} = 107$, $p < 0.01$) and 13 ($F_{1,89} = 123$, $p < 0.01$) for the El Cedro introduction experiment (there was only one food level in year 7). Population differences in growth rate were not evident in either year 4 ($F_{1,56} = 0.18$, $p = 0.68$) or 7 ($F_{1,113} = 1.1$, $p = 0.3$) or in the Aripo introduction ($F_{1,51} = 0.2$, $p = 0.9$), but by year 13 on the El Cedro there was a significant difference ($F_{1,89} = 8.6$, $p < 0.01$). Guppies from the high-predation site had faster intrinsic growth rates than did those from the low-predation site, although this difference is only evident at the high food level (figure 2), causing a significant food $\times$ population interaction ($F_{1,89} = 9.7$, $p < 0.01$).

4. DISCUSSION

In all comparisons with significant results guppies from downstream sites had faster growth rates than those from upstream sites. Moreover, differences in growth rate evolve quickly, becoming significantly slower in the El Cedro population within 13 years of the introduction of guppies from a high-predation locality into a low-predation locality (approximately 22 generations based on the generation time estimated in Reznick *et al.* (1997)). This pattern is more consistent with resource levels, rather than a size-refuge from predation, being the primary factor driving growth rate evolution in this system.

Why does rapid growth not evolve in response to predation as predicted in Arendt (1997)? Recent work (Bashey 2002) suggests that the size-refuge from *Rivulus* predation occurs at a smaller size than previously assumed. Moreover, population densities of guppies tend to be much greater at these sites than at high-predation sites; the larger offspring size typical of low-predation guppies provides an

Figure 2. Mean growth rates and standard deviations in the El Cedro and Aripo introduction experiments. Open bars are the upstream (low-predation) introduced population, filled bars are the downstream (high-predation) source population. Numbers in bars are samples sizes. (a) Results for El Cedro experiment at 4 and 13 years after introduction, where guppies were tested at two food levels. In both cases, the bars to the left are the lower food level. Downstream guppies grew significantly faster at high food levels in the 13 year assay. (b) Results for El Cedro 7 years and Aripo 11 years after introduction. In these assays, guppies were tested at a single food level. No differences among populations were detected.

advantage under such competitive situations (Bashey 2002). Given the poor growing conditions typical of low-predation sites, producing larger offspring may be a better strategy than producing fast-growing offspring.

Although we did not detect a significant drainage effect, closer examination of the south slope and north slope studies reveals that the difference in growth rate in both comparisons is large in one drainage area, but small in the other. Because productivity levels have not been measured at the populations used in this analysis, we have had to rely on a general correlation between upstream and low productivity versus downstream and high productivity. The inconsistent differences in growth rate among populations may occur because the relationship between predation and productivity is not always a strong one (Grether *et al.* 2001; Reznick *et al.* 2001). This variation among drainages is most likely to be the result of resource levels, rather than predation pressure, driving genetic variation in growth rate because predation pressures and life histories are known to differ consistently among these sites.

We were not able to detect a significant change in growth rate for the introduction experiments until year 13 in the El Cedro River. As previously reported (Reznick & Bryga 1987; Reznick *et al.* 1990, 1997), different life-history traits appear to evolve at different rates in this population. For example, significant differences in male age at maturity evolved in 4 years whereas differences in females did not appear until 7 years. It is possible that growth rate evolves more slowly than reproductive traits, or it may be more sensitive to resource levels in its expression. Guppies in the Aripo assay and the earlier El Cedro assays were raised on relatively low food levels, resulting in slow realized growth rates. In the 13 year El Cedro assay, it was only at the highest food level that significant differences in growth rate were found. It is possible that growth rate had evolved more quickly than we detected here, but that the single food level used in the 7 year assay for the El Cedro and 11 year assay for the Aripo was insufficient to reveal these differences.

Growth rate in guppies shows a co-gradient pattern with respect to resources. That is, slow growth has evolved in low-resource populations, where slow growth would be expected for any guppy regardless of growth potential. Based on measures of growth rate in the field using mark-recapture techniques, Reznick *et al.* (2001) argued that growth patterns are a direct consequence of the resources available at these sites. The results reported here raise the possibility that field measures may reflect evolved patterns rather than a direct measure of local productivity. Reznick *et al.* (2001) found that in the field, guppies at high-predation (downstream) sites grew, on average, 1.78 mm over a 12 day period whereas those from low-predation (upstream) sites grew *ca.* 0.98 mm (taken from their fig. 3). This translates into 45% slower growth at the upstream locations. If we convert our laboratory estimates of growth rate into millimetres per 12 days we get growth rates that are 2.6% slower for upstream populations (1.51 mm downstream versus 1.47 mm upstream) on the high food treatment and 26% slower (0.61 mm versus 0.45 mm) on the low food treatment for the south slope experiment. The north slope experiment is similar with 3.0% slower growth upstream than downstream (1.67 mm versus 1.62 mm) at high food and 16% slower (1.07 mm versus 0.90 mm) at low food levels. These values are all much lower than the 45% decrease measured in the field by Reznick *et al.* (2001). This suggests that field measures of growth rate are not simply due to the genetic differences in potential growth rate among upstream and downstream populations reported here but also incorporate differences in productivity in the two environments.

In conclusion, growth rates do not always evolve in an upstream-downstream comparison among populations. However, when they do evolve, the result is faster growth in downstream high-predation populations and slower growth in upstream low-predation populations. This pattern is the opposite of what we had predicted if a size-refuge from predation drives the evolution of growth rate. It is consistent with predictions for growth rate evolution based

on known patterns of resource availability. Upstream locations often have low productivity, and slow growth is often seen in organisms adapted to low-resource conditions. The population differences in growth rate seen in the laboratory are not sufficient to explain all of the difference in growth rate seen in the field. This means that field growth rates reflect both an evolved difference in growth rate and a difference in local productivity.

The authors thank F. Bashey, D. Elder, C. Ghalambor, M. Pires and two anonymous reviewers whose comments greatly improved this paper. This research was supported in part by the National Science Foundation.

REFERENCES

- Abrams, P. A., Leimar, O., Nylin, S. & Wiklund, C. 1996 The effect of flexible growth rates on optimal sizes and development times in a seasonal environment. *Am. Nat.* **147**, 381–395.
- Arendt, J. D. 1997 Adaptive intrinsic growth rates: an integration across taxa. *Q. Rev. Biol.* **72**, 149–177.
- Arendt, J. D. & Wilson, D. S. 1997 Optimistic growth: competition and an ontogenetic niche-shift select for rapid growth in pumpkinseed sunfish (*Lepomis gibbosus*). *Evolution* **51**, 1946–1954.
- Arendt, J. D. & Wilson, D. S. 1999 Countergradient selection for rapid growth in pumpkinseed sunfish: disentangling ecological and evolutionary effects. *Ecology* **80**, 2793–2798.
- Ayres, M. P. & Scriber, J. M. 1994 Local adaptation to regional climates in *Papilio canadensis* (Lepidoptera: Papilionidae). *Ecol. Monogr.* **64**, 465–482.
- Bashey, F. 2002 Causes and consequences of offspring size variation in the Trinidadian guppy (*Poecilia reticulata*). PhD thesis, University of California, USA.
- Berven, K., Gill, D. E. & Smith-Gill, S. J. 1979 Countergradient selection in the green frog, *Rana clamitans*. *Evolution* **33**, 609–623.
- Berven, K. A. 1987 The heritable basis of variation in larval developmental patterns within populations of the wood frog (*Rana sylvatica*). *Evolution* **41**, 1088–1097.
- Brown, J. J., Ehtisham, A. & Conover, D. O. 1998 Variation in larval growth rate among striped bass stocks from different latitudes. *Trans. Am. Fish. Soc.* **127**, 598–610.
- Conover, D. A. & Present, T. M. C. 1990 Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides from different latitudes. *Oecologia* **83**, 316–324.
- Conover, D. O. & Schultz, E. T. 1995 Phenotypic similarity and the evolutionary significance of countergradient selection. *Trends Ecol. Evol.* **10**, 248–252.
- Gotthard, K., Nylin, S. & Wiklund, C. 1994 Adaptive variation in growth rate: life history costs and consequences in the speckled wood butterfly, *Pararge aegeria*. *Oecologia* **99**, 281–289.
- Grether, G. F., Millie, D. F., Bryant, M. J., Reznick, D. N. & Mayea, W. 2001 Rain forest canopy cover, resource availability, and life history evolution in guppies. *Ecology* **82**, 1546–1559.
- Hambright, K. D. 1991 Experimental analysis of prey selection by largemouth bass: role of predator mouth width and prey body depth. *Trans. Am. Fish. Soc.* **120**, 500–508.
- Iwasa, Y. 1991 Pessimistic plant: optimal growth schedule in stochastic environments. *Theor. Popul. Biol.* **40**, 246–268.
- Johannesson, K., Rolan-Alvarez, E. & Erlandsson, J. 1997 Growth rate differences between upper and lower shore ecotypes of the marine snail *Littorina saxatilis* (Olivi) (Gastropoda). *Biol. J. Linn. Soc.* **61**, 267–279.
- Laugen, A. T., Laurila, A. & Merila, J. 2002 Maternal and genetic contributions to geographical variation in *Rana temporaria* larval life-history traits. *Biol. J. Linn. Soc.* **76**, 61–70.
- McPeck, M. A. 1995 Morphological evolution mediated by behaviors in the damselflies of two communities. *Evolution* **49**, 749–769.
- Magnhagen, C. & Heibo, E. 2001 Gape size allometry in pike reflects variation between lakes in prey availability and relative body depth. *Funct. Ecol.* **15**, 754–762.
- Mattingly, H. T. & Butler IV, M. J. 1994 Laboratory predation on the Trinidadian guppy: implications for the size-selective predation hypothesis and guppy life history evolution. *Oikos* **69**, 54–64.
- Neter, J., Kutner, M. H., Nachtsheim, C. J. & Wasserman, W. 1996 *Applied linear statistical models*, 4th edn. Chicago, IL: Irwin.
- Niewiarowski, P. H. & Roosenburg, W. 1993 Reciprocal transplant reveals sources of variation in growth rates of the lizard *Sceloporus undulatus*. *Ecology* **74**, 1992–2002.
- Persson, L., Andersson, J., Wahlstrom, E. & Eklov, P. 1996 Size-specific interactions in lake systems: predator gape limitation and prey growth rate and mortality. *Ecology* **77**, 900–911.
- Poorter, H. 1989 Interspecific variation in relative growth rate: on ecological causes and physiological consequences. In *Causes and consequences of variation in growth rate and productivity of higher plants* (ed. H. Lambers, M. L. Cambridge, H. Konings & T. L. Pons), pp. 45–68. The Hague, The Netherlands: SPB Academic Publishing.
- Reist, J. D. 1980 Predation upon phenotypes of brook stickleback, *Culaea inconstans*, by selected invertebrates. *Can. J. Zool.* **58**, 1253–1258.
- Reznick, D. 1982 Genetic determination of offspring size in the guppy (*Poecilia reticulata*). *Am. Nat.* **120**, 181–188.
- Reznick, D. N. & Bryga, H. 1987 Life-history evolution in guppies (*Poecilia reticulata*): 1. Phenotypic and genetic changes in an introduction experiment. *Evolution* **41**, 1370–1385.
- Reznick, D. N. & Bryga, H. A. 1996 Life-history evolution in guppies (*Poecilia reticulata*: Poeciliidae). V. Genetic basis of parallelism in life histories. *Am. Nat.* **147**, 339–359.
- Reznick, D. A., Bryga, H. & Endler, J. A. 1990 Experimentally induced life-history evolution in a natural population. *Nature* **346**, 357–359.
- Reznick, D. N., Rodd, F. H. & Cardenas, M. 1996a Life-history evolution in guppies (*Poecilia reticulata*: Poeciliidae). IV. Parallelism in life-history phenotypes. *Am. Nat.* **147**, 319–338.
- Reznick, D. N., Butler IV, M. J., Rodd, F. H. & Ross, P. 1996b Life-history evolution in guppies (*Poecilia reticulata*) 6. Differential mortality as a mechanism for natural selection. *Evolution* **50**, 1651–1660.
- Reznick, D. N., Shaw, F. H., Rodd, F. H. & Shaw, R. G. 1997 Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science* **275**, 1934–1937.
- Reznick, D., Butler IV, M. J. & Rodd, H. 2001 Life-history variation in guppies. VII. The comparative ecology of high- and low-predation environments. *Am. Nat.* **157**, 126–140.
- Seed, R. & Brown, R. A. 1978 Growth as a strategy for survival in two marine bivalves, *Cerastoderma edule* and *Modiolus modiolus*. *J. Anim. Ecol.* **47**, 283–292.
- Sinervo, B. & Adolph, S. C. 1994 Growth plasticity and thermal opportunity in *Sceloporus* lizards. *Ecology* **75**, 776–790.
- Werner, E. E. & McPeck, M. A. 1994 Direct and indirect effects of predators on two anuran species along an environmental gradient. *Ecology* **75**, 1368–1382.