

# Experimental and model analyses of the effects of competition on individual size variation in wood frog (*Rana sylvatica*) tadpoles

SCOTT D. PEACOR\* and CATHERINE A. PFISTER†

\*Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824 and Great Lakes Environmental Research Laboratory (NOAA), 2205 Commonwealth Blvd, Ann Arbor, MI 48105, USA; and

†Department of Ecology and Evolution, 1101 E. 57th Street, University of Chicago, Chicago, IL 60637, USA

## Summary

1. Size variation is a ubiquitous feature of animal populations and is predicted to strongly influence species abundance and dynamics; however, the factors that determine size variation are not well understood.

2. In a mesocosm experiment, we found that the relationship between mean and variation in wood frog (*Rana sylvatica*) tadpole size is qualitatively different at different levels of competition created by manipulating resource supply rates or tadpole density. At low competition, relative size variation (as measured by the coefficient of variation) decreased as a function of mean size, while at high competition, relative size variation increased. Therefore, increased competition magnified differences in individual performance as measured by growth rate.

3. A model was developed to estimate the contribution of size-dependent factors (i.e. based on size alone) and size-independent factors (i.e. resulting from persistent inherent phenotypic differences other than size that affect growth) on the empirical patterns.

4. Model analysis of the low competition treatment indicated that size-dependent factors alone can describe the relationship between mean size and size variation. To fit the data, the size scaling exponent that describes the dependence of growth rate on size was determined. The estimated value, 0.83, is in the range of that derived from physiological studies.

5. At high competition, the model analysis indicated that individual differences in foraging ability, either size-based or due to inherent phenotypic differences (size-independent factors), were much more pronounced than at low competition. The model was used to quantify the changes in size-dependent or size-independent factors that underlie the effect of competition on size-variation. In contrast to results at low competition, parameters derived from physiological studies could not be used to describe the observed relationships.

6. Our experimental and model results elucidate the role of size-dependent and size-independent factors in the development of size variation, and highlight and quantify the context dependence of individual (intrapopulation) differences in competitive abilities.

*Key-words:* density dependence, individual variation, size-variation, growth densatation, growth autocorrelation.

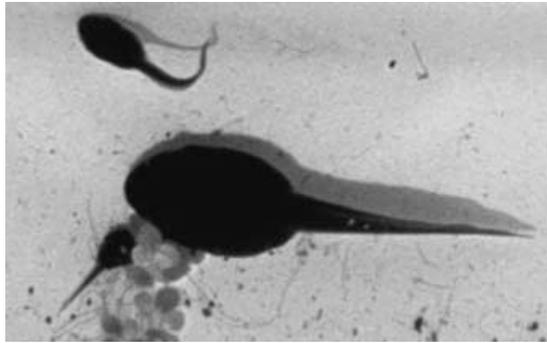
*Journal of Animal Ecology* (2006) **75**, 990–999

doi: 10.1111/j.1365-2656.2006.01119.x

## Introduction

Intrapopulation variation of individual growth rate is a widespread property demonstrated by the large size

variation observed in organisms from the same cohort reared together in controlled conditions (Wilbur & Collins 1973; reviewed in Uchmanski 1985; Lomnicki 1988). Even in nearly equal conditions, large variation in size can be observed, as illustrated for green frog tadpoles in Fig. 1 (see Kooijman 2000 for an example photograph of fish), owing solely to differential growth among individuals. The same factors leading to growth



**Fig. 1.** Example of within-cohort size variation. These three green frog (*Rana clamitans*) tadpoles are from the same cohort raised from the same egg mass together in a 300 L mesocosm. Their mass varied by two orders of magnitude.

rate variation can be expected to be equally important in populations of unequal age, although they are not as obvious.

Disentangling the mechanisms that underlie the development of size-variation is important for a number of reasons that fall under two broad categories. First, variation in size and other fitness components can play an important role in many ecological processes, including extinction risk (Conner & White 1999; Kendall & Fox 2002; Pfister & Stevens 2003), trophic interactions (Maret & Collins 1994), cohort survivorship (Rice *et al.* 1993; Ludsin & DeVries 1997; Rose *et al.* 1999) and population stability (Lomnicki 1988; Uchmanski 1999; Grimm & Uchmanski 2002). Differences in individual growth also can influence individual resource specialization (Bolnick *et al.* 2003) and the development of population size-structure (Ebenmann & Persson 1988) that can influence the aforementioned ecological processes.

Secondly, developing frameworks to understand the origin and development of size variation could elucidate important ecological factors (e.g. spatial heterogeneity, phenotypic effects on growth and fitness). Ecologists have performed numerous experiments in which individual variation was measured, or could have been measured without much additional difficulty. Frameworks to understand the origin of size variation could equip ecologists with an additional lens into interpreting ecological processes (Lomnicki 1988). The elucidation of processes from the examination of variation in a property is very familiar to ecologists, as the variation in population patterns across environmental gradients is used commonly to enhance our understanding of mean population processes (Connell 1961; Wellborn, Skelly & Werner 1996). This approach is also used commonly in physics, in which the variation of scattered particles reveal information about the particles, the object off which they scatter, and the particle-object interactions. We may be missing valuable information in ecological data when we focus on the mean and ignore the variation in animal size

(or other responses) (Hassell & May 1985; Lomnicki 1988).

However, we have surprisingly little understanding of the origin of individual size variation. One explanation for a commonly observed increase in size variation through time is that larger individuals have an advantage that confers faster growth, and therefore growth rate and size are positively correlated through time (denoted 'growth depensation' by Ricker 1958). Statistically, this results in a positive correlation in growth over time, as individuals experiencing higher growth at one time interval will experience higher growth at the next time interval. Because the factor underlying this change in size variation is due purely to size effects on growth, we denote it a 'size-dependent' factor (*sensu* Pfister & Stevens 2002).

The development of size variation may extend beyond size-dependent factors. Phenotypically based differences in foraging traits (Fuiman & Cowan 2003) that have a genetic basis (Arnold 1981; Conover & Munch 2002) or are learned (Palmer 1984; Dukas & Bernays 2000) can also generate differences in growth rate, and therefore size variation. For example, genetic differences that underlie varying levels of boldness in fish (Coleman & Wilson 1997) could translate into differential resource acquisition and hence affect size variation. Further, if an individual does well at acquiring food in one time period, this could both affect growth in that time period but also lead to a good condition that leads to better growth at the next time period (DeAngelis *et al.* 1993; Ludsin & DeVries 1997). Additionally, resources or other factors that affect growth may be heterogeneous, especially for sessile organisms, which will lead to unequal resource use among individuals. Thus, a number of non-size-based factors can underlie persistent growth rate differences and hence affect size variation. We denote this broad group of factors 'size-independent' factors to distinguish them from the size-dependent factors. Size-independent factors have been described quantitatively, with 'growth auto-correlation' (Pfister & Stevens 2002, 2003), 'residual autocorrelation' (Fujiwara, Kendall & Nisbet 2004) and 'memory' (DeAngelis *et al.* 1993; Imsland, Nelson & Folkvord 1998). Theoretical studies suggest that size-independent factors could play a substantial role in the development of size variation (DeAngelis *et al.* 1993; Imsland *et al.* 1998; Pfister & Stevens 2002; Fujiwara *et al.* 2004).

In this study the development of size-variation was examined in wood frog tadpoles, with the goal of determining the influence of size-dependent and size-independent factors. The effect of competition, which has been shown to affect size variation (Uchmanski 1985), was examined by varying resource level and tadpole density. We develop a model to interpret the strong observed effect of competition observed, and estimate the varying contribution of size-dependent and size-independent factors.

## Methods

### EMPIRICAL STUDY OF WOOD FROG SIZE VARIATION

The relationship between size variation and mean size of wood frog tadpoles at different competition levels, created by varying tadpole densities and resource supply rates, was examined. The study was performed at the University of Michigan's E. S. George Reserve experimental pond site in Michigan from May to June 1999 as part of a larger experiment that also examined the effect of predators on tadpole growth and behaviour (Peacor & Werner 2004).

Experiments were conducted in cylindrical 300-L wading pools that served as pond mesocosms. Pools were filled with well water and covered with lids constructed from 60% green shade cloth. Five-gallon buckets were placed in the pools to support the lids. Each pool received phytoplankton, periphyton and zooplankton collected from a local pond, and 150 g of dry oak leaves (predominantly *Quercus* sp.) to provide physical complexity. Before treatments were initiated, the pools sat for 9–10 days to allow plankton and periphyton population establishment. Fourteen egg masses collected from three closely situated (within 500 m) ponds in Scio Township, MI, were placed in two wading pools and, after hatching, tadpoles were fed rabbit chow. The tadpoles were combined prior to sorting into experimental treatments.

One resource level/tadpole density combination, hereafter the 'base' treatment, received 80 wood frog tadpoles that were fed ground rabbit chow distributed evenly throughout each pool every other day at a rate of approximately 1.5 g per day. A high-density treatment was implemented with twice the initial tadpole density (160 tadpoles/pool) but with the same resource level as in the base treatment. Two further treatments with one-quarter (denoted intermediate resource level) and one-eighth (denoted low resource level) the resource supply rate in the base treatment were implemented with 80 tadpoles. Thus, there was a base resource level/tadpole density treatment, and three manipulations that increased competition by either increasing tadpole density or reducing resource level. Initial tadpole mean mass determined by weighing 300 tadpoles was 22.2 mg. The initial relative size variation as measured by the coefficient of variation (CV; standard deviation divided by mean mass, Kokko *et al.* 1999) was 0.376.

Approximately one-half of the tadpoles were removed from the pools, weighed individually and returned on days 5, 11, 19 and 26 of the experiment (denoted sampling dates S1, S2, S3 and S4, respectively). On day 33, all tadpoles were removed and counted. Because some tadpoles showed early signs of metamorphosis (Gosner stage > 38; Gosner 1960) on the last date, which would reduce growth rates, the size variation at this date was not measured. Thus the final

date served only to quantify survivorship. Tadpole biomass at each sampling date was estimated as the product of the mean mass at the sampling date and the number of surviving tadpoles at the experiment end. Treatments were replicated four times in spatial blocks situated together in an open field. The standard deviation and CV were used to quantify absolute and relative size-variation, respectively.

Repeated-measures ANOVA was used to test the statistical significance of treatment effects on mean mass and mass CV. Mass data were log-transformed to test for relative, rather than absolute, differences in mass (Wootton 1994). Simple main effects (Neter, Wasserman & Kutner 1985) were examined to determine if treatment affected the dependent variables on particular sampling dates and whether treatments differed from each other on a given sampling date. Survivorship was high,  $92.7 \pm 3.6\%$  [mean  $\pm$  standard deviation (SD)] across all treatments, and there was no significant effect of treatment on survivorship (ANOVA,  $P = 0.96$ ). Therefore, mortality did not alter the patterns observed between mean mass and mass variation. One pool was dropped from all analyses because survivorship was notably lower (45% less) than all other pools. Data were analysed using SPSS version 12.0 (SPSS 2003). Data met assumptions of sphericity. ANOVA models used Type III sum-of-squares calculations. Results were considered significant below an  $\alpha$  of 0.05. For the simple main effects, Bonferroni adjustments corrected the  $\alpha$ -level for multiple comparisons.

### DEVELOPMENT OF A MODEL TO EXAMINE EMPIRICAL PATTERNS

A model was developed to determine the contribution of size-dependent and size-independent factors on the development of size variation in the empirical study. Because wood frog tadpoles are relatively mobile foragers, variation due to size-dependent factors is expected to arise from phenotypic differences (based on genetic, learned or condition differences; see Introduction) rather than environmental heterogeneity.

The growth rate of an organism can be expressed using an energy budget (Yodzis & Innes 1992), in which growth rate is equal to the rate acquired resources contribute to mass gain, minus a loss rate that these resources are expended on factors such as respiration. Typically, the physiological rates that determine gain and loss scale as  $w^b$  (Sebens 1982, 1987; Yodzis & Innes 1992; Brown *et al.* 2004) where  $b$  is a constant exponent. For example, in the case of gain, the exponent  $b$  is found experimentally to lie in the range of 0.6–0.8, and theoretical studies predict a value of 0.75 (Brown *et al.* 2004). Using this scaling relationship leads to a general and flexible growth equation (Sebens 1982, 1987; Uchmanski 1985; Brown *et al.* 2004):

$$\frac{dw}{dt} = a_1 w^b - a_2 w^b, \quad \text{eqn 1}$$

where  $w$  is size, the first term represents gain and the second term loss.

Growth eqn 1 forms the basis of bioenergetic models (Hewett & Johnson 1995) and other more specific growth equations including parabolic, logistic, linear and (for  $b_1 = 0.67$  and  $b_2 = 1$ ) von Bertalanffy (Wyzomirski *et al.* 1999). Typically eqn 1 (and its more specific forms) is used to describe particular species (or life history stages or size classes of species) or larger groups of multiple species (Yodzis & Innes 1992). In these cases, differences in the coefficients  $a_1$  and  $a_2$  are dependent on both organism traits and environmental characteristics. Any effects of size on the gain and loss rates are captured by the scaling exponents,  $b_1$  and  $b_2$ .

It is possible to simplify eqn 2 to examine wood frog growth in our experiment. Extensive experiments on wood frog growth as a function of different resource quantity and quality indicate that loss is negligible relative to positive gain under the conditions of this experiment (Schiesari 2004). That is, of the resources assimilated, the great majority are used towards gain relative to that lost to factors such as respiration. Indeed, this is consistent with the final mean size and total biomass gain in the present experiment (Appendix S1). This simplification would no longer hold once tadpoles are near stages of metamorphosis where growth rate slows; however, growth was not analysed in this range. Loss was therefore assumed to be negligible leading to a growth equation based only on the gain term:

$$\frac{dw}{dt} = a_1 w^{b_1}. \quad \text{eqn 2}$$

The manner that size variation can be affected by manipulating eqn 2 can be divided into two broad categories that correspond to size-dependent and size-independent factors. Equation 2 can be rewritten in a more general form as:  $dw/dt = a_1 f(w)$ . The function  $f(w)$  describes any potential size-dependent factors that affect growth, and therefore the difference in growth rates of individuals with different size within a population. We can therefore manipulate the effect of size-dependent factors on size-variation by manipulating the functional form of  $f(w)$ . In the case of growth eqn 2, this corresponds to changing the magnitude of the size-scaling exponent,  $b_1$ . For example, an increase in  $b_1$  will lead to increased size variation. Hereafter, we denote manipulation of  $f(w) = w^{b_1}$  through changes in  $b_1$  as describing the effect of size-dependent factors on growth and size variation.

Next consider factors other than size that affect the development of size variation. The coefficient in so-called allometric equations (e.g.  $a_1$  in eqn 2) that relate a dependent variable (e.g.  $dw/dt$  in eqn 2) to body mass, serve as normalization constants that are independent of size (Brown *et al.* 2004). We can therefore represent non-size-based individual differences in growth rate by varying the coefficient  $a_1$ . That is, variation in  $a_1$  describes 'inherent' differences in an individual's ability to grow (e.g. due to individual differences in activity

or access to better resources, see Introduction). Scenarios represented by the introduction (or increase) in the variation in  $a_1$  will have an increase in size variation as a function of mean size, as individuals with higher  $a_1$  will grow relatively more than individuals with lower  $a_1$ . We denote this manipulation of the growth equation as describing the effect of size-independent factors on growth and size variation. Note that when fitting data, the magnitude of the scaling exponent  $b_1$  can affect both the magnitude and units of the size-independent constant  $a_1$ .

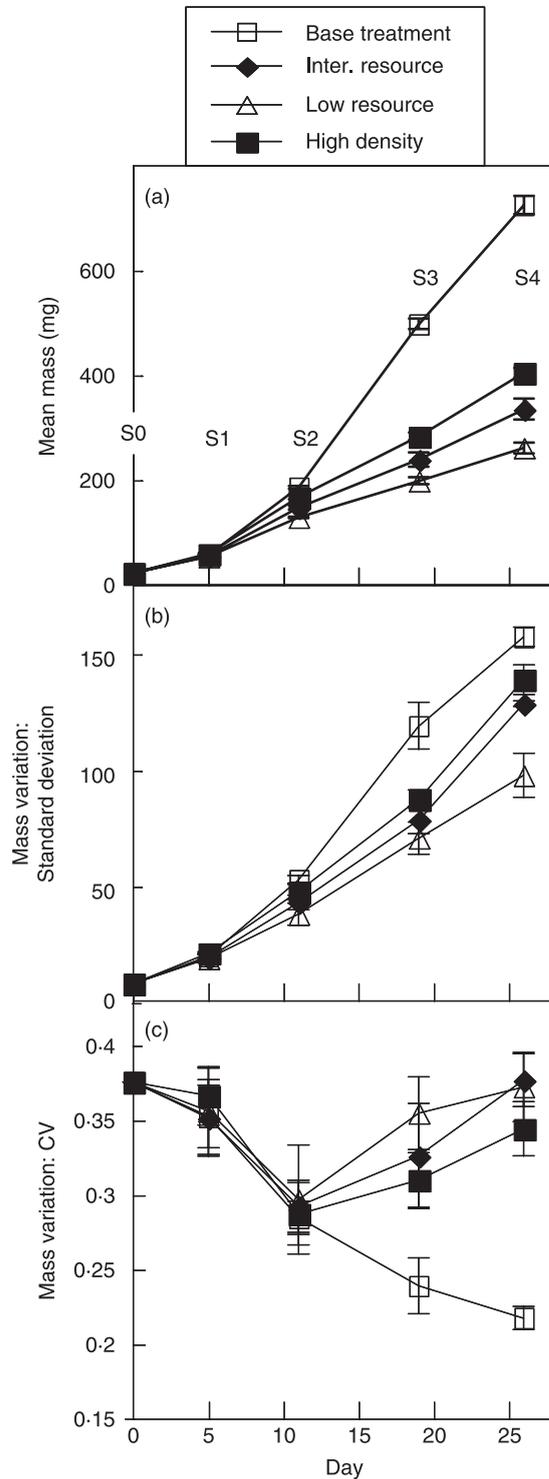
The manner in which we distinguish size-dependent and size-independent factors is analogous to the manner in which dependent and independent factors are distinguished in population growth equations. For example, in the general per-capita population growth equation,  $1/N dN/dt = rf(N)$ , the population growth rate is described by a density-independent coefficient term  $r$ , and density dependent contributions,  $f(N)$ . Note that there will be positive feedback between the size-dependent and size-independent factors in the growth model (eqns 1 and 2); if size-independent factor leads to faster growth for an individual, the consequent larger size could in turn confer an increased advantage due to size-dependent factors (i.e. if  $b_1 \neq 0$ ), a scenario that leads to large size variation in previous models (Pfister & Stevens 2003).

Using eqn 2, the growth of 144 individual tadpoles that began with the same initial mean mass and relative size variation as in the experiment was simulated. For simplicity, the model population's mass is initially normally distributed. Size-independent contributions were manipulated by giving different individuals different values of coefficient  $a_1$  using a normal distribution (with a known CV) of values of coefficient  $a_1$ . Smaller values from the distribution of  $a_1$  were assigned to the smaller individuals, as it was assumed that if size-independent factors are significant they would influence the initial size distribution. Size-dependent contributions to size-variation were manipulated by varying the absolute magnitude of  $b_1$ . We are interested in how factors affect the relative performance of individuals within a population, and thus examined the relative size variation (CV) as a function of mean size rather than after a defined period of time. That is, at a given mean performance (i.e. gain in mass), how did different individuals perform relative to one another? Note that the mean value of coefficient  $a_1$  is not reported, because it is arbitrary (i.e. it does not affect the relationship between mean and variation in size when using eqn 2).

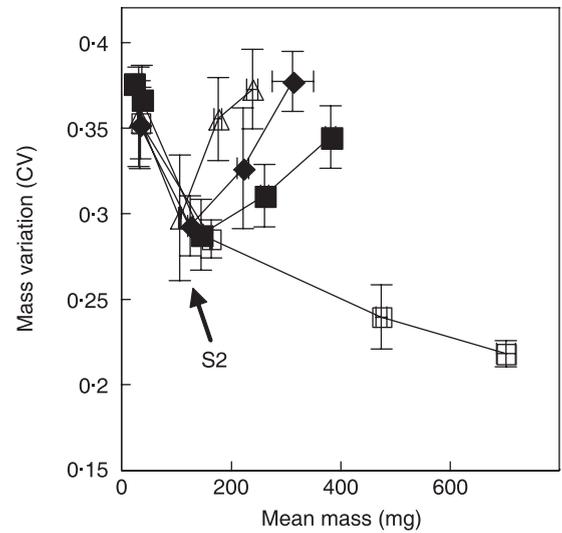
## Results

### WOOD FROG SIZE VARIATION AS A FUNCTION OF COMPETITION

Initially, tadpole mass increased at about equal rates in the different treatments; however, as time progressed, a



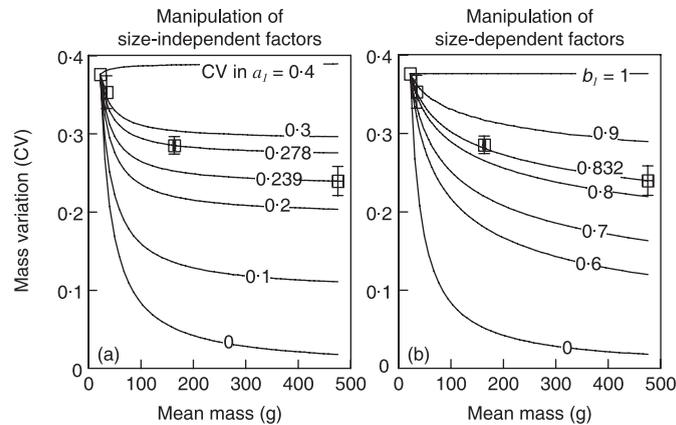
**Fig. 2.** (a) Mean size, (b) standard deviation in size and (c) the coefficient of variation (CV) of mean size, of wood frog tadpoles as a function of time (mean  $\pm$  SE). S0 indicates the initial measurements, and S1–S4 represent the first to fourth sampling date, respectively. The base treatment had the lowest competition level. Three manipulations led to higher competition; The intermediate and low resource level treatments reduced resource supply rates to 1/4th and 1/8th the base treatment level, and the high-density treatment had double the tadpole density.



**Fig. 3.** Relative size variation (mean  $\pm$  SE), CV, of wood frog tadpoles as a function of mean size. Symbols as in Fig. 2. Note that data for S1 and S2 (indicated with arrow) sampling dates are tightly grouped, but after this point there is divergence.

difference in mean size developed and increased (repeated-measures ANOVA, sample date–treatment interaction,  $F_{9,24} = 91$ ,  $P < 0.0001$ ), and was very large by the third sampling date (Fig. 2a). The SD of size increased over time in all treatments, indicating that there was ‘growth depensation’ as denoted by Ricker (1958). As with mean mass, treatment had little effect on SD early in the experiment, but was large by the end (Fig. 2b); SD was higher in treatments with higher growth rates corresponding to low competition. Thus, the faster the tadpoles grew, the larger the absolute difference in size variation among individuals within a mesocosm.

Although the absolute size variation increased (as measured by SD), when we standardize by mean size (i.e. calculate CV), we see that the relative differences in size among individuals decreased initially (Fig. 2c). As with mean mass and SD there was little difference among treatments initially, but after the second sampling date the CV in different treatments diverged (repeated measures ANOVA, sample date–treatment interaction,  $F_{9,24} = 5.2$ ,  $P = 0.0005$ ). Whereas there was no significant effect of treatment on CV on the second sampling date (simple main effect,  $F_{3,8} = 0.043$ ,  $P = 0.987$ ), there was a significant effect on the fourth sampling date (simple main effect,  $F_{3,8} = 22$ ,  $P < 0.001$ ). Indeed, after the second sampling date, the direction of the change in CV was actually in opposite directions (Fig. 2c). At the higher growth rate in the base treatment, CV continued to decrease; however, in the treatments with higher competition, CV increased. CV as a function of mean mass was also examined to help reveal information about the factors that affected size variation, and to facilitate the model analysis (Fig. 3). Increased competition led to larger CV at the same mean size.



**Fig. 4.** Model results of a simulated population with initial mean and variation in mass of tadpoles in the experiment. Empty squares represent experimental data from the base treatment. (a) Manipulate CV in coefficient  $a_1$  to vary size-independent factors in the absence of size-dependent factors ( $b_1 = 0$ ). Numbers on lines represent the magnitude of the CV in coefficient  $a_1$ . (b) Manipulate  $b_1$  to vary size-dependent factors on size variation in the absence of size-independent factors (CV in coefficient  $a_1$  equal to 0). Numbers on lines represent the magnitude of  $b_1$ . Note that the lowest line in both figures represents the predicted change in CV as a function of mass in the absence of size-dependent and size-independent factors on growth.

In the three treatments with equal initial tadpole density, and therefore equal initial tadpole biomass, biomass gain at the last two sampling dates (S3 and S4) was related linearly to the resource level addition ( $R^2 = 0.9999$  for linear regression of data collected on the third and fourth sampling dates, Fig. S1). Biomass gain in the high density treatment was not significantly different than in the base treatment ( $t$ -test,  $P > 0.25$  for both S3 and S4, Fig. S1).

#### MODEL EXAMINATION OF EMPIRICAL PATTERNS

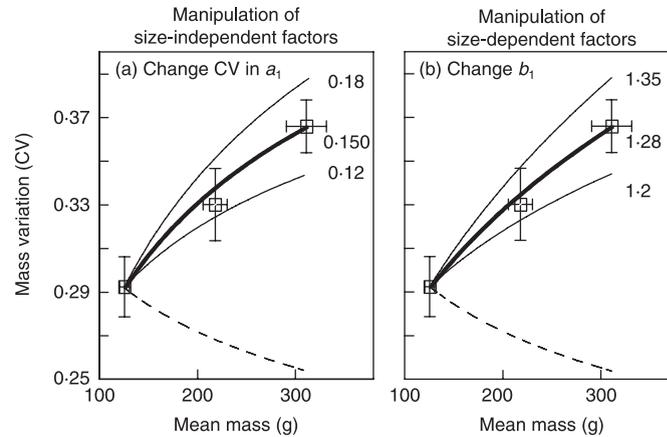
Consider first model analysis of the base treatment. The lowest lines in Fig. 4(a,b) illustrate the expected change in CV associated with the increase in mass observed in the experiment if there were no differences in individual growth. That is, all individuals grew at the same rate in the absence of size-dependent ( $b_1 = 0$ ) and size-independent ( $a_1$  equal for all individuals) factors. The resultant simulated CV in mass fell precipitously as a function of mean mass at a rate far greater than that observed in the experiment. This steep fall resulted from the fact that the absolute difference in size variation remained the same as the mean size increased. The large deviation between this model result and the empirical data (Fig. 4) indicates that significant persistent individual differences in tadpole growth existed (i.e. there was autocorrelation in individual growth rate). Note that growth to the third sampling date was analysed for this treatment, but to the fourth in other treatments (below), in order to examine changes in CV as a function of mean size over similar size ranges.

Next we use the model to examine the influence of size-independent factors on size-variation in the base treatment in the absence of size-dependent factors ( $b_1 = 0$ ). Using a nonlinear optimization routine (Microsoft Excel 'Solver', Microsoft Corporation, Redmond, Washington, USA) to minimize sum of

squares between the data and model relationships, the variance in the magnitude of coefficient  $a_1$  was found that best reproduced the relationship between mean and CV in mass of the initial data (S0) and third sampling date (S3) of the empirical data. The results produced a CV in coefficient  $a_1$  equal to 0.239, for which the resultant relationship between mean size and size variation is illustrated in Fig. 4(a). It is clear that with this best fit to the initial and final data points, the resultant curve greatly underestimates mass CV at the intermediate sampling dates (S1 and S2). As a corollary, the CV in coefficient  $a_1$  (0.278, Fig. 4a) that provides the best fit between S0 and an earlier sampling date (S2) overestimates CV at the endpoint (S3). These deviations arise because size-independent factors produce a more pronounced effect on relative size variation at lower mean size relative to high mean size than actually occurred in the experiment. Size-independent factors alone therefore cannot explain the observed patterns in the base treatment. Results for a range of values of CV in coefficient  $a_1$  are provided in Fig. 4(a) to illustrate the sensitivity to this variation.

Next, consider the effect of size-dependent factors in the absence of size-independent factors (i.e. coefficient  $a_1$  equal for all individuals). Using the same nonlinear optimization routine as above, a value of  $b_1 = 0.832$  provided the best fit of initial and final mean mass and variation in mass (Fig. 4b). In contrast to results of manipulating size-independent factors, this manipulation reproduced the relationship between mean and variation in mass over the whole range of sampling dates ( $r^2 = 0.998$ , contrast to  $r^2 = 0.84$  for the previous case). Indeed, it may appear that this curve was chosen to fit all of the data points, but it was not. Results for a range of  $b_1$  values illustrate the sensitivity of the relationship to changes in size-dependent growth (Fig. 4b).

The marked increase in size variation observed after the second sampling date (Fig. 3) in elevated competition treatments is examined next. Competition



**Fig. 5.** Results of model analysis of the increase in CV observed at high competition. Squares (error bars = SE of 12 mesocosms) represent the pooled data of the three high competition treatments from the second (S2) to fourth (S4) sampling date. In both panels, the lower dashed line is the best fitting line for the base treatment (see text) in which  $b_1 = 0.832$  and CV in coefficient  $a_1$  equal to 0. (a) Keeping  $b_1 = 0.832$  as in the best fit at low competition, an increase in CV in coefficient  $a_1$  equal to 0.150 reproduced the data at high competition (thick solid line). Numbers represent CV in coefficient  $a_1$ . (b) An increase in  $b_1$  to 1.28 from 0.832 reproduces the increase in mass CV seen at high competition (thick solid line). In (b) there are no size-independent factors affecting size variation (CV in coefficient  $a_1$  equal to 0). Numbers represent the magnitude of  $b_1$ . In both panels, the thin solid lines above and below the best fit lines are shown to illustrate the sensitivity of mass CV to changes in the size-independent and size-dependent factors.

evidently affected the relative advantage of different individuals, as size variation was much greater as a function of mean size. Our intention was to derive parameters that describe the general trends in the data, not specific values for each of the treatments with increased competition. The data were therefore pooled over all three treatments with elevated competition. In particular, changes in size-dependent and size-independent factors that could cause the marked increase in CV (~25% on average) as a function of mean mass (which increased by ~150% on average), observed from the second to the fourth sampling date, were determined.

A value of  $b_1 = 0.832$ , derived in the previous analysis for the base treatment, was used in eqn 2, and then the contribution of size-dependent and size-independent factors on size variation that reproduced the increase in CV observed in the higher competition treatments was determined. For size-independent factors, a value of CV in coefficient  $a_1$  equal to 0.150 provided the best fit (Fig. 5a) to the data. The results for CV in coefficient  $a_1$  equal to 0.12 and 0.18 are also provided to indicate sensitivity this manipulation. For size-dependent factors (with no size-independent contribution, i.e. CV in coefficient  $a_1$  equal to 0), a size-scaling exponent of  $b_1 = 1.28$  provided the best fit of the data (Fig. 5b). Model results for  $b_1 = 1.2$  and 1.35 are also illustrated to indicate the sensitivity to this parameter.

## Discussion

The experiment demonstrated that tadpole size variation changed dramatically as the strength of competition varied. This result was clear when competition was changed by manipulating either tadpole density or resource supply rate. When competition was least, the

relative size variation (CV) decreased as a function of size throughout the experiment. In contrast, when competition was higher, there was a marked increase in size variation as a function of mean size. To gain intuition into how these changes in the magnitude in CV represent changes in the relative performance of individual tadpoles, consider two tadpoles that are plus and minus one standard deviation from the mean. By definition, CV is equal to the SD divided by the mean. Thus, these two tadpoles would differ in size by 74% at the end of the high competition treatments in which CV ~0.37, but by only 41% in the low competition (base) treatment when CV ~0.21 (Figs 2 and 3). Therefore, increased competition almost doubled the difference in growth performance of paired tadpoles that differed by 2 SD.

The model analysis indicated that size-dependent differences in individual growth are primarily responsible for the observed relationship between mean size and size variation at low competition (Fig. 4b), whereas size-independent factors were not (Fig. 4a). The estimated value of the scaling exponent derived from the relationship between mean mass and size variation at low competition, 0.832, is close to the average value, 0.75, observed (and predicted theoretically) for animals (Brown *et al.* 2004). Thus, if we use this value from the literature for the scaling of individual growth and size, the model predicts the observed development of wood frog tadpole size variation fairly well, deviating from the actual data with a moderately steeper decrease in CV as a function of mean mass (Fig. 4b). This moderately steeper decrease suggests that the actual scaling factor for wood frogs is higher than 0.75, the average value for animals, or that other factors affected size variation. In particular, this deviation could suggest that size-independent factors are also

contributing to growth variation. Using the same methodology as in the previous section, if we assume that the size-scaling relationship is 0.75, then a CV in  $a_1$  of 0.026 increases the size variation to the required amount to reproduce the empirical data ( $r^2 = 0.988$ ). Thus size-dependent scaling factors alone with  $b \sim 0.83$ , or a moderate combination of size-independent factors combined with size-dependent factors, determined the observed decrease in size variation at low competition. In either case, size-variation is strongly dictated by a size-scaling relationship between mean size and growth rate similar to that determined from physiological studies.

The parameters needed to reproduce the relationship between mean size and size variation in treatments with higher competition are in stark contrast to those in the base treatment with the lowest competition. The model showed that an effect of competition on both size-independent factors, causing CV in coefficient in  $a_1$  approximately equal to 0.15, or an increase in size-dependent factors, by increasing the scaling relationship between size and growth ( $b_1$ ) to approximately 1.3, could underlie this pattern. In the latter case, the competition changed the size advantage from being less than proportional to size (i.e.  $b < 1$ ) to greater than proportional to size (i.e.  $b > 1$ ). It is important to note that slower growth due to increased competition does not necessarily imply that the relationship between mean mass and mass variation will be modified. It is plausible that all tadpoles would grow at equivalent lower rates and therefore size variation and mean size would change at reduced rates, but the relationship between mean mass and size variation would be the same.

One reason why trait (including size) differences could have a less pronounced effect on individual growth variation at lower competition is that any trait disadvantages do not limit resource acquisition at relatively high resource levels associated with lower competition. Therefore, all individuals would acquire (find and garner) and assimilate resources at nearly equivalent rates; but when resources are scarce at heightened competition, the effect of trait advantages in acquiring and assimilating resources will be more pronounced, leading to larger individual differences in growth (Uchmanski 1985; Lomnicki 1988). Further, work is required to disentangle which phenotypic differences, e.g. size- or other trait-based, are responsible. The possibility that size-independent factors may play a role is supported by laboratory experiments using marked tadpoles, in which we observed persistent individual differences, over the course of a week, in wood frog tadpole foraging behaviour (Peacor, unpublished data). We do not postulate here whether the origin of potential size-independent factors had a genetic (Arnold 1981; Conover & Munch 2002) or other basis, such as learned (Palmer 1984; Dukas & Bernays 2000), or positive correlation between growth and condition (DeAngelis *et al.* 1993; Ludsin & DeVries 1997).

One method to distinguish size-dependent and size-independent factors is to mark and follow the growth of individuals. Given these data, regression should reveal whether size has a large effect on growth rate, and positive correlation in the residuals of the size vs. growth relationship has been referred to as 'growth autocorrelation' and is indicative of size-independent processes (Pfister & Stevens 2003). Although a powerful approach, it is not always practical to collect data repeatedly on the same individual. Thus models that interpret size-variation in the absence of individual growth data, such as we present here, are needed.

An increase in size variation at higher competition levels, as reported here for wood frog tadpoles (see also Wilbur & Collins 1973), has been observed in a number of other animals (reviewed in Uchmanski 1985; Lomnicki 1988), including fish (Rubenstein 1981; Sogard & Olla 2000), and grasshoppers (Wall & Begon 1987). While little is known about the relative contribution of size-dependent and size-independent factors in these cases, there is evidence that in some fish species, size-independent behavioural differences between individuals (Fuiman & Cowan 2003) contribute to growth rate differences (Imsland *et al.* 1998; Wilson 1998). In addition, size can play a large role in social hierarchies of fish that lead to increased interference and larger inequities of resource distribution at low resource levels (Magnuson 1962; Rubenstein 1981). It is unlikely that interference played a significant role in the effect of competition on size variation in our study because the tadpoles foraged independently over relatively large areas. Rather, trait differences (size or other) must have affected foraging in other ways, such as by affecting the relative ability to locate, garner or assimilate resources.

The results in the high competition treatments have implications to modelling animal population dynamics. Increasingly, ecologists are using individually based models (IBM) to model ecological systems (DeAngelis & Mooij 2005; Grimm & Railsback 2005). One of a number of advantages (there are also disadvantages) of IBMs over other models, is that IBMs can represent and examine the implications of individual variation in phenotype. For example, a number of studies examining the population dynamics of fish have used IBMs. It is a standard protocol to use growth rate equations that are similar in form to eqn 1, such as bioenergetic models, to represent individual growth as a function of size for individual fish (Rose *et al.* 1999). However, our results indicate that under some conditions (e.g. high competition), this approach will fail to account for individual differences in growth that could affect model results. Indeed, higher competition enhancing the size variation of fish has been reported (Rubenstein 1981; Sogard & Olla 2000), and thus we expect similar modifications to eqn 1 would be needed to describe individual fish growth. For example, in models in which differential growth is important due to a fraction of individuals attaining higher reproductive success, modelling the individual differences accurately is

especially important. Our results suggest that a size-dependent scaling of growth rate on size well above that found from physiological studies, or introducing individual variation in the size-independent coefficients, may be required.

Although our analysis has assumed that resources are homogeneous and the mobility of wood frogs probably resulted in homogeneous resources, the basic growth equation has application to systems with heterogeneous resources. Of course, resource heterogeneity can lead to individual variation in growth if movement by individuals is limited. In addition, even in systems in which resources are initially homogeneous, restricted foraging can lead to persistent resource patchiness that can drive size differences for individuals with equivalent foraging abilities (Pfister & Peacor 2003). If modelled using eqn 1, persistent differences in resource availability, due to resource heterogeneity, can be represented by modifying coefficient  $a_1$  (Sebens 1987), with higher values corresponding to individuals that have had access to higher resources. Thus, variation in coefficient  $a_1$  can represent intrinsic organism trait differences among organisms or extrinsic differences due to conditions imposed by the environment.

Individual size variation is a ubiquitous feature of animal populations, and is predicted to affect numerous ecological processes (see Introduction). Size variation may also serve as an indicator of genetic variation proposed to affect community structure (Wilson 1998; reviewed in Agrawal 2003). Further, much in the way the variation in population patterns across environmental gradients enhances our understanding of mean population processes (Connell 1961; Wellborn *et al.* 1996), patterns of size variation may serve as a lens into processes that affect mean growth and consequently fitness (Lomnicki 1988). Building frameworks to understand how factors affect size-variation could help in the interpretation of many empirical studies that would typically focus on mean size. This study illustrated how the relationship between size variation and mean size can vary greatly as a function of competition, due to a shifting role for size-dependent or size-independent factors as competition varied. Finally, our results have important implications for modelling natural populations. Size is easily included as a state variable in population models and there is thus a rich history of modelling size-dependent demographics (Lefkovich 1965; Caswell 2001). In contrast, variance among individuals of non-size-based traits is described less easily in analytical formulations and requires more theoretical development.

### Acknowledgements

We thank D. Cholewiak, Trent Malcolm and Shannon McCauley for assistance with the experiments and M. Zimmerman for performing the statistical analysis. We thank Kent and Diana Hyne for permission to collect wood frog eggs on their property. We thank Jim Bence,

Ben Bolker, Stuart Ludsin, Chuck Madenjian and anonymous reviewers for providing helpful comments on this paper. Luis Schiesari provided valuable discussions on tadpole growth, and James Gillooly provided valuable discussions on allometric equations. A portion of this work was performed at the Chicago University Department of Ecology and Evolution and at the University of Michigan Biology Department. This work was supported by NSF grants DEB-9615523 and DEB-0089809 to E. Werner and S. Peacor, and OCE-9711802 to C. Pfister. This is GLERL contribution number 1389.

### References

- Agrawal, A.A. (2003) Community genetics: new insights into community ecology by integrating population genetics. *Ecology*, **84**, 543–544.
- Arnold, S.J. (1981) Behavioural variation in natural populations: 2. The inheritance of a feeding response in crosses between geographic races of the garter snake, *Thamnophis elegans*. *Evolution*, **35**, 510–515.
- Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D. & Forister, M.L. (2003) The ecology of individuals: incidence and implications of individual specialization. *American Naturalist*, **161**, 1–28.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology*, **85**, 1771–1789.
- Caswell, H. (2001) *Matrix Population Models*, 2nd edn. Sinauer, Sunderland, MA, USA.
- Coleman, K. & Wilson, D.S. (1997) Ecological and behavioural determinants of home range in juvenile pumpkinseed sunfish (*Lepomis gibbosus*). *Ethology*, **102**, 900–914.
- Connell, J.H. (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology*, **42**, 710–723.
- Conner, M.M. & White, G.C. (1999) Effects of individual heterogeneity in estimating the persistence of small populations. *Natural Resource Modeling*, **12**, 109–127.
- Conover, D.O. & Munch, S.B. (2002) Sustaining fisheries yields over evolutionary time scales. *Science*, **297**, 94–96.
- DeAngelis, D.L. & Mooij, W.M. (2005) Individually-based modeling of ecological and evolutionary processes. *Annual Review of Ecology, Evolution, and Systematics*, **36**, 147–168.
- DeAngelis, D.L., Rose, K.A., Crowder, L.B., Marschall, E.A. & Lika, D. (1993) Fish cohort dynamics – application of complementary modeling approaches. *American Naturalist*, **142**, 604–622.
- Dukas, R. & Bernays, E.A. (2000) Learning improves growth rate in grasshoppers. *Proceedings of the National Academy of Sciences USA*, **97**, 2637–2640.
- Ebenmann, B. & Persson, L. (1988) *Interactions in Size-Structured Populations: from Individual Behaviour to Ecosystem Dynamics*. Springer-Verlag, Berlin.
- Fuiman, L.A. & Cowan, J.H. Jr (2003) Behaviour and recruitment success in fish larvae: repeatability and covariation of survival skills. *Ecology*, **84**, 53–67.
- Fujiwara, M., Kendall, B.E. & Nisbet, R.N. (2004) Growth autocorrelation and animal size variation. *Ecology Letters*, **7**, 106–113.
- Gosner, K.L. (1960) A simplified table for staging anuran embryos and larvae, with notes on identification. *Herpetologica*, **16**, 183–190.
- Grimm, V. & Railsback, S.F. (2005) *Individual-Based Modeling and Ecology*. Princeton University Press, Princeton, NJ.

- Grimm, V. & Uchmanski, J. (2002) Individual variability and population regulation: a model of the significance of within-generation density dependence. *Oecologia*, **131**, 196–202.
- Hassell, M.P. & May, R.M. (1985) From individual behaviour to population dynamics. *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour* (eds R.M. Sibly & R.H. Smith), pp. 3–32. Blackwell, Oxford.
- Hewett, S.W. & Johnson, B.L. (1995) *Fish Bioenergetics Model 3*. University of Wisconsin Sea Grant Institute Report WIS-SG-91–250. Sea Grant Institute, Madison, Wisconsin, USA.
- Imsland, A.K., Nilsen, T. & Folkvord, A. (1998) Stochastic simulation of size variation in turbot: possible causes analysed with an individual-based model. *Journal of Fish Biology*, **53**, 237–258.
- Kendall, B.E. & Fox, G.A. (2002) Variation among individuals and reduced demographic stochasticity. *Conservation Biology*, **16**, 109–116.
- Kokko, H., Mackenzie, A., Reynolds, J.D., Lindström, J. & Sutherland, W.J. (1999) Measures of inequality are not equal. *American Naturalist*, **154**, 358–382.
- Kooijman, S.A.L.M. (2000) *Dynamic Energy and Mass Budgets in Biological Systems*. Cambridge University Press, Cambridge, UK.
- Lefkovich, L.P. (1965) The study of population growth in organisms grouped by states. *Biometrics*, **1965**, 1–18.
- Lomnicki, A. (1988) *Population Ecology of Individuals*. Princeton University Press, Princeton, NJ.
- Ludsin, S.A. & DeVries, D.R. (1997) First-year recruitment of largemouth bass: the interdependency of early life stages. *Ecological Applications*, **7**, 1024–1038.
- Magnuson, J.J. (1962) An analysis of aggressive behaviour, growth, and competition for food and space in medaka (*Oryzias latipes* (Pisces, Cyprinodontidae)). *Canadian Journal of Zoology*, **40**, 313–363.
- Maret, T.J. & Collins, J.P. (1994) Individual responses to population size structure: the role of size variation in controlling expression of a trophic polyphenism. *Oecologia*, **100**, 279–285.
- Neter, J., Wasserman, W. & Kutner, M.H. (1985) *Applied Linear Statistical Models*, 2nd, pp. 725–731. Richard D. Irwin, Burr Ridge, IL.
- Palmer, A.R. (1984) Prey selection by thaidid gastropods: some observational and experimental field tests of foraging models. *Oecologia*, **88**, 277–288.
- Peacor, S.D. & Werner, E.E. (2004) Context dependence of non-lethal predator effects on prey growth. *Israel Journal of Zoology*, **50**, 139–167.
- Pfister, C.A. & Peacor, S.D. (2003) Variable performance of individuals: the role of population density and endogenously formed landscape heterogeneity. *Journal of Animal Ecology*, **72**, 725–235.
- Pfister, C.A. & Stevens, F.R. (2002) The genesis of size variability in plants and animals. *Ecology*, **83**, 59–72.
- Pfister, C.A. & Stevens, F.R. (2003) Individual variation and environmental stochasticity: implications for matrix model predictions. *Ecology*, **84**, 496–510.
- Rice, J.A., Miller, T.J., Rose, K.A., Crowder, L.B., Marschall, E.A., Trebitz, A. & DeAngelis, D.L. (1993) Growth rate variation and larval survival: inferences from an individual-based size-dependent predation model. *Canadian Journal of Fish and Aquatic Science*, **50**, 133–142.
- Ricker, W.E. (1958) Handbook of computations for biological statistics of fish populations. *Fisheries Research Board of Canada Bulletin Number 119*.
- Rose, K.A., Rutherford, E.S., McDermot, D.S., Forney, J.L. & Mills, E.L. (1999) Individually-based model of yellow perch and walleye populations in Oneida Lake. *Ecological Monographs*, **69**, 127–154.
- Rubenstein, D.I. (1981) Individual variation and competition in the everglades pygmy sunfish. *Journal of Animal Ecology*, **50**, 337–350.
- Schiesari, L.C. (2004) *Performance tradeoffs across resource gradients in anuran larvae*. PhD Dissertation, University of Michigan.
- Sebens, K.P. (1982) The limits to indeterminate growth – an optimal size model applied to passive suspension feeders. *Ecology*, **63**, 209–222.
- Sebens, K.P. (1987) The ecology of indeterminate growth in animals. *Annual Review of Ecology and Systematics*, **18**, 371–407.
- Sogard, S.M. & Olla, B.L. (2000) Effects of group membership and size distribution within a group on growth rates of juvenile sablefish *Anoplopoma fimbria*. *Environmental Biology of Fishes*, **59**, 199–209.
- SPSS, 12.0 for Windows, Rel. 12 0 0 (2003) Chicago, SPSS Inc.
- Uchmanski, J. (1985) Differentiation and frequency-distributions of body weights in plants and animals. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, **310**, 1–75.
- Uchmanski, J. (1999) What promotes persistence of a single population: an individually-based model. *Ecological Modelling*, **155**, 227–241.
- Wall, R. & Begon, M. (1987) Population-density, phenotype and reproductive output in the grasshopper *Chorthippus-Brunneus*. *Ecological Entomology*, **12**, 331–339.
- Wellborn, G.A., Skelly, D.K. & Werner, E.E. (1996) Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics*, **27**, 337–363.
- Wilbur, H.M. & Collins, V. (1973) Ecological aspects of amphibian metamorphosis. *Science*, **182**, 1305–1314.
- Wilson, D.S. (1998) Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, **353**, 199–205.
- Wootton, J.T. (1994) Putting the pieces together: testing the independence of interactions among organisms. *Ecology*, **75**, 1544–1551.
- Wyszomirski, T., Wyszomirska, I. & Jarzyna, I. (1999) Simple mechanisms of size distribution dynamics in crowded and uncrowded virtual monocultures. *Ecological Modelling*, **115**, 253–273.
- Yodzis, P. & Innes, S. (1992) Body size and consumer-resource dynamics. *American Naturalist*, **139**, 1151–1175.

Received 18 January 2006; accepted 27 March 2006

### Supplementary material

The following supplementary material is available as part of the online article (full text) from <http://www.blackwell-synergy.com>

**Appendix S1.** Analysis of total biomass gain indicates that loss due to respiration is negligible.

**Figure S1.** Biomass gain as a function of resource level.