Developmental Thresholds and the Evolution of Reaction Norms for Age and Size at Life-History Transitions

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ABSTRACT: It is quite common in studies of life-history plasticity to find a negative relationship between the age at which various life-history transitions occur and the growth conditions under which individuals develop. In particular, high growth typically results in earlier transitions, often at a larger size. Here, we use a relatively general optimization model for age and size at life-history transitions to argue that current life-history theory cannot adequately explain these results. Specifically, most such theory requires key assumptions that are unlikely to be generally met. This suggests that some important component of the biology of many organisms must be missing from many of the models in life-history theory. We suggest that this missing component might be the phenomenon of developmental thresholds. There are at least two different types of developmental thresholds possible, and we incorporate these into our general optimality model to demonstrate how they can cause a negative relationship between growth conditions and age at a transition. If developmental thresholds are common throughout taxa, then this might explain the empirical results. Our model formulation and analysis also formalizes the popular Wilbur-Collins hypothesis for age and size at metamorphosis in amphibians. The results demonstrate that optimal combinations of age and size, and the slope of the reaction norm connecting them, depend on the existence and type of threshold assumed. Our results also provide an evolutionary framework that can be used to view the data and many of the proximate submodels derived from the Wilbur-Collins hypothesis.

Keywords: maturity, metamorphosis, plasticity, developmental thresholds, Wilbur-Collins model.

The ontogeny of most organisms is marked by a series of transitions between stages (e.g., hatch, metamorphosis, maturation), each of which can be characterized by the age and size at which it occurs. One of the principle goals of life-history theory is to explain intra- and interspecific patterns in the age and size of individuals at such transitions. Explanations are often sought through a consideration of potential trade-offs between making the transition earlier and at a smaller size versus doing so later at a larger size. For example, an earlier age at maturity will increase the probability of surviving to reproductive age, but it might do so at a cost of reduced size and, thereby, fecundity (Roff 1992; Stearns 1992; Charlesworth 1994). Similar arguments involving trade-offs have been constructed to explain other life-history transitions such as metamorphosis (e.g., Werner 1989).

One of the more conspicuous features of life-history transitions is that the combinations of age and size at which they occur often change plastically in response to environmental conditions (Roff 1992; Stearns 1992; Nylin 1998). Temperature (Atkinson 1994), growth rate (Berrigan and Charnov 1994), risk of predation (Crowl and Covich 1990; Peckarsky et al. 1993; Ball and Baker 1996), and time of season (Nylin et al. 1989; Blanckenhorn 1998; Johansson and Rowe 1999; Johansson et al. 2001) can all have important influences on the age and size at maturity. Most theoretical work that attempts to explain the evolution of these reaction norms in life-history transitions does so by considering how the form of the trade-off between an early versus a late transition changes with environmental conditions (e.g., Stearns and Koella 1986; Rowe and Ludwig 1991; Berrigan and Koella 1994; Sibly and Atkinson 1994).

Perhaps the most studied reaction norm in the life-history literature is the response of age and size at a transition to changes in growth rate. For example, there are many studies on the effects of food level on age and size at metamorphosis (or maturity) in a variety of taxa (reviews in Berrigan and Charnov 1994; Twombly 1996; Hentschel and Emlet 2000; Morey and Reznick 2000). A priori, there is no obvious reason to expect any regularity in response across different species. Indeed, of the several optimization models that have been developed, any pattern of response by both age and size appears to be possible

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given the appropriate specific assumptions (e.g., Stearns and Koella 1986; Stearns 1992; Berrigan and Koella 1994). Yet, the vast majority of taxa examined to date do exhibit a surprising regularity. In particular, most species display a reduced age at maturity or metamorphosis with increased growth conditions (reviews in Stearns and Koella 1986; Berrigan and Charnov 1994; Gotthard and Nylin 1995). Moreover, this is often accompanied by a larger size at the transition.

The regularity of this form of reaction norm, across a relatively broad range of taxa, suggests that some general factor, common to most species, might be responsible. A first reasonable inference might be that the particular assumptions of the subset of models that predict such a reaction norm are widely applicable. Indeed, much of the empirical literature has often been interpreted as a verification of these assumptions (e.g., Stearns and Koella 1986; Roff 1992; Stearns 1992). A closer examination of these models, however, reveals an interesting pattern. The vast majority of models that consider the evolution of age at maturity under different fixed growth conditions make at least one of the following two assumptions (see Abrams and Rowe 1996 and Abrams et al. 1996 for models with flexible growth). First, growth is described by the von Bertalanffy (VB) equation (von Bertalanffy 1957), and second, the appropriate measure of fitness is the intrinsic rate of increase (e.g., Stearns and Koella 1986; Sibly and Atkinson 1994). The first assumption has been questioned on a number of grounds (Kozlowski 1996; Day and Taylor 1997; Czarnoleski and Kozlowski 1998; T. J. Kawecki, D. Berrigan, and S. Carrol, unpublished manuscript). Although the VB equation is often a good descriptor of lifetime growth patterns, such patterns arise, in part, from the timing of resource allocation events related to maturation. Thus, such growth patterns should be derived as predictions rather than assumed in optimality models (e.g., Kozlowski 1996). Moreover, prereproductive growth in many organisms does not match the VB equation (see references in Day and Taylor 1997), and therefore additional factors must be operating, at least some of the time, to explain the observed reaction norms. With regard to the second assumption, the intrinsic rate of increase is not the appropriate fitness measure under many situations (Brommer 2000), and therefore, again, this assumption cannot provide the general explanation that we seek.

How then are we to explain this nearly ubiquitous pattern? We suggest that one missing component might be the phenomenon of developmental thresholds. A developmental threshold is simply a minimum size or condition that must be attained before a life-history transition can occur. There are currently two optimality models in the literature that do incorporate developmental thresholds. Rowe et al. (1994) supposed that individuals must reach some threshold condition before reproduction is possible, and T. J. Kawecki, D. Berrigan, and S. Carrol (unpublished manuscript) suppose that individuals lose a constant amount of mass after reaching maturity. This effectively imposes a threshold mass that must be reached before reproduction is possible because mass at maturation would have to exceed this constant. These two models differ in several other assumptions, however, and neither article examined how the presence of a threshold size or condition per se influences the model's predictions.

In fact, the vast majority of research on thresholds and their effect on age and size at life-history transitions has been motivated by a verbal model proposed by Wilbur and Collins (1973). Their model postulates a size threshold for the physiological ability to metamorphose, and it supposes that an organism can delay metamorphosis further after reaching this threshold in an adaptive manner in response to growth conditions. When growth conditions are good, Wilbur and Collins argued, there will be a long delay in metamorphosis; but when conditions are poor, individuals will metamorphose quickly after reaching the threshold. There have been a remarkable number of empirical studies aimed at testing elements of the Wilbur-Collins framework, including experiments with insects (Bradshaw and Johnson 1995), crustaceans (Ebert 1994; Twombly 1996), fish (Reznick 1990), and amphibians (Travis 1984; Alford and Harris 1988; Hensley 1993; Leips and Travis 1994; Tejedo and Reques 1994; Audo et al. 1995; Beck 1997; Morey and Reznick 2000). The results of these studies are somewhat mixed: some aspects of the model appear to be supported while others do not. For example, late increases in food supply often have no affect on development rate, despite the fact that Wilbur and Collins would predict a delay in the time to metamorphosis (reviewed in Morey and Reznick 2000). These mixed results have led many authors to alter the Wilbur-Collins framework slightly to accommodate their findings. This has resulted in the proliferation of several submodels, most of which are derived from the Wilbur-Collins framework (e.g., Hensley 1993; Leips and Travis 1994; Bradshaw and Johnson 1995; Twombly 1996; Hentschel 1999). For example, the apparent insensitivity of development rate in later-stage larval amphibians to food level has led to the hypothesis that development is fixed after a certain stage (e.g., Leips and Travis 1994). Most of these submodels are directed toward providing a proximate explanation for apparent deviations from the original verbal model of Wilbur and Collins rather than toward an ultimate (i.e., evolutionary) explanation. Notably, a similar threshold hypothesis was proposed earlier for *Drosophila melanogaster* (Bakker 1959) and has similarly been the subject of some empirical tests and modification (Gebhardt and Stearns 1988; Moed et al. 1999).

Because the Wilbur-Collins model is verbal (as is Bakker 1959), however, several of its features remain unclear. First, it is not clear what the overall pattern of plasticity is expected to be when growth conditions are enhanced. For example, high food levels mean that individuals will reach the threshold sooner but that they will wait longer after the threshold before undergoing the transition. Since these two effects work in opposition it is not clear whether the overall age at transition will increase or decrease. Second, Wilbur and Collins supposed that individuals would do best by delaying the transition once the threshold is reached if growth conditions are good, but they did not provide a clear argument for why this might be the case. A more formal treatment is required to determine whether or not this is in fact the optimal strategy.

In this article, we suggest that current life-history theory does not yet offer a satisfactory explanation for the common observation that age at maturity (or metamorphosis) is accelerated under high-growth conditions. We begin with a quite general model that demonstrates how, in the absence of assumptions about VB growth or the use of the intrinsic growth rate as a measure of fitness, age at maturity is predicted to increase with growth conditions. This prediction is opposite to the pattern found in nature. We then incorporate a developmental threshold into this general model in two different ways and explore its effect on predictions about optimal life-history transitions. Our analysis demonstrates that the addition of thresholds can reverse the predictions of the simple model and bring them into accord with the empirical observations. To the extent that developmental thresholds are common throughout taxa, this then provides one potential explanation for observed reaction norms. Finally, although it is not our purpose to review the literature directed toward testing the Wilbur and Collins (1973) model, because we incidentally formalize the ideas of Wilbur and Collins, we briefly compare earlier results and interpretations with our model assumptions and predictions.

The General Optimality Model

Most of the exposition is phrased in terms of age at maturity, but our results might be applied to other life-history transitions as well. We seek the age at maturity that maximizes an individual's lifetime reproductive success. Although some forms of density dependence can lead an evolutionarily stable life history that does not maximize lifetime reproductive success, we use lifetime reproductive success for two reasons. First, it is a simple and intuitive measure, and there are many forms of density dependence for which it is appropriate (Charnov 1990; Mylius and Diekmann 1995; Pásztor et al. 1996; Brommer 2000). Second, it represents a worst-case scenario for making the "correct" predictions. In particular, use of the intrinsic rate of increase as a fitness measure can, in itself, result in a negative relationship between age at maturity and growth conditions (as seen in the empirical data). Because this is certainly not a universally applicable fitness measure, however, it is necessary to construct a model without this assumption to determine the factors that can give rise to this prediction more generally.

Denoting size (or condition) at age t by $w(t)$, we suppose that growth occurs according to a differential equation of the form

$$\frac{dw}{dt} = f(w),$$
$$w(0) = w_i, \tag{1}$$

where w_i is the initial size. For instance, power function growth would have $f(w) = kw^b$, where $0 < b < 1$ and k is a constant, whereas linear growth would have $f(w) = kt$. We define an environment that increases growth conditions as one that results in the per unit or relative growth rate of individuals (i.e., $(dw/dt)/w$) increasing at all ages. Denoting this per unit growth rate by g and letting k be a parameter that represents growth conditions (with larger k corresponding to better growth conditions), this definition implies

$$\frac{\partial g(t, k)}{\partial k} > 0 \tag{2}$$

at all ages, t. Note that power function growth mentioned above satisfies this definition, as does linear growth, but the growth parameter usually employed in models using the von Bertalanffy equation does not (e.g., see Day and Taylor 1997).

We write the lifetime reproductive output of an individual with age at maturity t as

$$F(w(t))V(t), \tag{3}$$

where $F(w(t))$ is the expected lifetime reproductive output of an individual of size $w(t)$ at maturity and where $V(t)$ is the probability of surviving to age t. In the more general treatment of the appendix, $V(t)$ simply represents the value of reproducing at age t, which might incorporate the probability of surviving to age t as well as any seasonal change in the value of offspring. Note that for semelparous organisms the definition of F is straightforward and equal to fecundity. If the organism in question is iteroparous, then for simplicity we assume that reproduction occurs continuously in time, and in this case, F will also depend on adult mortality rate. Our results are valid in either case provided

that adult mortality rate is age and size independent. If the above is applied to other life-history transitions (e.g., age at metamorphosis), then F is the expected lifetime reproductive output of an individual at metamorphosis.

Here, for the sake of simplicity we assume that reproductive output, F, is proportional to size (see appendix for more general assumptions). Since $V(t)$ is the probability that the parent survives to maturity, we have $V(t) = e^{-\mu t}$, where μ is a constant, prereproductive mortality rate. From these assumptions, it follows that the optimal age at maturity, t^*, satisfies

$$g(t, k) = \mu \tag{4}$$

with $t = t^*$. The left-hand side of condition (4) gives the benefit that results from postponing maturity by a small increment at age t (which is an increase in size and, therefore, fecundity), and the right-hand side gives the cost (which is mortality). At early ages we expect the left-hand side to be larger than the right because a small delay in reproduction results in a large proportional increase in fecundity when individuals are small. At late ages, we expect the reverse because the proportional gain in fecundity from delaying reproduction is expected to be quite small for large individuals. It is optimal to mature when the two sides exactly balance (fig. 1).

To determine how the optimal age at maturity, t^*, changes when growth conditions increase, we implicitly differentiate condition (4) with respect to k, giving

$$\frac{dt^*}{dk} = \frac{-\partial g/\partial k}{\partial g/\partial t}. \tag{5}$$

From the second derivative condition for a maximum, the denominator of equation (5) is negative. Therefore, the optimal age at maturity changes in a direction given by the sign of $\partial g/\partial k$ (see appendix for a more general condition), and from definition (2), this is positive. Thus, age at maturity increases with growth conditions. Graphically, the relative growth rate curve, $g(t, k)$, increases at all ages as growth conditions increase, and therefore the point at which it crosses the mortality rate curve moves to the right (fig. 1). Increasing growth conditions increases the benefit to delaying maturity without altering the cost, thereby favoring a delay. This conclusion remains true if mortality rate decreases with size, if there is a time horizon due to seasonality, or if reproductive output, F, is proportional to some power of size (appendix).

Notice that the above results are valid only if the optimal age at maturity is >0. Mathematically, the analysis assumes that the optimum does not fall on the boundary of permissible ages at maturity. In some situations, however, it can be optimal to mature immediately because the costs on the right-hand side of condition (4) are larger than the benefits on the left-hand side for all ages (fig. 1, curve g_2). In particular, this can occur if growth conditions are low enough or if the mortality rate is high enough. In such cases, equation (5) is not valid, but these conditions are unlikely to be met in nature.

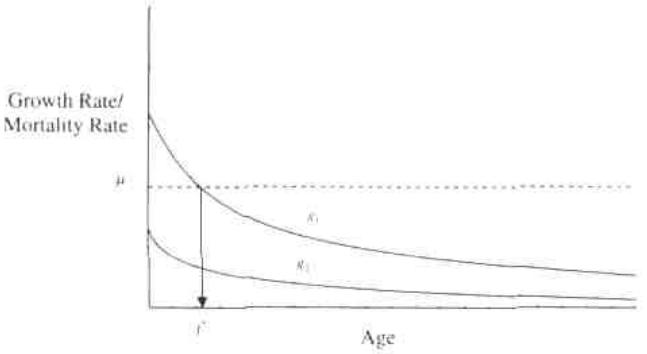

Figure 1: A graphical depiction of optimality condition (4) for two different levels of growth conditions. Curve g_1 is the per unit growth rate for high-growth conditions, whereas curve g_2 is for low-growth conditions. (In general, we expect the per unit growth rate to decline as an individual gets older.) Definition (2) implies that g_1 lies above g_2 at all ages. Dashed line is mortality rate. The costs and benefits balance at the age where the lines intersect. Notice that, for low-growth conditions, the per unit growth rate, g_2, lies below the mortality rate at all ages, and therefore it is optimal to mature immediately (i.e., $t^* = 0$). As growth conditions increase, the per unit growth rate curve moves upward, and therefore the intersection point (i.e., the optimal age at maturity) gets larger.

The Effect of Thresholds

We now determine how including a maturation threshold in the above model alters its predictions. From a mathematical perspective, there are at least two different ways in which a threshold might operate. For each of these, we present an example of the kind of biological mechanism that gives rise to the threshold, but there are undoubtedly other mechanisms that give rise to thresholds that are mathematically identical.

Following the conceptual framework of Wilbur and Collins (1973), it will be useful to decompose the optimal age at maturity, t^*, into the time until the critical size or threshold is reached, t_s, and the optimal time to delay maturity after reaching the threshold, t_d^*, with $t^* = t_s + t_d^*$. If w_s is the threshold size, then t_s is defined by $w(t_s) = w_s$. Only t_d^* can be adjusted adaptively in response to different growth conditions. This conforms to the model of Wilbur and Collins (1973), and it highlights the constraints imposed by a threshold.

Physical Thresholds

The first type of threshold explored occurs if an individual's reproductive potential increases continuously with size (or condition), but this reproductive potential cannot be realized until some critical size is exceeded. This might occur if an individual must reach a critical size before it is physically able to fit any reproductive output (e.g., live offspring or eggs) in its body. Alternatively, it might occur if there is another "state variable" in addition to size (e.g., physiological state) that must reach a critical value before reproduction is possible but that has no effect on fecundity. This then imposes a critical time, t_c, and thereby a critical size, w_c, that must be attained before reproduction can occur.

In either case, optimality condition (4) still gives the age at which the costs and benefits of delaying maturation are balanced. The threshold simply imposes a constraint on the lowest possible age at maturity. Graphically, we illustrate the outcome in the age-size plane by first drawing the reaction norm that would result across a range of growth conditions in the absence of a threshold and then drawing a horizontal line across these growth trajectories at the threshold (fig. 2). Slow-growing individuals that would mature at a small size in the absence of a threshold now must wait until the threshold is reached. Notice that they then mature after the age at which the cost and benefits are balanced because the presence of a threshold forces them to mature beyond that point. Fast-growing individuals that would mature at large sizes in the absence of a threshold are unaffected by its presence (fig. 2).

The results reveal that a physical threshold can cause the optimal age at maturity to decrease as growth conditions increase (fig. 2). In particular, as growth conditions increase, the age at which the threshold is reached (i.e., t_c) decreases. Because this is also the age at maturity for slow-growing individuals (fig. 2), age at maturity for these individuals thereby decreases. Notice, however, that this type of threshold cannot explain observations of an increase in size at transition with growth conditions. Moreover, fast-growing individuals mature at some point after reaching the threshold, and therefore age at maturity increases with an increase in growth conditions for these individuals, in opposition to most empirical evidence (fig. 2).

Overhead Thresholds

In the second type of threshold, an individual's potential fecundity starts from 0 once the threshold is reached and increases thereafter as size or condition increases. This can occur if the amount of resources that an individual has at its disposal is size dependent and if some amount of energy is required simply to become reproductively active, but this energy is not translated into fecundity. Any available resources over and above this overhead cost are then translated into fecundity. This imposes an "overhead" threshold size for reproduction since individuals smaller than this size cannot pay the overhead costs involved with reproducing (let alone pay for any reproductive output).

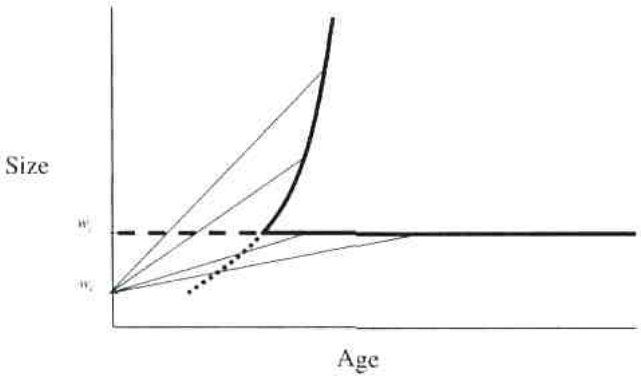

Figure 2: A plot of four hypothetical growth trajectories under a range of growth conditions. Bold curve represents the optimal switching curve (i.e., reaction norm) from growth to reproduction. The horizontal portion results from a lower bound on the size at which reproduction is possible from a physical threshold. Dotted dark curve is the extension of the bold switching curve that would result in the absence of a physical threshold. In the absence of a physical threshold, age at maturity increases with growth conditions. The horizontal line representing the threshold size is dashed in the portion of the age-size plane where the threshold has no effect (i.e., for high-growth conditions). Low enough growth conditions result in maturation immediately on reaching the threshold (and at a constant size). Larger growth rates exhibit a pattern of increased age at maturity with growth conditions.

Mathematically, we can specify an overhead threshold by supposing that reproductive output is proportional to size minus the threshold size, w_c; that is,

$$F \propto w(t) - w_c. \tag{6}$$

Therefore, the optimality condition (4) becomes

$$\frac{w(t)}{w(t) - w_c} g(t, k) = \mu \tag{7}$$

at $t = t^*$. Similar results can be obtained if fecundity has the form $F \propto [w(t) - w_c]^\alpha$ or $F \propto w(t)^\alpha - w_c^\beta$ (an example of the latter is considered below). Again, the left-hand side of equation (7) represents the benefit of postponing maturation, and the right-hand side represents the cost. The difference between this condition and condition (4) is the presence of w_c in the denominator of the left-hand side.

To determine how the optimal age at maturity changes when growth conditions increase, it is easiest to consider

the effect of increasing k on t_x and t_u^* separately. An increase in k will decrease the time until the threshold is reached just as with a physical threshold. To determine how t_u^* changes, we note that an individual that has just reached the threshold at age t_x faces the same decision as one that starts at size w_x at age 0. Therefore, t_u^* must satisfy condition (7), where $w(t)$ is determined by equation (1) but with $w(0) = w_x$. At $t_u = 0$, the denominator on the left-hand side of condition (7) is 0, and thus the benefit to delaying maturity past the time at which the threshold is reached is infinite; fecundity starts from 0 at the threshold, and therefore it always pays to delay maturity past the threshold to some extent.

A small increase in growth conditions, k, therefore changes t_u^* according to

$$\frac{dt_u^*}{dk} = -\frac{(\partial l/\partial k)[wg/(w - w_x)]}{\partial g/\partial t}. \tag{8}$$

Again, $\partial g/\partial t < 0$ because we are dealing with a maximum, and therefore the direction in which t_u^* changes as growth conditions increase is given by the sign of

$$\frac{\partial}{\partial k}\left(\frac{g}{\rho}\right), \tag{9}$$

where we have defined $\rho = (w - w_x)/w$ as the ratio of the above-threshold size to the actual size. Figuratively speaking, this can be thought of as the proportion of an individual's size that "counts" toward actual reproductive output. We have $\rho = 1$ if there is no overhead threshold, but with a threshold, $\rho < 1$, and this increases the benefit to postponing maturity. Also notice that as an individual grows, ρ eventually approaches unity; as size increases beyond the threshold, it is "felt" less and less. Also note that, for any given age, ρ increases as growth conditions, k, increase. Again, figuratively speaking, for any given age, a greater proportion of an individual's size counts toward reproductive output if it was raised under good growth conditions than if it was raised under poor growth conditions. The reason is simply that both will have the same threshold, but the individual raised under good conditions will be larger. Notice, though, that an individual's per unit growth rate, g, at this age will also increase with growth conditions, and therefore the sign of expression (9) will be determined by which of these has the biggest increase. As a result, for some growth models, t_u^* will increase with growth conditions, and under others, it will decrease. This is in marked contrast to physical thresholds in which t_u^* always increases with growth conditions if it changes at all.

This simple result demonstrates that the presence of an overhead threshold can cause an overall negative relationship between age at maturity and growth conditions in two different ways. First, if the optimal length of time to delay maturity after the threshold is reached (i.e., t_u^*) decreases with growth conditions (i.e., $dt_u^*/dk < 0$), then the overall age at maturity will certainly decrease because the time it takes to reach the threshold (i.e., t_x) decreases with growth conditions as well (i.e., $dt_x/dk < 0$). Second, even if t_u^* increases with growth conditions (as Wilbur and Collins [1973] supposed), then the overall age at maturity can still decrease if the decrease in t_x more than compensates. In the examples that follow, size at maturity also increases with growth conditions, although it is conceivable that a growth model could be chosen so that the opposite occurs.

Examples

To illustrate the above results, we consider two examples of overhead thresholds. The first uses linear growth; and the second, power function growth. Under linear growth we have $w(t) = w_i + kt$, and we assume that F is given by equation (6). In this case, optimality condition (7) solves to give

$$t^* = \frac{1}{\mu} + \frac{w_x - w_i}{k}. \tag{10}$$

This can be decomposed into the two components, $t_x = (w_x - w_i)/k$ and $t_u^* = 1/\mu$, which represent the time to reach the threshold and the optimal delay thereafter. Equation (10) shows that, in this example, age at maturity always decreases as growth conditions increase. The analogous model without a threshold is obtained by setting $w_x = 0$ in equation (10), which demonstrates that the presence of an overhead threshold is critical in reversing the prediction for how optimal age at maturity responds to growth conditions.

For power function growth, size as a function of age is given by

$$w(t) = [k(1 - b)t + w_i^{1-b}]^{1/(1-b)}. \tag{11}$$

As do many authors using power function growth, we assume that the amount of energy available for reproduction at age t is proportional to the size at that age raised to the power b (T. J. Kawecki, D. Berrigan, and S. Carrol, unpublished manuscript). Therefore, if there is a threshold level of energy that is required to pay the overhead costs of reproduction, we have $F \propto w(t)^b - w_x^b$, where w_x is the size that provides this threshold level of energy. With this formulation, the optimal age at maturity must be obtained numerically.

As with linear growth, an overhead threshold can result

in age at maturity decreasing as growth conditions increase. The top two panels of figure 3 (fig. 3*a*, 3*b*) demonstrate that as the threshold size decreases the reaction norm becomes more L-shaped. In fact, as the threshold becomes even smaller (fig. 3*c*), the curve bends further, and then has a slightly positive slope for high growth rates. This is expected since, in the extreme case where there is no threshold, we expect a positive relationship between age at maturity and growth conditions. We note that, in this example, the length of the postthreshold delay until the transition increases with growth conditions, but the decrease in the time until the threshold is reached more than compensates for this. Interestingly, if the exponent, b, is $<1/2$, then the length of the postthreshold delay actually decreases with an increase in growth conditions. Most evidence suggests that $b \approx 2/3$ to $3/4$ for power function growth, however, and therefore this case might be of less interest.

Predictions for Food Manipulation Experiments

Many studies, motivated by Wilbur and Collins (1973), have been conducted to look for maturation (or metamorphosis) thresholds as well as to explore how individuals' developmental programs respond to altered growth conditions (reviewed in Twombly 1996; Hentschel and Emlet 2000; Morey and Reznick 2000). One typical approach (following Alford and Harris 1988) is to alter growth conditions at various stages during an individual's development and then to examine how the age and size at maturity of these individuals compares with those whose growth conditions have remained constant (e.g., fig. 1 in Twombly 1996). Our formal model presented above provides an optimality framework within which we can conduct similar manipulations and compare them to results obtained from these previous experiments.

We focus solely on a model of an "overhead" threshold because physical thresholds cannot explain why size at the transition increases with growth conditions (in addition to age decreasing). We imagine that an experiment is conducted in which individuals are kept under either high- or low-growth conditions (H and L, respectively) throughout development. From the above model, we predict that high-growth individuals will mature earlier and at a larger size than low-growth individuals. This result is in accord with the most common empirical pattern for age and size at amphibian metamorphosis (Morey and Reznick 2000) and for maturation in many other taxa (Berrigan and Charnov 1994). We then need to examine the model's predictions when some high-growth individuals are switched to low growth at various stages of development (and vice versa). Experimenters have typically switched food levels at various stages, in an attempt to identify

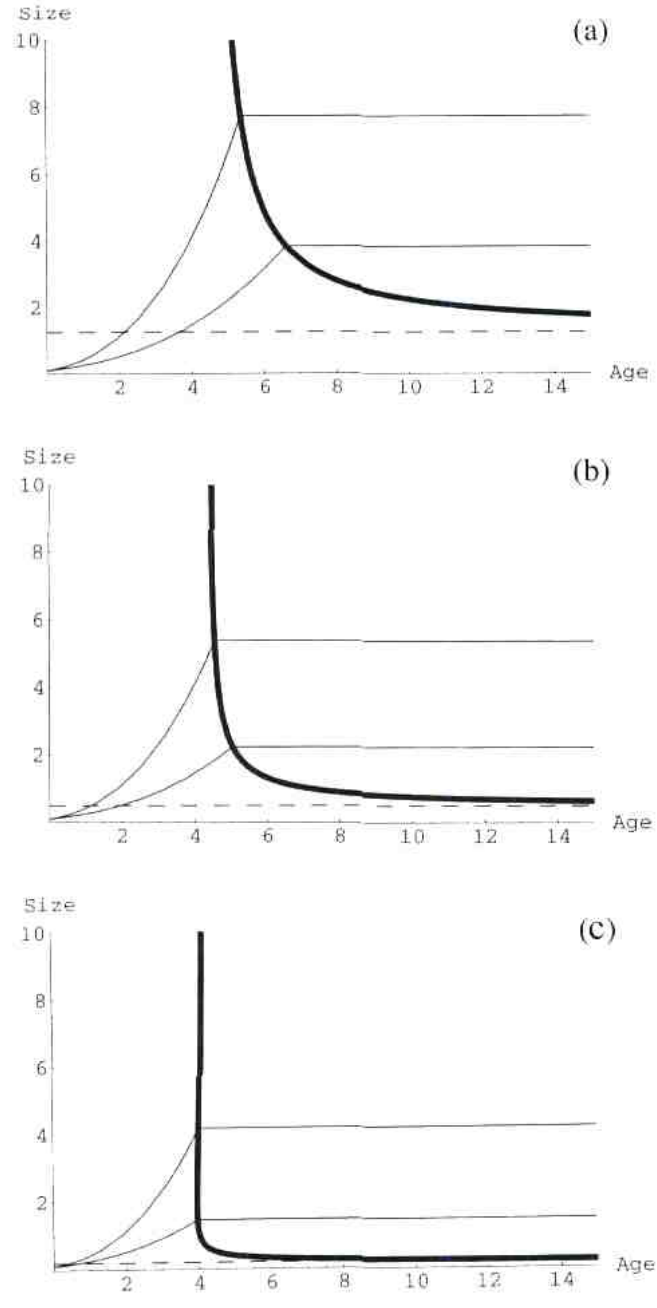

Figure 3: An example of the growth trajectories under two different growth conditions for power function growth and with an overhead threshold. Bold curves are the resulting switching curves (i.e., reaction norms). Dashed line is the threshold size. $b = 0.66$, $\alpha = 0.86$, $w_0 = 0.1$, $\beta = 1$, $\mu = 0.4$, $k = 0.5$, and $k = 0.85$ in *a*–*c*. *a*, $w_1 = 1.25$. *b*, $w_1 = 0.5$. *c*, $w_1 = 0.2$.

periods when development rate is and is not sensitive to growth conditions and to test the Wilbur and Collins (1973) prediction that low-growth conditions after the threshold will accelerate development (Travis 1984; Alford and Harris 1988; Hensley 1993; Ebert 1994; Leips and

Travis 1994; Tejedo and Reques 1994; Audo et al. 1995; Bradshaw and Johnson 1995; Twombly 1996; Beck 1997; Hentschel and Emlet 2000; Morey and Reznick 2000). We mimic such a manipulation with our model.

Consider a group of individuals that start out under high-growth conditions. If, at size $\hat{w}$, we switch half of these individuals to the low-growth treatment, what pattern of maturation do we expect between these two treatments (i.e., between HH and HL)? This question can be answered most easily by noting that, as far as the model's predictions are concerned, this experiment is equivalent to one in which we start with individuals of size $\hat{w}$ and simply initiate and maintain a high- and low-growth treatment for the remainder of development. Therefore, to predict what will happen in such experiments, we need only consider a hypothetical experiment in which there are two growth treatments and in which groups of individuals are started in the experiment at different initial sizes (fig. 4*a*).

The results presented earlier demonstrate that a large enough threshold causes a negative relationship between age at the transition and growth conditions. From the perspective of our hypothetical experiment, then, an alternative way to phrase this is that if individuals start out well below the threshold, then high-growth individuals will go through the transition earlier and at a larger size than low-growth individuals. Of course, because it is the presence of the threshold that causes this relationship, if individuals start out far enough above the threshold, then the reverse pattern is expected (fig. 4*a*). Therefore, as the starting size of an individual increases, the model predicts that there will come a point at which both high- and low-growth conditions result in the same age at transition, though high-growth conditions will give a larger size. Further increases in initial size will then given a positive relationship between growth conditions and age at transition (fig. 4). As a result, we can further conclude that if we instead switched the growth treatment of individuals at various stages during development, then we would expect a shift from a negative relationship between growth conditions and age at transition to one that is positive (fig. 4*b*).

Notice that if the positive relationship that is obtained when growth conditions are switched late in development is very steep, then it might well be indistinguishable from a vertical relationship in an experiment. This would generate a pattern in which development time appears to be fixed after some critical size, even though it is not.

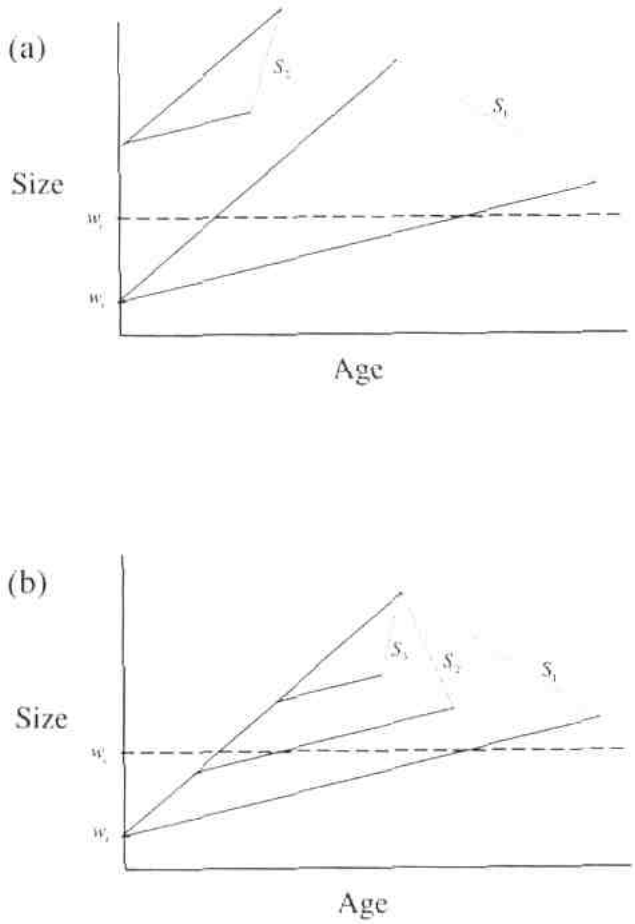

Figure 4: Plots of hypothetical switching curves for different growth conditions. *a*, The switching curves generated by a high- and low-growth treatment where the individuals are started either well below the threshold (S_1) or well above the threshold (S_2). The slope of the curve reverses as initial size increases because it is the threshold that causes a negative slope. *b*, The analogous plot of three switching curves that result from changing some individuals from high-growth conditions to low-growth conditions at different stages of development. Again, the slope of the switching curve changes from negative to positive as the change is made later and later because it is the threshold that causes a negative slope. Analogous plots can be made for experiments that switch individuals from low- to high-growth conditions.

Discussion

One of the most surprising results arising from our models was the difficulty we encountered in attempting to construct a simple model that offered a general explanation for the negative relationship between growth conditions and age at a transition, especially since this relationship is evident in much of the available empirical data (Stearns and Koella 1986; Berrigan and Charnov 1994; Gotthard and Nylin 1995). This discrepancy has apparently gone unnoticed for some time. This is probably because many prior models incorporated von Bertalanffy growth and/or they sought to maximize the intrinsic rate of increase, both of which can result in the observed pattern (Stearns and Koella 1986; Roff 1992; Stearns 1992). Although both assumptions may be valid in some systems, neither is likely to be generally

applicable, and therefore, models relying on these assumptions are unlikely to provide a general explanation. This suggests the need to seek new attributes of development that may be more broadly applicable to explain these empirical patterns. Here, we have demonstrated that developmental thresholds are one such possibility.

Thresholds and the Wilbur-Collins Model

Our work formalizes Wilbur and Collins's (1973) influential verbal model for age and size at metamorphosis and demonstrates that the inclusion of a threshold size can cause the optimal age at transition to decrease with increased growth conditions. Importantly, there are at least two functionally distinct types of thresholds, physical and overhead thresholds, and the distinction is critical in determining the shape of reaction norms. If the threshold merely sets the minimum size at which potential reproductive output can be realized (i.e., a physical threshold), then its effect is felt only by more slow-growing members of a population, and these individuals will appear to have an invariant or constrained size at transition (fig. 2). Fast-growing individuals, on the other hand, will have a reaction norm exactly as predicted in the general model without a threshold. If the threshold sets the minimum size at which an individual can pay the baseline costs of reproduction (i.e., an overhead threshold), then the threshold affects the optimal age and size of all growth classes and can result in a negative relationship between age and size at transition.

In Wilbur and Collins (1973), the time leading up to metamorphosis was split into two phases: pre- and postthreshold. The time spent in the prethreshold phase was completely constrained by growth conditions, whereas the time spent in the postthreshold phase could be adjusted adaptively in response to growth conditions. In particular, Wilbur and Collins assumed the following rule: if conditions are good (e.g., high growth), delay metamorphosis; if conditions are bad, metamorphose early. Yet, the form or even sign of the reaction norm for age and size at metamorphosis cannot readily be predicted by this verbal model because growth conditions have opposing effects on rates of development in the two phases of the life history. For example, slow growth will delay metamorphosis by lengthening the prethreshold phase, but it will accelerate metamorphosis by shortening the postthreshold phase. Our results demonstrate that if an overhead threshold is substantial enough, then the lengthening of the prethreshold phase is greater than the shortening of the postthreshold phase, causing an overall increase in age at metamorphosis (as seen in the data). Of course, the opposite overall pattern might obtain if the overhead threshold is very small.

Empirical Tests of the Model

We have illustrated how our optimality model can be used to make predictions for experiments in which food rations are manipulated at different stages of development. In particular, figure 4 illustrates the model's predictions when the optimal length of the postthreshold phase of development increases with growth conditions (as Wilbur and Collins assumed). Although our analysis with power function growth (assuming an exponent of 2/3 to 3/4) suggests that this is a common expectation, the model reveals that other predictions are also possible given different descriptions of growth. Therefore, although we would take the predictions of figure 4 to be among the most easily tested predictions of the model, failure to match these predictions does not, unfortunately, rule out a general model of developmental thresholds. This indeterminacy means that more definitive tests of the model are not possible without detailed information on the position of the threshold as well as an appropriate mathematical description of growth and the size/fecundity relationship. Of course, the prognosis is as bad or worse for the original Wilbur/Collins model and its derivatives because most of these are purely verbal arguments.

Despite these caveats, it is worth comparing our key predictions from the overhead model with the results from food manipulation experiments on insects, crustaceans, and amphibians, experiments that were conducted with respect to the original Wilbur-Collins framework (Travis 1984; Alford and Harris 1988; Reznick 1990; Hensley 1993; Ebert 1994; Leips and Travis 1994; Tejedo and Reques 1994; Audo et al. 1995; Bradshaw and Johnson 1995; Twombly 1996; Beck 1997; Hentschel and Emlet 2000; Morey and Reznick 2000). First, when larvae are exposed to constant food over the premetamorphic period, low-food larvae typically have delayed age and reduced size at metamorphosis. This prediction is in accord with our model, if the threshold size for metamorphosis is relatively large. Second, most manipulations reveal that size at metamorphosis is sensitive to changes in growth conditions, even if those changes occur late in the larval period. Specifically, larvae moved from high to low food ration will have reduced size compared to those remaining at high food (or vice versa). This observation is also in accord with our model predictions.

Finally, most previous studies have found that development rate of larvae is unaffected by changing food conditions, when those changes occur at later development stages. Recall that the Wilbur-Collins model predicts that development rate will respond to growth conditions after the threshold has passed (presumably at later stages). Specifically, if growth conditions decline, the Wilbur-Collins model predicts that larvae will escape these conditions by

accelerating development. Therefore, this general empirical result is in opposition to the key prediction of the Wilbur-Collins model. Notably, recent experiments by Morey and Reznick (2000) contrast with these earlier results and are in accord with the Wilbur-Collins predictions. Morey and Reznick (2000) found that at all larval stages tested, larvae responded to food deprivation by accelerating development. The lack of a response by late-stage larvae to food manipulations has been interpreted as an indication that development rate is fixed at some early stage and is, therefore, insensitive to conditions after this stage (e.g., Hensley 1993; Leips and Travis 1994; Hentschell 1999). Although fixed development rates may occur in some species, this would offer only a proximate instead of ultimate explanation for the observations.

Our model demonstrates that development rate can either increase or decrease when food is reduced (fig. 4). The direction of the effect depends on the size of the larvae at the time of food reduction relative to the threshold. Manipulations occurring before the threshold will slow development, while those after the threshold will speed development. Therefore, predictions can only be precise if the threshold size is known. Moreover, development may appear to be fixed after some stage simply because the opposing effects of food reductions before and after the threshold will cancel one another out. Unfortunately, only Morey and Reznick (2000) have precisely identified the threshold size and then manipulated food at different distances from that threshold. Finally, as seen in our figure 3, there are large regions of the optimal switch curve where there is little variance in age at maturity, despite the fact that it is unconstrained in our model, and large variance in size at maturity. This would appear, to the experimenter, as a fixed development rate, with flexible size at maturity. This is also the most common pattern found by experimenters (Travis 1984; Alford and Harris 1988; Reznick 1990; Hensley 1993; Ebert 1994; Leips and Travis 1994; Tejedo and Reques 1994; Audo et al. 1995; Bradshaw and Johnson 1995; Twombly 1996; Beck 1997; Hentschel and Emlet 2000).

Environmental Determination of Growth

One of the primary limitations of our model is that it sets growth rate as a function that is fixed by the environment. Although this is typical for life-history models (Roff 1992; Stearns 1992), it is not in accord with our knowledge of the adaptive foraging strategies of individuals. For example, we know that foragers can "choose" a growth rate that balances the often conflicting demands of gaining energy and avoiding predation (Lima and Dill 1990; Lima 1998). Allowing such flexible foraging strategies in life-history models is known to affect and even reverse the sign of predictions for age and size at maturity (Abrams and Rowe 1996; Abrams et al. 1996). Moreover, aspects of the environment other than growth and predation, including time constraints (e.g., Rowe and Ludwig 1991) and temperature (e.g., Berrigan and Charnov 1994) can also act directly and through flexible growth to affect age and size at any life-history transition. We have not included these factors in this treatment, though the framework can easily accommodate these and others. These facts argue that tests of the model need to be limited to carefully controlled growth experiments where other factors, such as predation risk, can be controlled. Finally, we have assumed, in accord with most of the experimental literature, that all variation in growth is environmental rather than genetic. There is, however, no reason to expect that genetic variation in growth rates would change our qualitative predictions.

Defining and Explaining Thresholds

There is currently evidence for developmental thresholds in many systems, including threshold sizes for metamorphosis or maturation in insects, crustaceans, amphibians, and fish (see Roff 1992, p. 126) To date, most thresholds have been defined proximately as physiological constraints, without any clear connection to fitness components. For example, Wilbur and Collins (1973) describe thresholds as endocrinological mechanisms that initiate metamorphosis. There are two problems with such proximate definitions. First, there is no explicit connection between the mechanism underlying the constraint and fitness. Details about these connections are required to understand how the threshold affects optimal age and size for subsequent transitions. We have illustrated two types of thresholds (physical and overhead) that have very different effects, and it is reasonable to assume that there are other possible types of thresholds with other effects on age and size at transitions as well. Therefore, considerable effort should be directed toward understanding the mechanisms underlying particular thresholds under study and the connections between these mechanisms and components of fitness.

Second, the proximate nature of these definitions, ours included, leaves the question of how these thresholds evolve untouched. Recent work by Morey and Reznick (2000; also see references therein) has revealed interspecific variation among toads in the threshold size for metamorphosis. They found that species from more temporary environments had a lower threshold size than those from more permanent habitats. On one level, this makes sense; species in temporary environments are under strong selection to metamorphose rapidly to escape deteriorating environments. However, if thresholds can indeed evolve as this suggests,

what are the evolutionary forces that keep threshold sizes large in permanent habitat species? More generally, what is the advantage of any threshold at all? An answer to this question will require a detailed understanding of the physiological mechanisms underlying the threshold. A promising system for exploration is amphibian metamorphosis, where a great deal of effort has been directed toward understanding developmental mechanisms (reviewed in Denver 1997).

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APPENDIX

A More General Model

Here we consider a more general set of assumptions than those of the text. The optimality condition for the general fitness expression, expression (3), is

$$\frac{dF}{dt} \times \frac{1}{F} = -\frac{dV}{dt} \times \frac{1}{V}, \tag{A1}$$

where V represents the "value" of undergoing the transition at different ages and is a function of age and possibly size as well; that is, $V(t, w(t))$ (examples of possible choices for V are considered below). Implicitly differentiating equation (A1) gives dt^*/dk as

$$\frac{dt^*}{dk} = \frac{-\frac{\partial}{\partial k}\left(\frac{dF/dt}{F} + \frac{dV/dt}{V}\right)}{\frac{\partial}{\partial t}\left(\frac{dF/dt}{F} + \frac{dV/dt}{V}\right)}. \tag{A2}$$

The second-order condition required for t^* to give a maximum implies that the denominator of equation (A2) is negative, and therefore the sign of dt^*/dk is given by the sign of the numerator:

$$\frac{dt^*}{dk} \propto \frac{\partial}{\partial k}\left(\frac{dF/dt}{F} + \frac{dV/dt}{V}\right). \tag{A3}$$

If, as in the text, we assume that $V(t) = e^{-rt}$, then expression (A3) shows that the optimal age at maturity will increase provided that the first term is positive, that is, provided that the per unit rate of increase of reproductive output increases with growth conditions. As a result, even though the per unit growth rate always increases with growth conditions by definition (2), it is nevertheless possible to choose a function, $F(w)$, such that the per unit rate of increase of reproductive output decreases with growth conditions. This requires a very specific form of F, however, and therefore this is unlikely to provide a general explanation for the observed empirical patterns.

Perhaps one of the most reasonable, general choices for F is $F(w) \propto w^{\beta}$. In this case, the right-hand side of expression (A3) becomes

$$\frac{\partial}{\partial k}\left[\beta g(t^*, k) + \frac{dV}{dt} \times \frac{1}{V}\right]. \tag{A4}$$

Under a time constraint, we suppose that $V(t)$ is a function of time only, and therefore expression (A4) has the same sign as $\partial g/\partial k$; the optimal age at maturity always increases with growth conditions as in the text. If mortality rate is size dependent, then the second term in the parentheses of expression (A4) is $-\mu(w(t^*))$, and therefore expression (A4) becomes

$$\beta\frac{\partial g}{\partial k} - \frac{d\mu}{dw} \times \frac{\partial w}{\partial t}. \tag{A5}$$

If mortality rate decreases with increased size, then clearly this will be positive; the optimal age at maturity again increases with growth conditions. If the reverse holds, then whether the optimal age at maturity increases or decreases with growth conditions will depend on the relative magnitude of the terms in expression (A5).

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