

# The effect of size-dependent growth and environmental factors on animal size variability

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## Abstract

The origin of variation in animal growth rate and body size is not well understood but central to ecological and evolutionary processes. We develop a relationship that predicts the change in relative body size variation within a cohort will be approximately equal to the relative change in mean per unit size growth rate, when only size-dependent factors affect growth. When modeling cohort growth, relative size variation decreased, remained unchanged, or increased, as a function of growth rate-size scaling relationships, in a predictable manner. We use the approximation to predict how environmental factors (e.g., resource level) affect body size variation, and verified these predictions numerically for a flexible growth model using a wide range of parameter values. We also explore and discuss the assumptions underlying the approximation. We find that factors that similarly affect mean growth rate may differently affect size variation, and competition may increase body size variation without changing size-independent relationships. We discuss implications of our results to the choice of growth equations used in models where body size variation is an important variable or output.

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## 1. Introduction

Variation in individual growth rate, reproductive output, and other properties that influence fitness, is distinctive of animal populations. A number of ecologists have argued that it is imperative that we consider the implications of such individual variation for population and community properties (Hassell and May, 1985; Lomnicki, 1988; DeAngelis et al., 1993; Grimm and Uchmański, 2002). For example, numerous studies indicate that body size variation can have influential effects on ecological variables, including population abundance, dynamics, and extinction risk (Lomnicki, 1988, 1999; DeAngelis et al., 1993; Grimm and Uchmański, 2002; Kendall and Fox,

2002; Pfister and Stevens, 2003). But a perusal of any ecological journal shows that there is a focus on the mean value of such properties, with little attention to variation. Given that individual variation is a fundamental component of evolution, and thus entire disciplines in biology, it is perhaps surprising that it is often ignored in ecological studies.

The large variation in size observed in animals from the same cohort reared together in controlled conditions illustrates the great propensity of individuals to develop and grow at different rates (Haynes and Hitz, 1971; Wilbur and Collins, 1973; McCaughan and Powell, 1977; Seed and Brown, 1978; Rubenstein, 1981a; Lomnicki, 1988; see Kooijman, 2000; Peacor and Pfister, 2006, for example photos of fish and tadpoles, respectively). In this case, the age and origin are the same, thus any variation can be ascribed to initial differences among individuals in size at birth and subsequent differences among individuals in growth rate that occurred under nearly equal conditions.

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Empirical studies reveal that such individual variation can be a function of environmental context, such as the association of increased size variation with an increased level of competition (Wilbur and Collins, 1973; Rubenstein, 1981a; Uchmański, 1985; Irwin et al., 1999).

The origin of within cohort variability in size (hereafter termed size variation) can be partitioned into two broad categories, which we denote “size-dependent” and “size-independent” factors. Size-dependent factors arise from the advantages or disadvantages to growth that size itself incurs. Numerous studies document how properties such as physiological processes (e.g. metabolism) or factors related to consumption rate (e.g. territory size, ingestion rate, activity level) scale as a function of size. Thus, if stochastic environmental, maternal, or other factors cause an initial size variation, the effect of size on growth can influence the manner in which size variation progresses. Size-independent factors arise from a number of non-size-based processes that can differentially affect individual growth. For example, phenotypically based differences in traits that affect growth (e.g., due to behavioral, morphological, life historical, and physiological traits differences) could affect size variation. Such persistent differences could have a genetic basis (Arnold, 1981; Conover and Munch, 2002; Sanford et al., 2003) or could be learned (Palmer, 1984; Dukas and Bernays, 2000). Additionally, stochastic effects could cause variation in conditional states (i.e., energy level or disease load) that could affect growth over long periods of time (DeAngelis et al., 1993; Ludsins and DeVries, 1997). Finally, resources or other factors that affect growth may be heterogeneous, which could lead to persistent unequal resource use or assimilation among individuals and therefore affect size variation (Pfister and Peacor, 2003). Such size-independent factors that can affect size variation have been referred to as “growth autocorrelation” (Pfister and Stevens, 2002, 2003), “residual autocorrelation” (Fujiwara et al., 2004), and “memory” (DeAngelis et al., 1993; Imsland et al., 1998).

Although important to understanding evolutionary and ecological problems, we know very little about how size-dependent and size-independent factors affect size variation. In this paper, we examine how size-dependent factors alone can affect within-cohort variation in size. We develop a simple analytical approximation for the general relationship between changes in size variation and changes in growth rate. Given moderate initial variation in size and nonlinearity in how growth changes with size, we show that our analytical approximation accurately predicts actual changes in variation, ascertained using numerical methods (e.g., based on the true probability density function (PDF) obtained by solving partial differential equations (PDEs)). When applied to growth following a widely used and flexible growth equation, our approximation reveals strong dependence of size variation on environmental factors that affect growth rate, and the scaling relationships between size and factors that affect growth rate. The simple nature of the analytical approximation helps provide a conceptual

understanding of how parameter changes in the flexible growth equation can lead to surprising changes in how initial size variation is propagated. Our findings have important implications for the development and interpretation of models used to examine the consequences of size variation, and on the effects of environmental factors, such as competition and temperature, on the origin of size variation.

## 2. An approximate relationship between individual size variation and mean growth rate

We derive an analytical approximation that relates size-variation (CV) and individual growth rate ( $g(w) = dw/dt$ ) in the absence of size-independent factors. Thus our approximation addresses how initial variation in size changes over time as the individuals grow, when the only factor causing different individuals to grow differently is their size, and size distributions are not influenced by size-dependent mortality. Symbols used in the main text are described in Table 1.

Our approach treats size at some future time as a transformation of initial size. We therefore can take advantage of methods from statistics used to determine distributions of transformed variables. We use  $w = \mathbf{w}(w_0, t)$ , in which  $\mathbf{w}$  is a function that transforms initial size ( $w_0$ ) of an individual into its final size ( $w$ ) at time  $t$ . The delta method yields an approximation for the variance in size of a population of individuals after transformation (e.g., Seber, 1982; Rice, 1995):

$$\sigma^2(t) \cong \sigma_0^2 \left[ \frac{\partial \tilde{w}}{\partial \tilde{w}_0} \right]^2. \quad (1)$$

The variance of individual size is  $\sigma_0^2$  initially, and  $\sigma^2(t)$  at time  $t$ . To simplify notation we use  $\tilde{w} = \mathbf{w}(\tilde{w}_0, t)$  to represent the size at time  $t$  of an individual in the population that starts at

Table 1  
Symbols used in models

| Symbol          | Meaning   |
|-----------------|---|
| $t$             | Time  |
| $w$             | Final size at time $t$  |
| $w_0$           | Initial size  |
| $\mathbf{w}$    | Function that transforms initial size into final size                                   |
| $\mathbf{w}_0$  | “Inverse function” of $\mathbf{w}(w_0, t)$ that transforms final size into initial size |
| $\sigma_0^2$    | Initial variance  |
| $\sigma^2(t)$   | Variance at time $t$  |
| CV <sub>0</sub> | Initial coefficient of variation  |
| CV( $t$ )       | Coefficient of variation at time $t$  |
| $\bar{w}_0$     | Mean initial size   |
| $\bar{w}$       | Mean size at time $t$   |
| $\tilde{w}$     | Size of individual at time $t$ that starts at $\tilde{w}_0$                             |
| $\tilde{w}_0$   | Initial size of individual that starts at $\tilde{w}_0$ (thus = $\bar{w}_0$ )           |
| $g(\cdot)$      | Growth rate   |
| $f_i(\cdot)$    | PDF of size at time $t$   |
| $f_0(\cdot)$    | PDF of size at time zero  |

the mean initial size,  $\bar{w}_0$ . To keep symbolism parallel, we substitute  $\tilde{w}_0$  for  $\bar{w}_0$ . Note that, whereas  $\tilde{w}_0$  is equal to  $\bar{w}_0$  by definition, that  $\tilde{w}$  is only an approximation of mean size at time  $t$ ,  $\bar{w}$ .

Dividing both sides of Eq. (1) by  $\sigma_0^2$  and taking the square root leads to

$$\frac{\sigma(t)}{\sigma_0} \cong \frac{\partial \tilde{w}}{\partial \tilde{w}_0}. \quad (2)$$

Dividing the numerator and denominator of the right-hand side of Eq. (2) by  $dt$  (an application of the chain rule for partial derivatives) and recalling that  $g(w) = dw/dt$  leads to

$$\frac{\sigma(t)}{\sigma_0} \cong \frac{g(\tilde{w})}{g(\tilde{w}_0)}. \quad (3)$$

This equation indicates that the ratio of the standard deviation at time  $t$  and initial standard deviation is approximately equal to the ratio of the growth rates at time  $t$  and initial growth rate.

Dividing both sides of Eq. (3) by  $\tilde{w}/\tilde{w}_0$  and using the definition for coefficient of variation,  $CV = \text{standard deviation}/\text{mean}$ , we arrive at an expression for the relative size variation (rather than absolute as in Eq. (3)):

$$\frac{CV(t)}{CV_0} \cong \frac{g(\tilde{w})/\tilde{w}}{g(\tilde{w}_0)/\tilde{w}_0}. \quad (4)$$

The approximation in Eq. (4) arises from the approximations needed for Eq. (1), from which Eq. (3) is derived, and also uses  $\tilde{w}$  as an approximation of  $\bar{w}$ .

Eq. (4) provides a key (approximate) relationship: *Relative size variation will change in proportion to the relative change in the per unit size growth rate.* The qualitative nature of this result is intuitive. If the per unit size growth rate of larger individuals is greater than that of smaller individuals (right-hand side of Eq. (4)), then we expect the distribution to spread more rapidly than the mean size increases, causing the CV to increase. Individuals above the mean increase in size proportionally more and individuals below the mean increase in size proportionally less than individuals of average size. What is perhaps surprising, however, is the simplicity of this equation, and further, as we will see, its accuracy under a wide range of conditions.

### 3. Exact solution to changes in the size distribution

Here we present an exact solution to how the size distribution changes as a cohort grows, and describe how we calculate the CV given these size distributions. We use the resulting CVs in the rest of the paper to investigate how CVs change as a cohort grows under different conditions. Whereas we compare these true CVs with results from our analytical approximation, the primary purpose of the approximation is to predict and help understand these changes in CV. The PDF (relative abundance by size) at time  $t$ , given the PDF at the initial time zero, can be shown

to equal (e.g., by solution of PDEs—Appendix B):

$$f_t(w) = f_0(w_0) \frac{g(w_0)}{g(w)}, \quad (5)$$

$$w_0 = \mathbf{w}_0(w, t),$$

where  $f_t(\cdot)$  is the PDF of size at time  $t$ ,  $f_0(\cdot)$  is the PDF of size at time zero, and  $\mathbf{w}_0(w, t)$  is a function that returns size at time zero given a specified size at time  $t$ . Note that  $\mathbf{w}_0$  is the “inverse function” of  $\mathbf{w}(w_0, t)$ . Thus, for size  $w$ , the probability density at time  $t$  is given by first finding the corresponding initial size and initial probability density for that initial size, and multiplying this density by a ratio of growth rates. This ratio represents how the localized size distribution is contracting or expanding over the time period (Appendix A). The reciprocal of this same ratio of growth rates evaluated for  $w = \tilde{w}$  was used in Eq. (3). Using Eq. (5) we can then determine the CV from the definitions:

$$\bar{w} = \int w f_t(w) dw,$$

$$\sigma^2(t) = \int (w - \bar{w})^2 f_t(w) dw. \quad (6)$$

These integrals usually cannot be solved analytically and thus will require numerical integration (Appendix B).

### 4. Development of size variation using a commonly used and general growth model

Here we examine how relative size variation (CV) changes as a cohort grows according to a general and flexible growth model, using the true CVs obtained by numerical integration of Eq. (6) (Appendix B). The general growth model we consider here is given by

$$g(w) = \frac{dw}{dt} = a_1 w^{b_1} - a_2 w^{b_2}, \quad (7)$$

where  $a_1$  and  $a_2$  are coefficients of gain in size due to assimilation and loss due to respiration, respectively, and are due to traits independent of size. We will call this equation, which balances gain and loss with changes in growth, the Putter balance equation (Pütter, 1920; Ricklefs, 2003). Any differences in the growth due to size are captured by the exponents,  $b_1$  and  $b_2$ , which are scale factors that affect growth as a function of size (Sebens, 1982, 1987; Uchmański, 1985; Werner, 1988; Brown et al., 2004). This model captures the idea that growth rate can be viewed as resulting from an energy budget (Yodzis and Innes, 1992), in which growth rate is equal to the rate acquired resources contribute to growth, minus the rate these resources are expended on factors such as respiration, and that rates that determine gain and loss are well approximated by power functions with constants that scale contributions to growth as a function of size (Sebens, 1982, 1987; Yodzis and Innes, 1992; West et al., 2001; Brown et al., 2004). If the rate is proportional to size, the exponent is one, whereas if the rate decreases (increases) faster than

proportional to size, the exponent is less than (greater than) one. This growth equation forms the basis of bioenergetic models (Hewett and Johnson, 1995) and other more specific growth equations (Wyzomirski et al., 1999) including parabolic, logistic, linear, (for  $b_1 = 2/3$  and  $b_2 = 1$ ) weight-based von Bertalanffy with isomorphic growth, and (for  $b_1 = 1$  and  $b_2$  variable) Richards'. The scaling exponents  $b_1$  and  $b_2$  may take on a wide range of values, and even for the same species,  $b_1$  may be greater or smaller than  $b_2$  depending on environmental factors such as temperature (see Discussion).

We examine the development of size variation over a large range of growth conditions by manipulating the relative contributions of gain and loss represented by  $a_1$  and  $a_2$  in the Putter balance equation, and the size-dependent scaling of gain and loss by manipulating  $b_1$  and  $b_2$ . To determine mean size as a function of time, we solve Eq. (6) using numerical integration (Appendix B). In each case a cohort starts with an initial truncated (at zero to prevent negative sizes) normal size distribution with mean size 1 and variance 0.1 (CV of 0.316), and grows until mean size increases 10-fold.

We also apply the analytical approximation to this growth model. Applying Eq. (4) to a cohort growing according to Putter balance equation, the size variation is predicted to be

$$CV(t) \cong CV_0 \frac{a_1 \tilde{w}^{b_1-1} - a_2 \tilde{w}^{b_2-1}}{a_1 \tilde{w}_0^{b_1-1} - a_2 \tilde{w}_0^{b_2-1}}. \tag{8}$$

Our principal motivation in using this approximation (Eq. (8)) is to identify and understand qualitative trends in the development of size variation, and how they relate to model parameter values. In addition, our analysis allows us to evaluate whether the approximation is robust when using this growth model together with moderately large initial variation and large changes in size over time.

For simplicity, first consider the relationship between size variation and mean size when loss is negligible ( $a_2 = 0$ ) and therefore  $g(w) = a_1 w^{b_1}$ . The analytical approximation of size variation and mean size (Eq. (8)) then reduces to

$$CV(t) \cong CV_0 \left( \frac{\tilde{w}}{\tilde{w}_0} \right)^{b_1-1}. \tag{9}$$

This relationship predicts that if larger size provides a proportionately larger increase in growth rate ( $b_1 > 1$ ), then the relative size variation will increase, whereas if larger size provides a proportionately smaller increase in growth rate ( $b_1 < 1$ ), then the relative variation will decrease. These qualitative patterns were supported by CVs obtained from our numerical evaluation for growth according to  $g(w) = a_1 w^{b_1}$  for a range of  $b_1$  (Fig. 1a), and the CVs generated by the analytical approximation were in close quantitative agreement with the numerically derived values. In the special case of exponential growth (i.e.  $b_1 = 1$ ), Eq. (9) predicts a constant CV over time, and the

relationship is exact for this case (DeAngelis and Coutant, 1979; Uchmański, 1985, Appendix A).

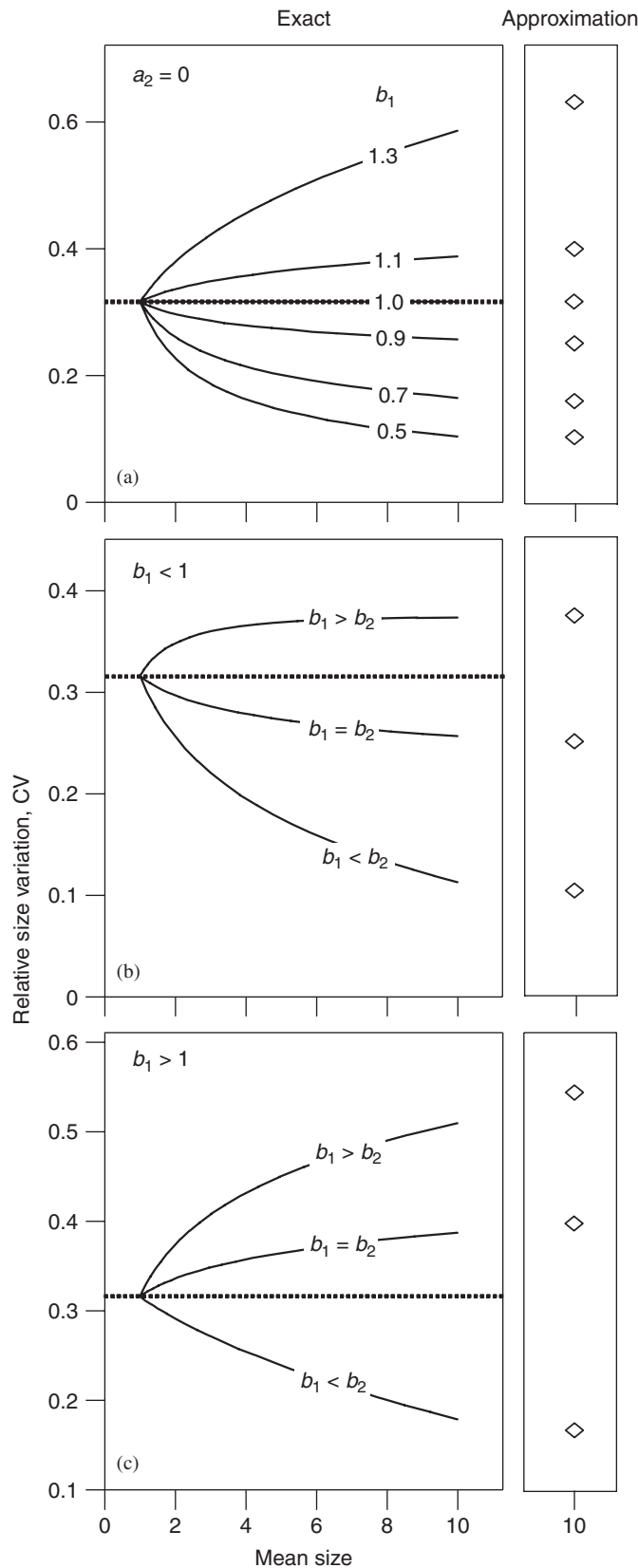
We next consider the relationship between size variation and mean size with the inclusion of a loss term. Our analytic approximation suggests that the inclusion of a loss term and any increase in its magnitude can either increase or decrease size variation, with the direction of the effect of loss being a function of the relative magnitudes of the scaling relationships (Eq. (8)). Specifically, the approximation indicates that an increase in loss causes an increase in relative size variation if the size dependence of gain is greater than the size dependence of loss, i.e.  $b_1 > b_2$ . In contrast, it suggests that there will be no effect if  $b_1 = b_2$ , and a decrease if  $b_1 < b_2$ . The magnitude of these effects is a function of the relative magnitude of loss relative to gain. We confirmed these patterns for  $b_1 < 1$  (Fig. 1b) and  $b_1 > 1$  (Fig. 1c) over a range of scaling of size and loss in which  $b_2$  is less than, equal, or greater than  $b_1$ , and demonstrated close quantitative agreement between true CVs derived by numerical integration and values from the approximation. Particularly noteworthy is that the addition of a loss term can reverse the trend in relative size variation as a function of mean size. That is, when  $b_1 < 1$  size variation decreases without loss (Fig. 1a), but can increase if  $b_1 < 1$  and  $b_1 > b_2$  with loss (Fig. 1b). Similarly, when  $b_1 > 1$  size variation increases without loss (Fig. 1a), but can decrease if  $b_1 > 1$  and  $b_1 < b_2$  with loss (Fig. 1c). These results show that seemingly complex and varied relationships between size variation and mean size can arise from size-dependent effects alone (i.e., without size-independent effects).

To gain intuition into the effect of the scaling of gain and loss with size, consider the effect of an increase in loss (i.e. an increase in  $a_2$ ) for a species in which larger size has a greater effect on loss than gain, i.e.  $b_1 < b_2$ . If  $b_1 < b_2$  the mean per unit size growth rate will decrease as the animals grow, and thus according to Eq. (8) the relative size variation will also decrease. The increase in loss will reduce the growth rate of both large and small individuals. However, the negative effect of loss for larger individuals relative to smaller individuals will be greater than the positive effect that size has on growth (since  $b_1 < b_2$ ). Thus, as the animals grow, the effect of the increase in loss will have a proportionately larger negative effect on growth of the larger individuals relative to smaller individuals, and consequently the increase in loss will reduce relative size differences.

We next present a more complex example over larger changes in size, in order to illustrate a scenario in which the dependence of size variation on size changes sign, and to further illustrate the robustness of the analytical approximation. For growth of a cohort over time according to Putter balance equation ( $b_1 = 0.8$ ,  $b_2 = 0.6$ ,  $a_1 = 1$ ), in the absence of loss ( $a_2 = 0$ ) mean size increased nearly four orders of magnitude, whereas with loss ( $a_2 = 0.8$ ) the increase in mean size was reduced by approximately 10-fold (Fig. 2a). The observed negative curvature without loss is characteristic of a scaling relationship of size and



growth rate less than one. In contrast, with loss, there is an initial positive curvature, because scaling of loss is less than that of gain, and loss is initially large relative to gain (80%



as determined by the relative magnitude of  $a_1$  and  $a_2$ ). As time progresses, the magnitude of loss relative to gain decreases (because  $b_2 < b_1$ ), and therefore the positive curvature disappears, and the signature of the scaling of gain increases until nearly similar to the case without loss. These changes are reflected in the individual variation in size (Fig. 2b). As seen previously (Fig. 1), CV falls with increasing size without loss, and when  $b_1 < 1$  there is a positive effect of the addition of loss because  $b_2 < b_1$ . With the given parameters, an interesting scenario arises in which there is an initial increase in relative size variation as a function of mean size that peaks and then falls with increasing size. This follows directly from the general analytical approximation (Eq. (4)), in which the change in CV is proportional to the per unit size growth rate; a peak is expected if the derivative with respect to size of the per unit size growth rate is equal to zero. For the Putter balance equation, this occurs when

$$w = \left( \frac{a_2 (b_2 - 1)}{a_1 (b_1 - 1)} \right)^{1/(b_1 - b_2)} \tag{10}$$

and for our example this predicted peak in CV occurs when size is equal to 10.5, which is very close to the actual value obtained by numerical analysis (Fig. 2b).

### 5. General predictions based on the growth model

In the previous section we examined how scaling relationships of gain and loss combine to affect the relationship between size variation and mean size. In this section, we use these results to derive three more general predictions.

1. Environmental factors can have a dramatic effect on size variation even in the absence of size-independent factors, and the effect of the environmental factor on size variation is strongly dependent on scaling relationships of size and growth.

Effects of environmental factors on growth can be represented by manipulating parameters in the Putter balance equation (Sebens, 1987). We can therefore use the approximate relationship for size variation (Eq. (8)) to predict how changes in environmental factors will affect size variation. Consider a reduction in resource level, which can be represented in the Putter balance equation by a

←  
 Fig. 1. Development of relative variation in body size (CV) as a function of mean size (arbitrary units) for animals growing according to the Putter balance equation (Eq. (7)) using different parameter values ( $\bar{w}_0 = 1$ ,  $\sigma_0^2 = 0.1$  ( $CV_0 = 0.316$ )). Left-hand panels present numerically calculated CV. For comparison, the right-hand panels show the results of the analytical approximation (Eq. (8)) and the same initial CV and mean size, and a final mean size of 10. (a)  $b_1$  (magnitude indicated by numbers on lines) is varied when there is no loss ( $a_2 = 0$ ). (b) Relationship with loss ( $a_2 = 0.5$ ),  $b_1 < 1 = 0.9$ , and  $b_1 = b_2, b_1 < b_2 = 1.1$ , and  $b_1 > b_2 = 0.6$ . (c) As in (b) for  $b_1 > 1$  ( $= 1.1$ ),  $b_2 = 0.9, 1.1$  and  $1.3$ . In all cases,  $a_1 = 1$ . Note that the results shown in the figure are invariant to equal ratios of  $a_1$  and  $a_2$ . The analytical approximations were very accurate (within 8% of true values calculated numerically) for all combinations of loss and gain.

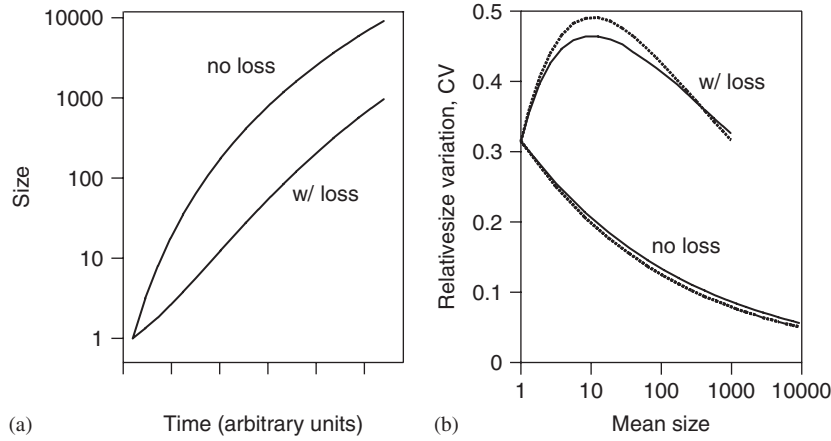


Fig. 2. Example in which relative size variation reverses as a function of mean size and in which mean size increases greatly. (a) Mean size as a function of time for growth according to the Putter balance equation (Eq. (7),  $\bar{w}_0 = 1$ ,  $CV_0 = 0.316$ ,  $b_1 = 0.8$ ,  $b_2 = 0.6$ ,  $a_1 = 1$ ) for a case without ( $a_2 = 0$ ) and with ( $a_2 = 0.8$ ) loss. (b) The corresponding relationships of size variation and mean size (solid lines). The dotted lines are results of the analytical approximation (Eq. (8)). The approximation at each point in time is made using only the initial mean and variation in size, and the size at the time the approximation is made of an individual that was originally of mean size.

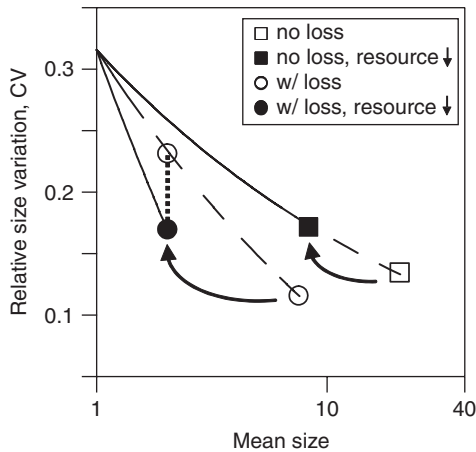


Fig. 3. Example of an environmental effect on size variation, as measured by CV for growth according to the Putter balance equation (Eq. (7),  $\bar{w}_0 = 1$ ,  $CV_0 = 0.316$ ,  $b_1 = 1$  and  $b_2 = 0.75$ ). A reduction in resource level is represented by decreasing  $a_1$  from 1.0 to 0.5 for cases without loss ( $a_2 = 0$ , squares) and with loss ( $a_2 = 0.3$ , circles). Empty and filled symbols represent cases without and with the resource reduction, respectively. Arrows connect curves without and with the reduction in resource level with the same assumption about losses. Comparing with and without resource reduction at the same mean size (but therefore different times) a reduction in resource level led to a decrease in relative size variation with losses and no change in relative size variation without losses (compare filled and empty circle connected by dotted line).

decrease in the magnitude of  $a_1$ . If loss is negligible relative to gain, then the approximation predicts that a reduction in resource level will have *no effect* on the relative size variation as a function of size. That is, mean size and size variation will change at a slower rate, but the relationship between mean size and size variation will be unaltered. In contrast, if loss is not negligible, then a reduction in resource level will have a positive or negative effect on size variation depending on the relationship of  $b_1$  and  $b_2$ . Numerical results confirm these predictions (Fig. 3), in

which a reduction in resource level, represented by 50% reduction in  $a_1$ , has a dramatically different effect on size variation as a function of mean size for two cases with different relative contributions of loss. This environmental effect on size variation arises when there is a difference in the scaling relationships of gain and loss. We note that competition is one way resource levels (and thus  $a_1$ ) might be altered, and thus our results suggest that size dependence alone should lead to changes in size variation in response to changes in the extent of competition, i.e., other inherent differences among individuals are not required (see Discussion). Similar predictions can be made for environmental factors that affect loss represented by changes in  $a_2$  (e.g., an increase in temperature, Sebens, 1987).

2. Size variation can yield information on the scaling relationships between size and growth not possible from measurements of mean size alone

Inferences on the relationship between individual growth rate and size based on analysis of only mean size as a function of time can be seriously incorrect. As animals grow, they will likely encounter changes in the environment caused by exogenous or endogenous (e.g. through reduced resource levels) factors that will cause the underlying relationship to be obscured when only considering mean size. In such cases, individual variation can yield information into the relationship between size and growth rate not available from analysis of mean growth. This can be illustrated by considering growth in a system where resources are constant and limiting (i.e. nearly all resources are consumed). In this case, we assume organisms assimilate resources equivalently, and for simplicity that losses are negligible (i.e., with  $g(w) = a_1 w^{b_1}$  and  $a_1$  and  $b_1$  the same for all individuals at a specified time). Our assumptions of fully utilized and constant resources combined with no losses implies that the sum of growth rates over individuals in the cohort must be a constant and

balance the resource supply rate. We model this situation by

$$\frac{dw_i}{dt} = cR \left( \frac{w_i^{b_1}}{\sum_{j=1}^n w_j^{b_1}} \right). \quad (11)$$

Here  $R$  is the resource supply rate,  $c$  is the conversion efficiency of resources into size (mass), and the term within large braces is the proportion of the total resource supply rate that is acquired by the  $i$ th individual. The actual CVs obtained numerically for growth according to Eq. (11) ( $b_1 = 0.75$ ,  $\bar{w}_0 = 1$ ,  $CV_0 = 0.316$ ) are illustrated in Fig. 4. Because resources are supplied at a constant rate and all resources are consumed, mean size increased linearly. Therefore an analysis of size as a function of time might incorrectly conclude that because mean growth rate is independent of size that  $b_1 = 0$ . This apparent discrepancy can occur because other factors (in this case limited resource supply) influenced mean growth, causing the relationship between size and growth over time to deviate strongly from the scaling relationship of size and growth. In contrast, we obtain a more accurate estimate of  $b_1$  by analyzing the change in size variation as a function of mean size. Rearranging Eq. (9) and replacing  $\tilde{w}$  by  $\bar{w}$  leads to the approximation

$$b_1 \cong 1 + \frac{\ln(CV(t)/CV_0)}{\ln(\bar{w}/\bar{w}_0)}. \quad (12)$$

Using the initial and final CVs and mean sizes (see Fig. 4 caption) obtained numerically in Eq. (12) yields  $b_1 = 0.766$ , which is close to the true value of 0.75. This example illustrates that individual variation can offer a lens into

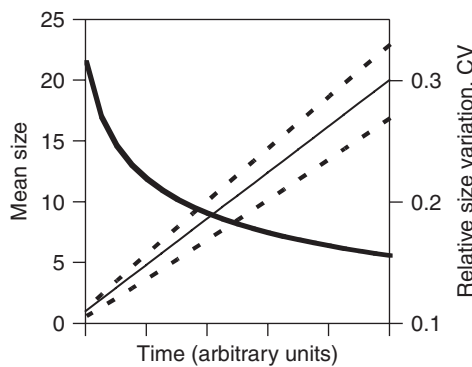


Fig. 4. Example for which size variation yields more reliable information into size-dependent growth than mean growth. Mean (straight solid line) and variation (CV, curved solid line) in size as a function of time when growth is limited by a constant and limiting resource supply and follows Eq. (11) ( $\bar{w}_0 = 1$ ,  $CV_0 = 0.316$ ,  $b_1 = 0.75$ ). Dashed straight lines represent the size of individuals that were initially greater and less than the mean size by one standard deviation. Mean size increased 20-fold leading to a decrease in size variation to  $CV = 0.156$ . The linear increase in mean size indicates that mean growth rate was independent of size, which could incorrectly be interpreted as indicating  $b_1 = 0$ . A close approximation of the correct scaling relationship ( $b_1 = 0.75$ ) can be derived from the data by examining the change in size variation as a function of mean size (Eq. (12), see text). These results are independent of the magnitude of the coefficients  $c$  and  $R$ .

how size-dependent processes and competition interact, beyond what is possible if only mean growth is considered.

3. Different environmental factors that have the same effect on mean growth can have very different effects on size variation

This prediction is a corollary of our second prediction. We illustrate this prediction by examining the effect of two factors that reduce the growth rate of a simple “base” case in which gain is proportional to size ( $b_1 = 1$ ), and there is no loss ( $a_2 = 0$ ). In this simple case, relative size variation does not change as mean size increases. Next, we introduce two factors that reduce growth by 75%. The first factor reduces growth rate by reducing gain (by reducing  $a_1$ ), whereas the second factor reduces growth rate by increasing loss (by increasing  $a_2$ ). In this example, the loss scaling factor ( $b_2$ ) is 0.75 which is less than  $b_1$ . Whereas these two manipulations cause nearly identical reductions in mean size achieved by a cohort, they have dramatically different effects on size variation (Fig. 5); the first factor has no effect, whereas the second has a pronounced positive effect. Importantly, this prediction and example further highlight how individual variation can yield insight into animal growth not available from changes in mean size alone.

## 6. Discussion

Although patterns of size variation have long been recognized (Ricker, 1958; Magnuson, 1962; Uchmański, 1985; Lomnicki, 1988; DeAngelis et al., 1993) we have an incomplete understanding of their origin. We developed an intuitive approximate relationship between individual size variation and growth rate; namely that relative size variation changes in proportion to the relative change in the mean per unit size growth rate. Our approximation works well for a widely applicable growth model, showing that the scaling of size-dependent growth processes has profound effects on size variation, and that changes in environmental factors have very different but predictable effects on size variation depending on growth rate properties (results summarized in Table 2).

Our results suggest that size variation will develop very differently for different species, or even different populations as a function of context, given the large range of scaling relationships expected for different species and populations. When compared across species, scaling relationships derived from physiological studies are remarkably robust over many orders of magnitude of body size (Peters, 1983; West et al., 2001). However, within species there is large variation in the values of scaling exponents (Sebens, 1982; Peters, 1983). For example, a review of intraspecific scaling exponents of respiration rate yielded exponents ranging from below 0 to greater than 2, with many values deviating by greater than 50% in both positive and negative directions (Glazier, 2005) from the mean value of 0.75 found across species (Peters, 1983). Further, even within a species, context can strongly affect scaling relationships (reviewed in Kozłowski et al., 2004).

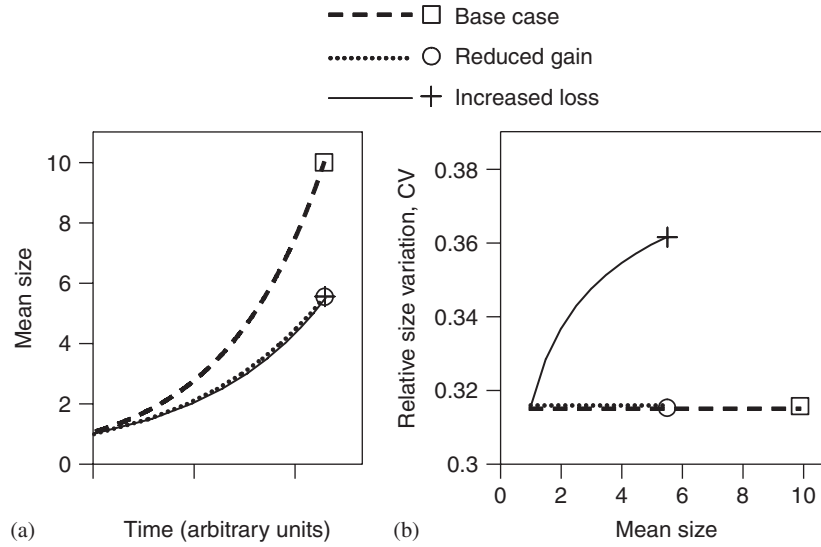


Fig. 5. Example of two factors having similar effects on mean growth rate, but very different effects on size variation. Exact numerical results using the Putter balance equation (Eq. (7),  $\bar{w}_0 = 1$ ,  $CV_0 = 0.316$ ), are shown in which a base treatment [ $a_1 = 1$ ,  $b_1 = 1.0$  and  $a_2 = 0$  (no loss), represented by dashed line and square symbol] is manipulated first, by decreasing gain ( $a_1 = 0.75$ , dotted line and circle symbol) and second, by increasing loss (by increasing  $a_2$  to 0.32 with  $b_2 = 0.75$ , solid line and + symbol). (a) The manipulations had nearly identical negative effects on growth rate (curves of mean size as a function of time nearly overlap). (b) In contrast, the two manipulations had very different effects on size variation; the decrease in gain has no effect on the relative size difference as a function of mean size (overlaps with base treatment), however the increase in loss has a positive effect on relative size variation as a function of mean size.

Table 2

Summary of predicted changes in relative size variation as a function of mean size when growth is described by the Putter balance equation (Eq. (7)) (NA indicates not applicable, downward and upward arrows indicate decrease and increase, respectively)

| Contribution of loss? | Size-dependent gain and loss relationships | Change in relative size variation as function of size | Effect of increase in loss coefficient ( $a_2$ ) relative to gain on change in relative size variation |
|-----------------------|--|---|--|
| No ( $a_2 = 0$ )      | $b < 0$                                    | ↓   | NA   |
|                       | $b = 0$                                    | None  | NA   |
|                       | $b > 0$                                    | ↑   | NA   |
| Yes ( $a_2 > 0$ )     | $b_1 < b_2$                                | ↓ or ↑  | ↓  |
|                       | $b_1 = b_2$                                | ↓ or ↑  | None   |
|                       | $b_1 > b_2$                                | ↓ or ↑  | ↑  |

Bayne et al. (1977) showed for a mussel species that metabolism scaled with size with an exponent of 0.35 and 0.84 during different seasons. Strong and Daborn (1980) showed, for the isopod *Idotea baltica*, that  $b_1$  (describing ingestion) decreased from approximately 0.94–0.71 with increasing temperature, while  $b_2$  (describing metabolism) increased from approximately 0.68–1.14 with increasing temperature. Thus for the same species, an environmental factor changed the ratio of  $b_1$  and  $b_2$  from greater than 1, to less than 1, which is predicted to lead to a decrease in size variation. Further, published scaling relationships are typically based solely on physiological factors including metabolism and respiration measured in laboratory settings, where the animals are isolated from important ecological processes. Behavioral factors such as competitive hierarchies (Magnuson 1962; Jobling, 1983) or access to additional resources (Werner and Gilliam, 1984; Ludsins

and DeVries, 1997) could strongly influence scaling factors. For example, size plays a large role in competitive hierarchies in fish. Jobling (1983) showed that competitive hierarchies in Arctic charr led to scaling relationship between food intake and size greater than 1, and this relationship increased at reduced feeding frequency which heightened the competitive hierarchy. Therefore, we expect that the wide range of magnitudes, and relative magnitudes, of  $b_1$  and  $b_2$  explored here are represented in natural settings.

We found methods from statistics, based on viewing future size as a transformation of initial size, useful. Although these methods are limited to evaluating changes in size distributions when growth of the cohort is the only influence on the relative abundances of different sizes, they provided us a way to understand how size variation could respond in apparently complex ways to changes in growth



model parameters. Our analysis explored hypotheses and properties that could be derived from considering a single focal process. The analytical approximation was derived to guide qualitative predictions, as numerical methods can provide nearly exact quantitative values of how size variation changes. Nevertheless, we were initially somewhat surprised by how accurately the approximation predicted changes in relative size variation, and described in some detail the nature of the approximation and its influence.

Future work should consider how the size-dependent growth we investigated interacts with other processes. PDE approaches can often be useful to gain insight into how size distributions respond in such more complex situations. For example, PDEs have been used to explore the effects of size-dependent mortality and persistent individual differences in growth rate that may have a genetic basis (size-independent factors, see Introduction). Indeed, DeAngelis and Coutant (1982) used a PDE approach to show how a bimodal size distribution can develop from an initial unimodal distribution as a consequence of a size-dependent growth rate relationship derived from the field. For some yet more complex situations, such as stochasticity in daily growth that is temporally correlated, PDE analysis cannot be used and individually based simulation is required (DeAngelis et al., 1993).

Our results suggest an alternative mechanism can lead to the frequently observed effect of competition on animal size variation, where increased competition is associated with an increase in relative size variation as a function of mean size in a number of animals (reviewed in Uchmański, 1985) including frog tadpoles (Wilbur and Collins, 1973, Peacor and Pfister, 2006), fish (Rubenstein, 1981a; Irwin et al., 1999) and grasshoppers (Wall and Begon, 1987). This relationship is typically hypothesized to indicate that competition magnifies inherent non-size-based phenotypic differences (i.e. size-independent factors, see Introduction) among individuals in their ability to grow, and therefore that competition magnifies or reveals these individual differences not otherwise apparent. This mechanism could be expressed in the Putter balance equation by introducing variation in the coefficient  $a_1$  or  $a_2$  to capture the inherent phenotypic differences in growth, and increasing this variation at high competition (as in Uchmański, 1985). In some cases, such inherent differences have been supported by direct quantification of individual phenotypic differences (Rubenstein, 1981b; Jobling and Koskela, 1996), adding strength to the hypothesis. However, our results show that a decrease in resource levels, that would accompany an increase in competition, could cause an increase in size variation via size-dependent factors alone. In this scenario, if decreasing resources associated with increased competition has a proportionally larger negative effect on gain than loss, then an increase in size variation would result when the scaling of size-dependent gain exceeded that of size-dependent loss ( $b_1 > b_2$ , as in Figs. 1 and 3). Such a difference is plausible given the large range

of potential values for these exponents. Thus the mechanism proposed here could underlie the increased size variation observed with increased competition, and could also play a role even in the cases for which a contribution of inherent phenotypic differences is established. To accurately model and describe the effects of competition on size variation, it is therefore important to account for such size-dependent effects.

Our results have implications to the development and inferences drawn from individually based models (IBMs) used to examine the population or community dynamics of specific ecological communities. A principal motivation underlying the use of IBMs is that they can capture processes occurring at the individual level that combine in complex ways to affect patterns at the population and community level (DeAngelis and Gross, 1992; Grimm and Railsback, 2005). For example, a number of studies have used IBMs to predict the survival of fish cohorts in complex environmental contexts (Rice et al., 1993; Letcher et al., 1996; Martinez-Garmendia, 1998; Rose et al., 1999). Because predation is size selective, variation in growth rate is hypothesized to have a large effect on survivorship. But many IBMs start a cohort with a size distribution at a young age and apply a growth model to all individuals, with parameters based on the relationship between mean size and age. Our results show that one should not assume that the resulting size variation will match what would be obtained if the correct individual growth versus size relationship were used (Fig. 5). We urge that when the goal is to predict how individual variation affects population processes, correct prediction of among individual variation in size-at-age and/or growth be one consideration when selecting among growth models. Ideally, the correct scaling relationship between individual growth rate and size should be used within IBMs, but often information to base a scaling relationship on is limited. It is therefore important when constructing IBMs that use size-dependent processes to consider how robust model predictions are to the choice of the growth equation.

For analogous reasons, models constructed to examine the contribution of size-independent factors to the origin of size variation (e.g., DeAngelis et al., 1993; Imsland et al., 1998; Pfister and Stevens, 2002) could underestimate the influence of size-dependent factors, if size dependence were represented in a way that departs from the true scaling. For example, Pfister and Stevens (2002) found that size-dependent growth in an IBM model cannot account for increases in variability patterns observed in field studies. The scaling factor of size-dependent growth (gain) in their IBM lies between 0 and 1, and there is no loss term. Therefore the size-dependent contribution should be a decrease in relative variation as growth proceeds. Alternative growth models that include loss could produce the opposite pattern, and thus inferences depend upon the selected model having correctly represented how contributions to individual growth rate scale with size. Whereas theoretical studies clearly point to the importance and need

to understand size-independent factors (DeAngelis et al., 1993; Imsland et al., 1998; Pfister and Stevens, 2002), further work is required to understand the relative contribution of size-dependent and size-independent factors, and their potential interactions.

## 7. Conclusions

Increasing attention devoted to size variation suggests that understanding its origin is important to a wide range of ecological problems (Lomnicki, 1988, 1999; Grimm and Uchmański, 2002; Kendall and Fox, 2002; Bolnick et al., 2003; de Roos and Persson, 2003). Further, size variation may provide clues into how species interactions and environmental conditions affect growth and survival in general (Lomnicki, 1988), by for example, indicating the magnitude of competition (Wilbur and Collins, 1973; Wall and Begon, 1987) and predation risk (Ziamba et al., 2000). A critical step is increased measurements of individual-based data (Pfister and Stevens, 2002) to understand the interaction of size-dependent and size-independent contributions to size variation. Our results, which complement those from earlier studies using PDEs (e.g., DeAngelis and Huston, 1987), illustrate the large range of potential relationships between mean size and size variation due to differences in the contributions and scaling of components of growth, and the effect of environmental factors on these relationships. This large range of relationships, however, can arise solely from size-dependent growth where relative size variation changes approximately in proportion to the changes in mean per unit size growth rate.

## Acknowledgments

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## Appendix A. Basis for the analytical approximation for variance and consideration of nonlinear influences

Our application of the delta method to obtain an analytical approximation of how the variance in size changes as a cohort grows is based on the Taylor series. Recall that if a function  $S(x)$  and its  $n+1$  derivatives are continuous in an interval containing any two values of  $x$ ,  $w$  and  $\mu$ , the function evaluated at  $w$  is equal to the Taylor series expanded about  $\mu$  with remainder:

$$S(w) = S(\mu) + S^{(1)}(\mu)(w - \mu) + \frac{S^{(2)}(\mu)}{2!}(w - \mu)^2 + \cdots + \frac{S^{(n)}(\mu)}{n!}(w - \mu)^n + R_n(w, \mu),$$

$$R_n(w, \mu) = \int_{\mu}^w \frac{(w - \tau)^n}{n!} S^{(n+1)}(\tau) d\tau. \quad (\text{A.1})$$

Here  $S^{(n)}(\mu)$  denotes the  $n$ th derivative of the function  $S(x)$  evaluated at  $x = \mu$ . For many functions the remainder term  $R_n(w, \mu)$  vanishes. In practice, many applications of the Taylor series use just the first several terms to approximate the function, as these terms will frequently dominate.

The usual delta method approximation we used includes only the first two terms of the series, so that

$$w(t) \cong \mathbf{w}(\bar{w}_0) + (w_0 - \bar{w}_0) \frac{g(\mathbf{w}(\bar{w}_0))}{g(\bar{w}_0)}. \quad (\text{A.2})$$

From this the expected value of size at time  $t$  is approximated by

$$\bar{w} \cong E(\mathbf{w}(\bar{w}_0) + \mathbf{w}^{(1)}(\bar{w}_0)(w_0 - \bar{w}_0)) = \mathbf{w}(\bar{w}_0). \quad (\text{A.3})$$

Here  $\mathbf{w}$  is a function returning size at time  $t$ , given initial size as an argument, and is identical to the  $w$  used in the main text, but the second argument,  $t$ , has been dropped to simplify notation. Then the delta method approximation of the variance is obtained, using this approximation of  $\bar{w}$ ,

$$\begin{aligned} \sigma^2(t) &= E[(w - \bar{w})^2] \cong E[\mathbf{w}(\bar{w}_0) \\ &\quad + \mathbf{w}^{(1)}(\bar{w}_0)(w_0 - \bar{w}_0) - \mathbf{w}(\bar{w}_0)]^2 \\ &= (\mathbf{w}^{(1)}(\bar{w}_0))^2 E[(W_0 - \bar{w}_0)^2] = (\mathbf{w}^{(1)}(\bar{w}_0))^2 \sigma_0^2. \end{aligned} \quad (\text{A.4})$$

This leads directly to Eq. (1) in the main text.

While the delta method is usually applied as in Eq. (A.4), it is straightforward (but algebraically messy) to extend the approach to include higher order terms. In the main text we restricted our attention to the approximation that uses the first two terms of the Taylor series because our purpose in presenting the approximation was to aid intuition about how variance in size develops for a cohort. Here we develop the approximation including the third (quadratic) term, as an aid to understanding of how nonlinearities can influence the approximation.

In a similar fashion to Eq. (A.3), the expected value of size at time  $t$  with the quadratic term included is

$$\begin{aligned} \bar{w} &\cong E\left(\mathbf{w}(\bar{w}_0) + \frac{\mathbf{w}^{(2)}(\bar{w}_0)}{2}(W_0 - \bar{w}_0)^2\right) \\ &= \mathbf{w}(\bar{w}_0) + \mathbf{w}^{(2)}(\bar{w}_0) \frac{\sigma_0^2}{2}. \end{aligned} \quad (\text{A.5})$$

This emphasizes that in general  $\bar{w} \neq \mathbf{w}(\bar{w}_0)$ , i.e., the average size is not equal to the size of the individual that was at average size initially. Incorporating the quadratic term either leads to an increase or decrease from the linear approximation depending on whether  $\mathbf{w}$  is an accelerating (positive second derivative) or decelerating (negative second derivative) function of the initial value for size. The absolute value of the adjustment depends on both the magnitude of the second derivative and the variance.

Now using the new approximation for mean size from Eq. (A.5) and incorporating the quadratic term (i.e., the

third term in Eq. (A.1)) when approximating  $w$ , the approximation for variance given by (A.4) is modified to

$$\sigma^2(t) \cong E \left( \left[ \left[ w(\bar{w}_0) + w^{(1)}(\bar{w}_0)(W_0 - \bar{w}_0) + \frac{w^{(2)}(\bar{w}_0)}{2}(W_0 - \bar{w}_0)^2 - \left[ w(\bar{w}_0) + w^{(2)}(\bar{w}_0) \frac{\sigma_0^2}{2} \right]^2 \right] \right]^2 \right). \quad (\text{A.6})$$

After algebraic simplification this can be expressed as

$$\sigma^2(t) \cong \{ (w^{(1)}(\bar{w}_0))^2 \sigma_0^2 \} + \{ w^{(1)}(\bar{w}_0) w^{(2)}(\bar{w}_0) E((W_0 - \bar{w}_0)^3) \} + \left\{ \left( \frac{w^{(2)}(\bar{w}_0)}{2} \right)^2 \left[ E((W_0 - \bar{w}_0)^4) - (\sigma_0^2)^2 \right] \right\}. \quad (\text{A.7})$$

In Eq. (A.7), the first term is the original delta method approximation based on the first two terms of the Taylor series. The second term represents an interaction between the initial skew in the distribution and the nonlinear (quadratic) term (third term of Eq. (A.1)). If both the skew and the second derivative have the same sign, the effect of this term is to cause an increase over the linear approximation. The third term is also related to skew and is always positive because the squared second derivative must be positive and the term in square braces is of the form  $E[X^2] - (E[X])^2$  and  $E[X^2] > (E[X])^2$ . Thus we have the somewhat surprising result that curvature caused by a non-zero second derivative will generally increase the variance (provided the initial distribution is symmetric) over the linear approximation, regardless of the direction of the curvature in the relationship. Although individuals with size initially below (with a positive second derivative) or above (with a negative second derivative) the mean will end up closer to the center of the distribution than assumed by the linear approximation, the opposite effect on the other side of the mean produces larger squared deviations on average. However, when considering the CV rather than variance, a positive second derivative could cause a decrease rather than increase in comparison with the linear approximation, because  $\sigma(t)$  (square root of Eq. (A.7)) could increase proportionately less than the reciprocal of the mean (reciprocal of Eq. (A.5)) decreases.

To further explore the nature of the delta method approximation, we compare the size distribution arising from the approximation with the actual size distribution, when organisms grow according to the logistic model:

$$\begin{aligned} \frac{dw}{dt} &= g_1 w - \frac{g_1}{w_{\max}} w^2, \\ w(w_0, t) &= \frac{w_{\max}}{(w_{\max}/w_0 - 1) \exp(-g_1 t) + 1}, \\ w_0(w, t) &= \frac{w_{\max}}{((w_{\max} - w)/w) e^{g_1 t} + 1}. \end{aligned} \quad (\text{A.8})$$

Fig. A1a shows a normal PDF for initial sizes (truncated at zero), a final PDF after logistic growth (i.e., using Eq. (A.8)), and a final PDF corresponding to growth

following the approximation (Eq. (A.2)) used in the derivation of the delta method approximation for CV (Eq. (4)). The PDFs were calculated by Eq. (5), but for approximate logistic growth the ratio of growth rates on the right-hand side of the equation becomes  $g(\bar{w}_0)/g(\bar{w})$ . As for logistic growth, for approximate logistic growth the functions  $g(\cdot)$  and  $w(\cdot)$  applied in Eq. (5) followed Eq. (A.8). We chose an initial distribution, parameters, and time period for growth that accentuate and illustrate the differences between the approximation and the actual distribution for true logistic growth ( $\bar{w}_0 = 5$ ,  $CV_0 = 0.316$ ,  $g_1 = 1$ ,  $g_{\max} = 20$ ,  $t = 2.0$ ). These parameters lead to an 277% increase in mean size.

The initial probability density for sizes 2 and 8 were equal, but after logistic growth the probability density declined substantially for a size corresponding to an initial size of 2, and increased substantially for an initial size of 8. The probability density corresponding to the analytical approximation remained equal and decreased only slightly after growth (Fig. A2 panel b). Fig. A2, panels c and d, show a more detailed view of the PDFs after growth for sizes corresponding to initial size ranges of  $2 \pm 0.2$  and  $8 \pm 0.2$ . Individuals near 2 in initial size were spread over a wider range of sizes after growth than before growth, whereas individuals initially near 8 were spread over a narrower range after growth. This reflects the different growth ratios  $g(w(w_0))/g(w_0)$  in different parts of the initial size distribution, which is ignored by the approximation. The approximation spreads the entire size distribution based on the ratio at the mean of the initial distribution  $g(w(\bar{w}_0))/g(\bar{w}_0)$ , which in this case leads to only modest change in spread from the initial size distribution. After growth, the locations along the  $X$ -axis for these size intervals also differed between logistic growth and growth according to the approximation. For the logistic scenario we modeled, the average growth ratio between an initial size of 2 and the initial mean (equal to 5) was greater than the ratio at the mean, leading to a stretching of this portion of the distribution relative to what the approximation assumes and an underestimate of the difference in total growth for individuals starting at sizes of 2 and 5. Likewise, the average ratio between an initial size of 5 and 8 is less than the ratio at the mean, and thus the difference in total growth for individuals starting at these sizes is overestimated by the approximation.

In the above example we deliberately chose a starting size distribution, logistic parameters, duration for growth, and focal sizes to emphasize differences between the true logistic PDF and that presumed by the approximation. Even so, the overall location and spread of the approximate distribution has roughly tracked the true distribution. While the approximate mean of 14.79 is somewhat over the true mean of 13.85, and the approximate CV of 0.109 is substantially below the true CV of 0.149, the approximation has still captured the substantial decline in CV for this example deliberately chosen to emphasize errors due to the approximation. At least in part the

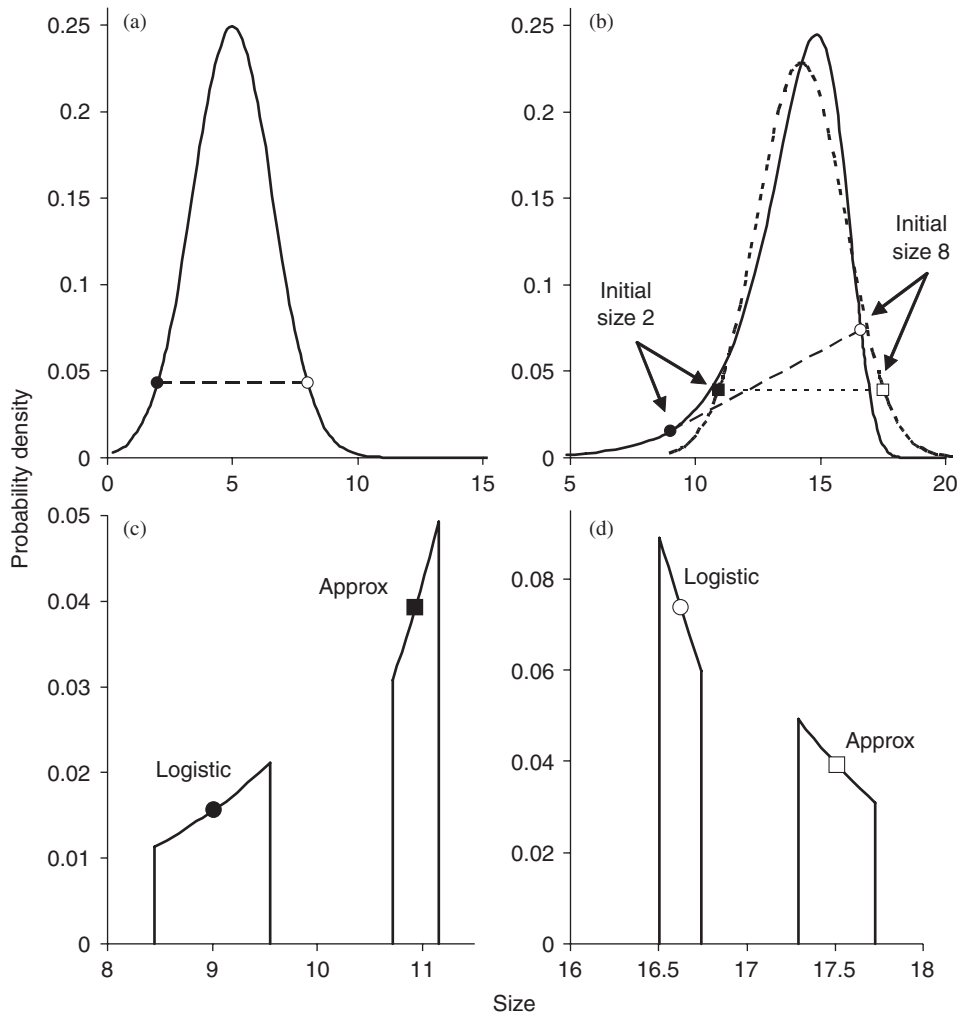


Fig. A1. Illustration of local expansion of a size distribution and its relationship to the analytical approximation based on the delta method. (a) The initial size distribution (probability density function, PDF) for a truncated (at zero) normal distribution ( $\bar{w}_0 = 5$ ,  $CV_0 = 0.316$ ). Circles are located on PDF curve for sizes of 2 (solid) and 8 (open), and are connected by a long dashed line emphasizing that the probability density is the same for these two sizes that are equal distance from the initial mean. (b) The PDF after logistic growth ( $g_1 = 1$ ,  $g_{max} = 20$ ,  $t = 2.0$ ) (solid curve) as well as an approximation to the PDF after growth based on the same linearization as our analytical approximation for the CV (dashed curve). Symbols on PDF curves show sizes of individuals that were initially of size 2 (solid symbols) or size 8 (open symbols). Circles are used for actual logistic growth and are connected by a long dashed line, and squares connected by a short dashed line are used for approximate logistic growth. The connecting lines emphasize that the probability density remains equal for individuals of size 2 and 8 according to the approximation, whereas probability density increases for the initially larger size relative to the initially smaller size for actual logistic growth. (c) Expanded portion of the final PDFs after growth corresponding to individuals that were of initial size  $2 \pm 0.2$  for logistic (solid circle on curve) or approximate logistic (solid square on curve) growth. (d) Same as panel c for the portion of the PDFs corresponding to initial size  $8 \pm 0.2$ , using open symbols instead of solid ones.

approximate CV bears a relationship to the true CV because the stretching of the distribution below the mean is balanced by its contraction above the mean, although there is some underestimation because the approximation cannot account for the skew (see general discussion above). Some may be surprised by how well the approximation performs, viewing the linearization as assuming that  $w(w_0)$  changes linearly with time. In fact, the analytical approximation is based on a less severe assumption of a linear relationship between  $w(w_0)$  and  $w_0$  with slope determined by the ratio of initial and final growth rates for an initial size equal to the mean and intercept given that slope determined by  $w(w_0)$ . These assumptions are strictly true for some models where

size changes quite nonlinearly with time, such as exponential growth ( $dw/dt = a_1 w$ ) or the “length-based” von Bertalanffy ( $dw/dt = a_1 - a_2 w$ ), where size ( $w$  here) is usually considered to be length, and for these the approximation is exact.

### Appendix B. Derivation of the exact distribution of size at time $t$ and calculation of the associated variance

We use two distinct methods to derive the (exact) PDF for size at time  $t$ ,  $f_t(w)$ , and then calculate the associated variance (and CV). The first approach, from statistics, is based on considering size at time  $t$  as a transformation of



initial size, and thus relates to our delta method approximation. The second is based on solving a partial differential equation describing the dynamics of a size-structured population. Rather than follow individuals, this method quantifies how the density of individuals as a function of size changes through time (DeAngelis and Coutant, 1979). PDEs have the advantage that they can be adapted to incorporate additional influences on size distributions such as size selective mortality and recruitment (DeAngelis and Huston, 1987).

The first approach is intended for deriving the PDF for a transformed random variable (Larsen and Marx, 1981, pp. 92–93). Let  $w_0$  represent the size of some individual at time 0, with PDF  $f_0(w_0)$  and cumulative distribution function (CDF)  $F_0(w_0)$ . The solution of the differential equation  $dw/dt = g(w)$  at time  $t$ , given an initial size  $w_0$ , is obtained by the function  $w(w_0, t)$ . The inverse function  $w_0(w, t)$  returns the initial size given the size at time  $t$ . We obtain the PDF for  $w$  at time  $t$  by first expressing the CDF for  $w$  at time  $t$  in terms of the CDF for  $w_0$ ,  $F_t(w) = F_0(w_0(w, t))$ , which holds when  $w(w_0, t)$  is a one-to-one monotonic function, as is the case for the growth models we are considering. Next, we differentiate this CDF with respect to  $w$  to obtain (by definition) the PDF  $f_t(w)$ :

$$f_t(w) = \frac{dF_0(w_0(w, t))}{dw} = \frac{dF_0(w_0(w, t))}{dw_0(w, t)} \frac{dw_0(w, t)}{dw} = f_0(w_0(w, t)) \frac{dw_0(w, t)}{dw}. \tag{B.1}$$

We then divide the numerator and denominator of the last term in Eq. (B.1) by  $dt$ , and recalling that  $dw/dt = g(w)$ , obtain Eq. (5).

The second approach to obtain the PDF is to use the method of characteristics to solve a set of PDEs. In this approach we consider a PDE that describes the dynamics of a size-structured population for the special case where individual growth is occurring in the absence of mortality or recruitment to the population. For this case, the appropriate PDE is (DeAngelis and Huston, 1987)

$$\frac{\partial N(w, t)}{\partial t} + \frac{\partial}{\partial w}(g(w, t)N(w, t)) = 0. \tag{B.2}$$

Here,  $N(w, t)$  represents the density of animals of size  $w$  at time  $t$ . Eq. (B.2) can be rewritten in the form  $N_t + cN_w = b$ , where  $N_t$  and  $N_w$  are partial derivatives of  $N$  with respect to  $t$  and  $w$ , respectively:

$$N(w, t) + g(w(t)) \frac{\partial N(w, t)}{\partial w} = -N(w, t) \frac{\partial g(w(t))}{\partial w}. \tag{B.3}$$

The method of characteristics recognizes that Eq. (B.3) can be rewritten as the pair of coupled ordinary differential equations:

$$\begin{aligned} \frac{dN}{dt} &= b = -\frac{\partial g(w)}{\partial w} N, \\ \frac{dw}{dt} &= c = g(w). \end{aligned} \tag{B.4}$$

Consequently,

$$\begin{aligned} N(w, t) &= N(w_0, 0) \exp\left(-\int_0^t \frac{\partial g(w)}{\partial w} d\tau\right) \\ &= N(w_0, 0) \exp\left(-\int_{g(w_0)}^{g(w(w_0, t))} \frac{1}{g} dg\right) \\ &= N(w_0, 0) \frac{g(w_0)}{g(w(w_0))}. \end{aligned} \tag{B.5}$$

In obtaining Eq. (B.5),  $\partial g/\partial w$  could be equated with  $dg/dw$  because the former does not depend upon  $t$ . Without loss of generality, we can assume  $\int N(w, 0) dw = 1$  (if this is not true we can normalize the distribution so it is), so that  $N(w, 0) = f_0(w_0)$ . With this substitution in Eq. (B.5) we again obtain Eq. (5).

With an equation giving the PDF at time  $t$  in hand (Eq. (5)), the task is then to determine variance (and CV). This requires that Eq. (5) be substituted for  $f_t(w)$  in Eq. (6) and the resulting integrals evaluated. The resulting integrals generally cannot be solved analytically and numerical integration is required. These integrals have the general form  $\int h(w)f_t(w) dw$ , where  $h(w)$  is either  $w$  or  $(w - \bar{w})^2$ , for the mean and variance, respectively. We used a simple brute force approach of varying  $w$  over the range of  $K$  values with non-negligible probability density (from a lower value  $L$  to a higher value  $U$ ) in small increments, and calculating  $\sum_{i=1}^{i=K} h(w_i)f_t(w_i)\delta_i$ , where  $\delta_i$  is the size increment for which  $f_t(w_i)$  is assumed to apply. The limit of this summation as  $\delta_i \rightarrow 0$  is the desired integral, so the summation can be used in place of the integral after checking that  $\delta$  are small enough so the answer would not appreciably change with further decreases in the increment size. Normally, one would use equal size increments, but this is not generally possible here because this would require that  $w_0(w, t)$  be known (so that Eq. (B.1) can be applied to obtain  $f_t(w)$  for the desired  $w$  in the summation). For a given  $w_0$ , however, we can numerically solve the growth model (differential equation) to obtain  $w$ . We therefore specified a sequential series of  $K$  values of  $w_0$ , found the corresponding  $w$  at later times (after growth) by numerically solving the differential equation for each initial size, and then used these resulting sizes in the summation. In this case (for a distribution truncated at zero),  $\delta_1 = (w_2 - w_1)/2 + w_1$ ,  $\delta_i = (w_{i+1} - w_{i-1})/2$ ,  $1 < i < K$ , and  $\delta_K = \delta_{K-1}$ . Based on preliminary testing we used 1000 equally spaced increments, between 0 and 5 in our numerical integrations presented in main text.

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