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NOTES AND COMMENTS

VON BERTALANFFY'S GROWTH EQUATION SHOULD NOT BE USED TO MODEL AGE AND SIZE AT MATURITY

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The study of life-history evolution has enjoyed considerable success in melding theoretical prediction with empirical observation (Roff 1992; Stearns 1992). Often relatively simple models yield remarkably accurate predictions. One area of particular interest has been the study of age at maturity (Kozłowski 1992; Bernardo 1993; references therein). Several models have been proposed to explain variation in age at maturity across species, and each usually employs a different set of assumptions regarding mortality rates, growth, fecundity, and the appropriate measure of fitness. Results are often sensitive to the choice of these components; therefore, it is important to know when simple formulations are adequate. Here we focus on one of these components: the growth function.

In the first section, we present the general modeling framework common to most of the aforementioned studies and consider how to choose an appropriate growth equation. We suggest that the growth trajectory should be specified by two separate equations: a prematurity equation in which essentially no surplus energy is devoted to reproduction and a postmaturity equation in which all (determinate growth) or some (indeterminate growth) surplus energy is devoted to reproduction. Logical inconsistencies can arise in models of the evolution of age and size at maturity when such a specification is not made.

We believe that the von Bertalanffy (VB) equation is misused in both indeterminate and determinate growth models of maturity. Under indeterminate growth, a separate specification of pre- and postmaturity growth curves is usually not employed. Under determinate growth, in which such a separate specification is made, the VB equation often fails to provide an appropriate description of prema-

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turity growth. Here we consider determinate growth models in detail and review evidence for the shape of prematurity growth curves. We demonstrate that using a more suitable equation for prematurity growth alters predictions in a qualitative way. Finally, we consider indeterminate growth models in detail and propose a suitable specification for modeling age and size at maturity in this setting.

MODELING AGE AND SIZE AT MATURITY

Many models for optimal age and size at maturity can be placed within a general theoretical framework based on the Euler-Lotka equation. Additionally, the majority assume continuous reproductive output (see Kozłowski and Wiegert 1986) and an instant switch for the onset of maturity. Maturity is regarded as the point at which an organism begins to devote some surplus energy to reproduction. The two most common fitness measures employed are lifetime reproductive output, R_0, and the Malthusian parameter, r (Kozłowski 1993). Our analysis focuses primarily on R_0, because it is simplest and it is an appropriate fitness measure under many important forms of density-dependent population regulation (see Charnov 1990; Mylius and Diekmann 1995). We assume that mortality can be reasonably described by an initial burst of mortality (p) followed by constant juvenile and adult mortality rates (see the appendix for notation). This is probably most appropriate when changes in mortality result from reproductive costs rather than size or age dependency. Under these assumptions, we have

$$R_0 = pe^{-j\alpha} \int_0^\infty e^{-ax} m(x + \alpha)\, dx, \tag{1a}$$

and a necessary condition for maximizing R_0 is

$$\frac{\int_0^\infty e^{-ax} \frac{\partial m}{\partial \alpha}\, dx}{\int_0^\infty e^{-ax} m\, dx} = j. \tag{1b}$$

Equation (1b) is an optimization condition and reveals the trade-off between the relative rate of gain in fecundity from postponing reproduction (left-hand side) and the corresponding relative rate of decrease in the probability of surviving to maturity (right-hand side). The optimal age at maturity occurs when these two factors exactly balance. To make more use of equations (1), we need to specify how an organism grows and how size is related to reproductive success. We follow most treatments in assuming that increased size translates into increased fecundity, and we refer to the function of mass versus age as the growth trajectory.

What properties should a suitable growth trajectory exhibit? A common although sometimes implicit assumption is that growth and reproduction are "competing" energy sinks (for evidence, see Roff 1992, pp. 150–157; Stearns 1992, app. 2D). Thus, the onset of maturity involves a reduction of energy devoted to growth to "fuel" reproduction (Kozłowski 1992). As a result, the growth trajectory used in such a model should exhibit a fundamental change at this point

(Kozłowski and Wiegert 1986; Kozłowski 1992). Therefore, a very important property that any suitable growth specification should have is a distinction between pre- and postmaturity growth processes.

The prematurity growth trajectory should describe pure growth. Its shape should reflect the size-age relationship when all available resources are devoted to growth. Two common postmaturity growth patterns are modeled: determinate and indeterminate growth. Determinate growers devote most surplus energy to reproduction after maturity; thus, their postmaturity trajectory should be flat. Indeterminate growers show a gradual decline in the energy devoted to growth and an increase devoted to reproduction; thus, their postmaturity trajectory should be increasing but gradually plateau.

The importance of having separate equations for pre- and postmaturity growth is illustrated by considering the optimization procedure. The previous specification of growth results in a trajectory in which the pre- and postmaturity pieces are spliced together at α. To determine if α is optimal, we vary α and determine the resultant change in fitness. When increasing α, we need to continue along the prematurity trajectory slightly longer and then switch to a postmaturity trajectory at a larger size. When decreasing α, we need to switch to a postmaturity trajectory at a smaller size. Thus, we require a prematurity trajectory that describes "pure growth" and a family of postmaturity trajectories indexed by α that describes growth when some significant amount of energy is devoted to reproduction.

The two most common choices of growth equation for life-history models are the VB equation, which, using the approximation mass = length^3, specifies growth rate as

$$\text{VB:} \quad \frac{dw}{dt} = 3kw^{2/3}(w_{\infty}^{1/3} - w^{1/3}) \tag{2}$$

(Roff 1984, 1986; Stearns and Koella 1986; Charnov 1989; Shine and Charnov 1992; Berrigan and Koella 1994), and the production relation, which specifies growth rate as a power function (PF) of mass, that is,

$$\text{PF:} \quad \frac{dw}{dt} = kw^c \tag{3}$$

(Roff 1983, 1986; Kozłowski and Wiegert 1986, 1987; Kozłowski and Uchmanski 1987; Kozłowski 1992). In both equations, the parameter k is usually interpreted as a growth rate or habitat quality parameter; a large k corresponds to a productive habitat because it gives a larger growth rate.

The PF equation is often an accurate representation of prereproductive growth, and its use in determinate growth models thus follows quite naturally; size is simply assumed to remain constant after maturity. Later we consider how this equation might be suitably extended to model indeterminate growth also. The VB equation has been used in both determinate and indeterminate growth models. It has gained widespread use, largely because it is believed to be an accurate description of *lifetime* growth in many organisms, it is simple, and there are many empirical estimates of its parameters (however, see Roff 1980 for a discussion of some shortcomings). We suggest, however, that it is usually inappropriate for

modeling age and size at maturity under determinate growth, and using it alone for modeling age and size at maturity under indeterminate growth is always inappropriate. We consider each of these cases in turn.

Models of the evolution of age and size at maturity under determinate growth *do* separate pre- and postmaturity growth phases. Some equation describing prematurity growth is used, followed by a family of constant functions after maturity.

What should the prereproductive growth trajectory used in age at maturity models look like? Before maturity, surplus energy is devoted primarily to growth. Thus, the prereproductive growth rate should be proportional to the rate of energy acquisition minus the rate at which energy is used for maintenance. The shape of the resulting growth trajectory will depend on how this difference scales with body mass. Several lines of evidence suggest an approximate scaling of $mass^{0.7}$ (Farlow 1976; Blueweiss et al. 1978; Case 1978; Lavigne 1982; Reiss 1989), which results in a concave-up trajectory. Such trajectories are believed to be the norm (at least for early growth stages) (Ricker 1979; Sibly and Calow 1986), which is often the justification for modeling determinate growth as a power function of mass with an exponent of two-thirds to three-fourths (Reiss 1989; Charnov 1993). Evidence also suggests, however, that larvae and juveniles of many other organisms such as cephalopods (Jackson and Choat 1992; references therein), fish (Brett and Shelbourne 1975; Brett 1979; Roff 1983; Deegan and Thompson 1987; Tzeng and Yu 1988; Comyns et al. 1989; Hovenkamp and Witte 1991), amphibians (Nagai et al. 1971; Alford and Harris 1988), and reptiles (Schoener and Schoener 1978) exhibit concave-up trajectories (see also Alford and Jackson 1993). These observations suggest that the power function is often a good choice for describing prematurity growth.

Although the VB equation is often thought of as an indeterminate growth equation, it has been employed as the prematurity equation under determinate growth as well (Roff 1984, 1986; Stearns and Koella 1986; Berrigan and Koella 1994). We suggest, however, that because the VB equation describes *lifetime* growth, it is not likely to be an accurate representation of prematurity growth in many organisms. This problem is often exacerbated by using empirically estimated parameter values. The pattern of growth embodied by the parameter estimates of a given species describes the age-specific schedule of resource allocation to growth and reproduction *after* that species has "solved" the life-history optimization problem. Thus, by using these parameters in the VB equation for prereproductive growth, one is largely neglecting the reason that the organism might postpone maturity in the first place, namely, to increase size and hence fecundity.

The use of the VB equation can alter predictions of age at maturity away from those obtained using the power function in a nontrivial way. Under determinate growth, size remains constant after maturity, which is taken to imply that fecundity, $m(\alpha)$ also remains constant. Therefore, equations (1a) and (1b) become

$$R_0 = \frac{pe^{-j\alpha}m(\alpha)}{a}$$

and   (4)

$$\frac{dm/d\alpha}{m} = j.$$

The solutions to equations (2) and (3) (with $c = 2/3$) for arbitrary, nonzero initial sizes are

$$\text{VB:} \quad w(t) = (w_\infty^{1/3}(1 - e^{-kt}) + w_0^{1/3}e^{-kt})^3 \tag{5}$$

and

$$\text{PF:} \quad w(t) = (1/3\ kt + w_0^{1/3})^3. \tag{6}$$

We assume fecundity is proportional to the rate of availability of surplus resources, which is given by equations (2) and (3) by substituting in size at maturity (Kozłowski and Wiegert 1986, 1987; Kozłowski 1992).

Calculating the optimal age at maturity for each case using equation (4) yields

$$\text{VB:} \quad \alpha = \ln\left[\frac{(w_\infty^{1/3} - w_0^{1/3})}{w_\infty^{1/3}} \cdot \frac{3k+j}{k+j}\right] \cdot \frac{1}{k} \tag{7}$$

and

$$\text{PF:} \quad \alpha = \frac{2}{j} - \frac{3w_0^{1/3}}{k}. \tag{8}$$

Although their forms differ, equations (7) and (8) are both decreasing functions of j as expected from the general consideration of equation (1b). One very important difference, however, is the effect of the growth rate parameter, k. The VB age at maturity is a decreasing function of k over nearly its entire range, whereas the PF age at maturity is an increasing function of k everywhere (fig. 1). It is interesting that most previous treatments employing the VB equation have assumed $w_0 = 0$, which makes equation (7) everywhere decreasing in k and equation (8) independent of k. Clearly, neglecting even a small initial size will change the qualitative nature of equation (8) as a function of k everywhere, whereas it may do so only for very small values of k in equation (7).

These results illustrate that even in this simple model, using a more suitable growth specification has a major *qualitative* effect on prediction. This is easily intuited: the VB equation is asymptomatic; therefore, using it for prereproductive growth restricts the maximum size and hence fecundity that is attainable. In a sense, increasing the growth rate parameter allows an individual to approach this maximum sooner and thereby mature earlier, but it never allows for an increase in the maximum. Thus, there is a decreasing benefit to postponing maturity as k
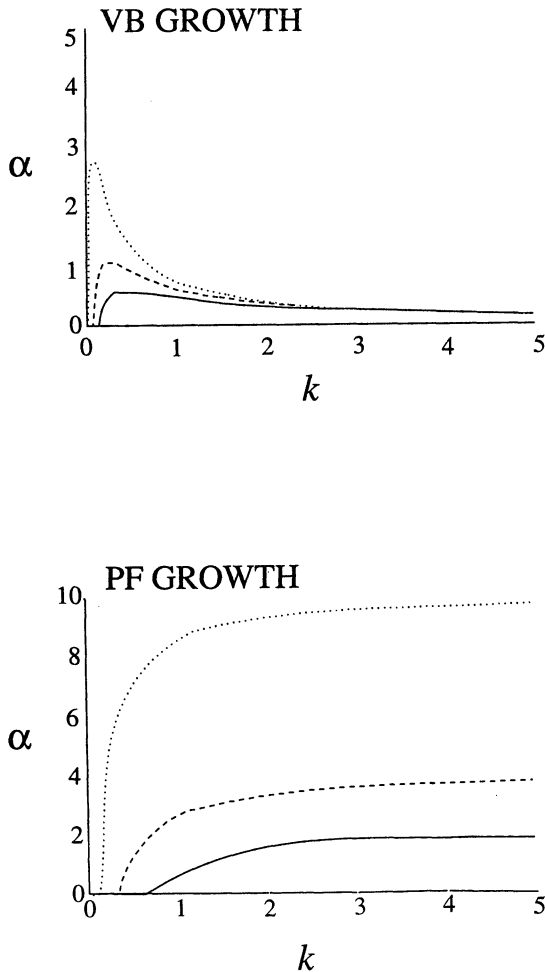
VB GROWTH

PF GROWTH

Fig. 1.—The relationship between predicted age at maturity and the growth rate parameter, k, under both VB and PF growth. *Dotted line, $j = 0.2$; dashed line, $j = 0.5$; solid line, $j = 0.9$.* Both growth functions use $w_0 = 0.1$, and the VB function also uses $w_\infty = 10$. Note the different scale on the α-axis for VB versus PF. Under VB growth, for most values of k, as the productivity of the habitat increases (increasing k), the model predicts an earlier age at maturity. Under PF growth, as the productivity of the habitat increases, the model predicts a later age at maturity.

increases. Under PF growth, however, increasing k always allows for an increase in size and fecundity. This can be more easily seen in the corresponding size at maturity equations obtained by substituting equations (7) and (8) into equations (5) and (6) (fig. 2):

$$\text{VB:} \quad w(\alpha) = w_\infty \left(\frac{2k}{3k + j} \right)^3$$
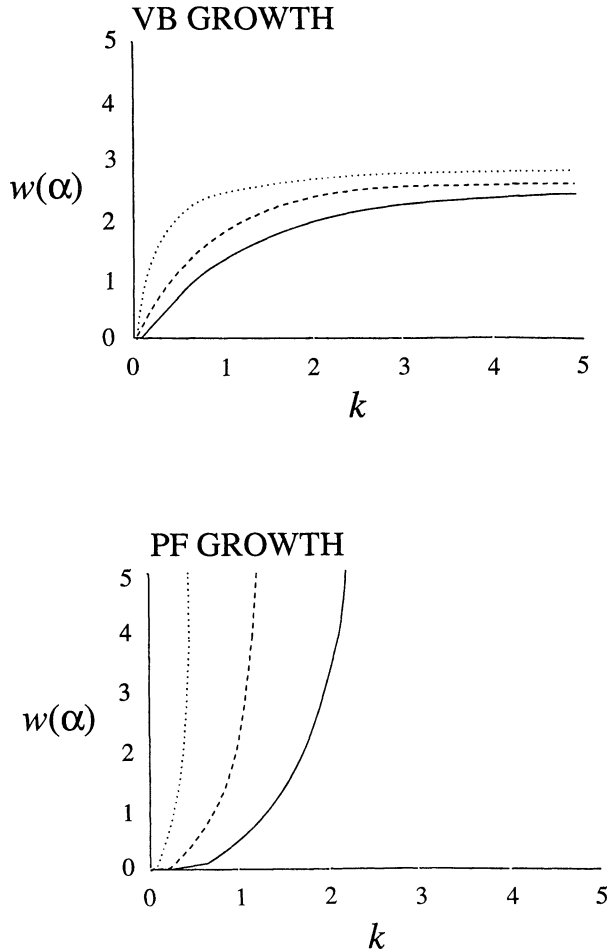
VB GROWTH

PF GROWTH

Fig. 2.—The relationship between predicted size at maturity and the growth rate parameter, k, under both VB and PF growth. *Dotted line, $j = 0.2$; dashed line, $j = 0.5$; solid line, $j = 0.9$.* The VB function uses $w_\infty = 10$. Under VB growth, as habitat productivity increases, the predicted size at maturity increases but reaches a maximum. Under PF growth, as habitat productivity increases, the predicted size at maturity increases dramatically and has no upper limit.

and

$$\text{PF:} \quad w(\alpha) = \left(\frac{2k}{3j}\right)^3.$$

These expressions reveal that under PF growth, increasing the growth rate parameter allows an individual to mature later at a much larger size (and fecundity), but under VB growth there is maximum attainable size. Indeed, it follows from the optimality condition (4) that for any S-shaped prematurity growth trajectory,

the optimal age at maturity must occur before the trajectory begins to plateau (i.e., the inflection point). To see this, note that fecundity, $m(\alpha)$, is proportional to the rate of availability of surplus resources, and under determinate growth this is simply dw/dt evaluated at $t = \alpha$. Consequently, equation (4) requires that $d^2w/dt^2 > 0$, which implies that the optimal age at maturity must occur where the growth trajectory is concave up. Thus, with an S-shaped prematurity equation, the inflection point acts as a definite ceiling on the optimal age at maturity.

Using r as the fitness measure also produces different predictions. Numerical solutions under VB and PF growth show that, although the α versus k relationship has the same qualitative shape, large quantitative differences still result. This point can also be intuited. When r is used as the fitness measure, there is an additional source of decreasing benefit to postponing reproduction. In an increasing population, a premium is placed on early reproduction because this will increase r. Regardless of the growth trajectory used, this effect will be present if the population size is increasing.

Stearns (1992, pp. 147–148) noticed similar discrepancies in the α versus k relationship when comparing a model using PF growth (Kozłowski and Wiegert 1987) with one using VB growth (Stearns and Koella 1986). However, because the two models also used different fitness measures (R_0 vs. r), he suggested this to be the cause. Our results suggest that this explanation is not complete. Predicted age at maturity decreases as k increases only when there is a decreasing benefit to postponing reproduction. If r is the fitness measure, this decrease results from an increasing population size. However, the use of VB growth also results in a decrease in the value of postponing maturity. The Stearns and Koella model confounds both of these factors, while the Kozłowski and Wiegert model incorporates neither.

In advocating the use of an equation such as the PF for growth before maturity, we do not suggest that a plateau in prereproductive growth never occurs. Indeed, if prereproductive growth is extended indefinitely, it must eventually asymptote because of physical constraints. If such an effect is believed relevant, then it should be explicitly included in the model. The prior considerations, however, reveal how important it is to have good information about where the inflection point should be on such a curve.

INDETERMINATE GROWTH

In the original formulation of the VB equation by Pütter (1920; as cited in Ursin 1967) and von Bertalanffy (1957, 1960; see also Ricker 1979; Reiss 1989), growth rate was envisioned to result from the difference between catabolism (tissue breakdown) and anabolism (tissue synthesis). No explicit account was made of a change in energy allocation at maturity because interest centered on understanding growth through a consideration of total energy input and output. Thus, the VB equation embodies prereproductive growth, age at maturity, and postmaturity growth all in one composite description. Consequently, using the VB equation alone in an optimization model under indeterminate growth implicitly assumes that the change in energy allocation at maturity does not affect postmaturity

growth; the postmaturity growth curve does not change when α is varied in the optimization procedure.

What is required for age at maturity models is an equation that is faithful to the growth processes that occur under different choices of this age. Therefore, because the PF appears to be a reasonable description of prematurity growth, we consider how it might be extended for use as the postmaturity trajectory when modeling indeterminate growth. To remain consistent with both the empirical evidence and determinate growth models, we suggest using a power function for prematurity growth but then employing an exponential decline in resource allocation to growth after maturity. We note that this is merely intended as a suitable description of indeterminate growth that is consistent with the life-history model in which it will be used. We assume that the organism can acquire resources at a rate proportional to a power function of its size as before. Growth rate and fecundity are given by

$$\frac{dw}{dt} = ukw^{2/3} \tag{10}$$

and

$$m = (1 - u)kw^{2/3},$$

respectively (Kozłowski and Wiegert 1986; Kozłowski 1992). Here u is simply the proportion of resources devoted to growth. It equals 1 before maturity and $\exp(-[t - \alpha]h)$ after maturity, where h scales the rate of exponential decline.

The solution to the prematurity growth equation (10), with $u = 1$, is the same as before (given by eq. [6]), and the solution to the postmaturity growth equation (10), with $u = \exp(-[t - \alpha]h)$, is

$$w(t^*) = \left[\frac{1}{3}\frac{k}{h}(1 - e^{-ht^*}) + w(\alpha)^{1/3}\right]^3$$

or, by using equation (6) evaluated at α,

$$w(t^*) = \left[\frac{1}{3}k\left(\frac{1 - e^{-ht^*}}{h} + \alpha\right) + w_0^{1/3}\right]^3, \tag{11}$$

where $t^* = t - \alpha$ is the time since maturity. Equation (11) specifies a family of postmaturity trajectories indexed by α. A growth trajectory constructed by piecing together equations (6) and (11) at α has a sigmoidal shape and the favorable property that it is still smooth (differentiable) at α. The parameter h scales the rate of exponential decline in postmaturity resources devoted to growth and thus determines how quickly the growth trajectory plateaus after maturity (fig. 3). Thus, changing age at maturity also changes final size (and fecundity), but the rate of growth plateau after maturity can be varied independently.

CONCLUSION

The idea of employing a logically sound growth relation that is consistent with the life-history model being used is not new. Roff (1983, 1984, 1992, pp. 204–207)
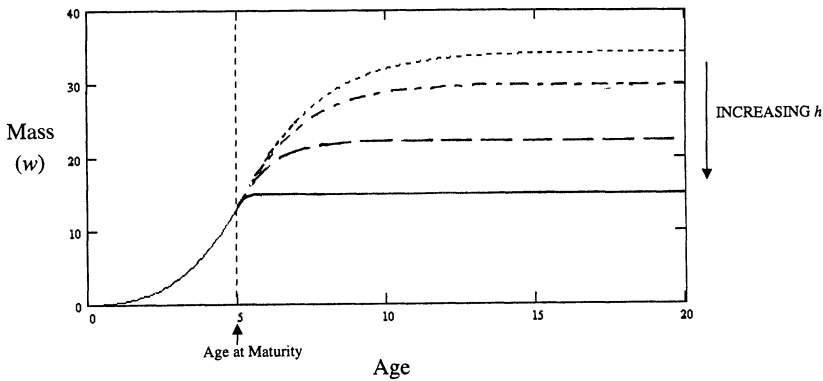
Fig. 3.—A plot of the indeterminate growth equation presented in the text. Here $\alpha = 5$, and a sequence of values for the constant h are shown. The constant h determines the rate of postmaturational growth plateau.

and Charnov (1993, pp. 85–86, chap. 8) have suggested that a model based on resource allocation is preferable to one based on VB growth. Similarly, Kozłowski and Wiegert (1986; see also Kozłowski 1992) have advocated the use of resource allocation and power function relations such as equations (3) and (10) in life-history theory. The implications of not using such growth relations, however, have not previously been investigated. Others have voiced concern over the simplicity of many current life-history models and have questioned why such models should match observation so well (Bernardo 1993; Charlesworth 1994, p. 255).

We suggest that, for models of age at maturity using VB growth, concern is warranted on two accounts. First, using the VB equation under indeterminate growth fails to acknowledge the change in resource allocation at maturity; growth is not specified by two equations. Second, because the VB equation is asymptotic, using it for prereproductive growth often does not accurately reflect the trajectory of an organism that is devoting all energy to growth. The results we present demonstrate that even in the simplest models, using a more suitable growth equation can substantially alter predictions.

Most determinate growth models of age and size at maturity *do* employ separate equations for pre- and postmaturity growth. This is probably because of the simplicity of the situation; it is natural to use a family of constant functions after maturity because determinate growers stop growing. Obtaining a suitable family of postmaturity equations under indeterminate growth, however, presents a greater problem. Most approaches to modeling maturity under indeterminate growth that do account for resource allocation decisions involve some type of dynamic optimization (e.g., control theory, dynamic programming). Because these methods are conceptually and computationally more difficult, the approach suggested here offers an advantage. Although equation (11) has a largely descriptive motivation, it reduces such dynamic optimization procedures to a simple, two-variable optimization problem.

It is also notable that incorporating a switch at maturity in the growth rate

function does not necessarily produce a "corner" in the size-versus-age trajectory. For example, our use of an exponential function for u in equation (10) results in a smooth growth trajectory (fig. 3). Indeed, any specification for u that makes growth rate a continuous function of size will have this property. We also note that use of an exponential function in equation (10) gives the postmaturity trajectory a particularly simple form; it is just the prematurity trajectory with a different time parameter (compare eqq. [11] and [6]).

NOTE ADDED IN PROOF

A recent article by Kozłowski (1996) demonstrates that dynamic optimization models based on resource allocation decisions often generate *lifetime* growth curves that are well approximated by the von Bertalanffy equation. His models have VB growth as a prediction (rather than an assumption) and might explain why the VB equation is often a good description of lifetime growth.

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APPENDIX

TABLE A1

A LIST OF NOTATION

Variable	Definition
w	Body mass
w_0	Initial body mass (at independence)
w_∞	Asymptomatic body mass for VB equation
m	Fecundity
x	Age
α	Age at maturity
u	Proportion of resources devoted to growth
j	Juvenile mortality rate
a	Adult mortality rate
p	Initial burst of mortality before constant juvenile mortality rate
k	Growth rate parameter, presumably a function of environmental quality
r	Intrinsic rate of increase
R_0	Lifetime reproductive output

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