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Reaction norms for age and size at maturity in response to temperature: a puzzle for life historians

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Ectotherms mature later at smaller size when growth rates are lowered by reductions in food quality but they mature later at larger sizes when growth rate is lowered by reductions in temperature. We argue that this general pattern has been neglected by life history theorists and suggest that an explanation for these strikingly different responses to two environmental cues might be found by considering correlations between the growth coefficient of the Bertalanffy equation and asymptotic size in a model for the evolution of age and size at maturity.

Recent work on life history traits, and on age and size at maturity in particular, illustrates the power of the natural selection approach as a tool for generating quantitative and testable predictions (Kozlowski 1992, Roff 1992, Stearns 1992, Bernardo 1993, Charnov 1993). One major area of progress has involved the evolution of reaction norms for age and size at maturity. Reaction norms are phenotypic responses to variable environments and are now known, in some cases, to have a genetic basis (e.g., Gebhardt and Stearns 1988, 1993a, b). Several models make predictions about the evolution of the shape and position of these reaction norms as a function of changes in growth, mortality, and fecundity regimes (reviewed in Roff 1992, Stearns 1992). This work has focused explicitly on the consequences of changes in the opportunities for growth caused by reductions in food quality.

In this paper we discuss a puzzle associated with the differing reactions to cues that influence growth, and we suggest that an explanation for the puzzle might involve differential effects of temperature and food quality on correlations between components of a model for individual growth. The puzzle involves the surprisingly different responses of age and size at maturity to changes in temperature versus food quality. We might have predicted that decreased temperature or decreased food quality would have similar effects on age and size at maturity because both factors reduce immature growth rate. However, they do not have similar effects; in fact, the responses of most ectotherms are polar opposites. In most ectotherms, decreased food quality reduces growth rate and typically results in delayed maturation at a *smaller* size. Decreased temperatures also reduce growth rate. However, decreased temperature usually results in delayed maturity at a *larger* size (Ray 1960, Atkinson 1994). We seek complementary evolutionary and physiological explanations for this broad pattern.

Atkinson (1994) reviews over 100 studies of the effects of temperature on age and size at maturity in ectotherms; and in more than 80% of the cases, decreased temperature leads to maturation later at a larger size. Despite the generality of this response, a satisfactory explanation has yet to be produced by life history theory. In fact, the characteristic response to temperature turns out to be remarkably difficult to predict using models for the evolution of age and size at maturity (Sibly and Atkinson 1994; and see below). Optimality models for reaction norms of age and size at maturity assume that individuals assess the opportunities for growth in the environment and then mature at a size that results from the maximization of fitness in the face of one or more specified tradeoffs. The machinery for calculating optimal responses to various environmental conditions is fairly well developed, and these calculations often predict delayed maturity at smaller size when immature growth rate is lowered (e.g., Stearns and Crandall 1984, Stearns and Koella 1986, Perrin and Rubin 1990). Ectotherms, however, mature later and at larger sizes when reared at colder temperatures, even though lower temperatures also reduce growth rates when food and other resources are not limiting (reviewed in Ray 1960, Atkinson 1994). This observation has no generally satisfactory explanation. Most explanations focus on potential performance advantages to larger size under cold conditions (reviewed in Atkinson 1994). Atkinson points out that they are either flawed or suffer from lack of generality.

How can we generate predictions of delayed maturity

Table 1. Summary of models that predict delayed maturity at a larger size when growth rate is reduced. Note that here we only consider models which assume a saturating model for individual growth. These models generally predict delayed maturity at a smaller size when growth rate is reduced if the critical assumptions listed here are relaxed. Additional details in the text.

Source	Critical assumptions
Stearns and Koella (1986)	Juvenile mortality increases rapidly as growth rate decreases. Offspring survivorship increases when adults delay maturity.
Perrin and Rubin (1990)	Fixed life span.
Kindlmann and Dixon 1992	Gonadal growth rate constrained and increasing with temperature.
Berrigan and Koella (1994)	Juvenile mortality increases more than linearly as growth rate increases.
This commentary	Growth coefficient and asymptotic size inversely related as a power function with exponent between 0 and −1.

at larger size when the opportunities for growth are reduced by decreased temperature while still predicting delayed maturity at a smaller size when growth rate is reduced by decreased food quality? At least four quantitative models have been proposed that apply to animals with indeterminate growth (Table 1). We focus on models which assume that individual growth can be described with the Bertalanffy equation because this growth model applies widely to ectotherms such as fish, lizards, shrimps and insects. Here we summarize these four cases, argue that they are unlikely to provide general explanations for ectotherm responses to temperature, and suggest an additional possibility.

Case 1: If juvenile mortality increases strongly as growth rate decreases, Stearns and Koella (1986) predict delayed maturity at a larger size when growth is slow. This counter-intuitive prediction depends on a strong correlation between growth rate and juvenile mortality and an assumed increase in offspring quality as a function of adult age and size at maturity. This explanation seems unlikely because egg size is relatively invariant in many species of ectotherms (e.g. in insects, Hinton 1979). However, females could alter egg quality without altering egg size. **Case 2**: Perrin and Rubin (1990) predict dome shaped reaction norms for age and size at maturity when life span is fixed. These models predict that as growth slows from rapid to intermediate rates, the optimal age and size at maturity increases. At very low growth rates organisms mature earlier than expected because they run out of time. This results from the assumption that life span is fixed. Notice that here and in case three (below) delayed maturity at a larger size is only predicted for one portion of the potential growth trajectory. This may be true in some organisms. For example, Ashburner (1989) points out that *Drosophila* reared at successively lower temperatures first mature later at larger sizes and then later at smaller sizes as temperature decreases. Unfortu-

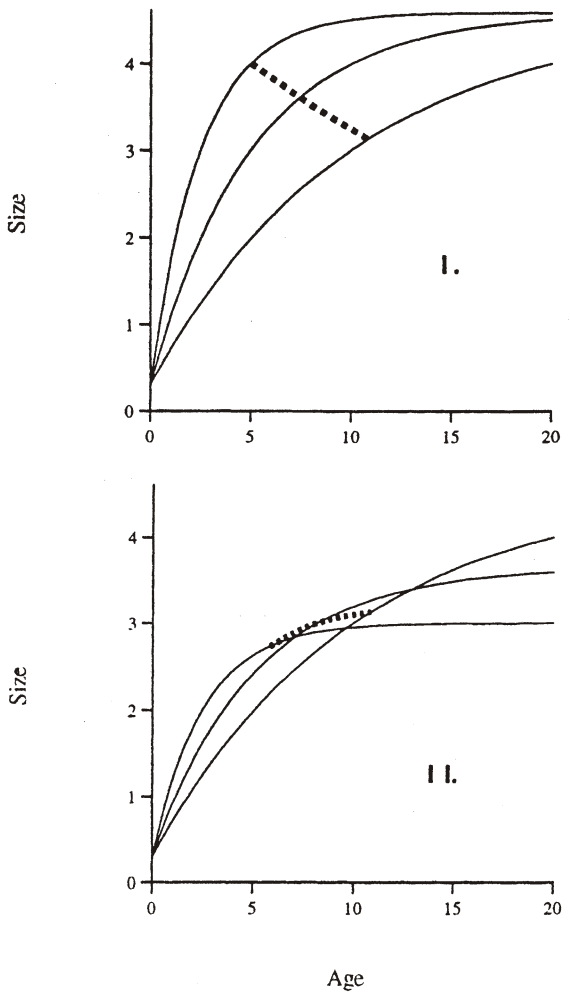

Fig. 1. Hypothetical family of growth curves overlaid by two reaction norms for age and size at maturity. Where a reaction norm intersects a growth curve is the age and size at maturity that maximizes some fitness measure. In the models described here growth ceases at maturity. Otherwise identical models with indeterminate growth behave in a very similar fashion. In case I, the organism matures later but at a *smaller* size as growth rate decreases. In case II, the organism matures later but at a *larger* size as growth rate decreases. These optimal ages and sizes at maturity were obtained (see text) by assuming that selection acts on the age at maturity to maximize the net reproductive rate (R_0). The only cost of delayed maturity is the increased risk of death prior to maturation and the only benefit to delayed maturity is increased fecundity. The cost of delayed maturity is imposed by assuming a constant juvenile mortality rate and the benefit is implemented by assuming a linear increase in fecundity with size. Note that if the asymptotic size decreases as the growth coefficient decreases then this model predicts delayed maturity at a smaller size as the growth coefficient decreases unless juvenile mortality rate increases dramatically when growth rate increases.

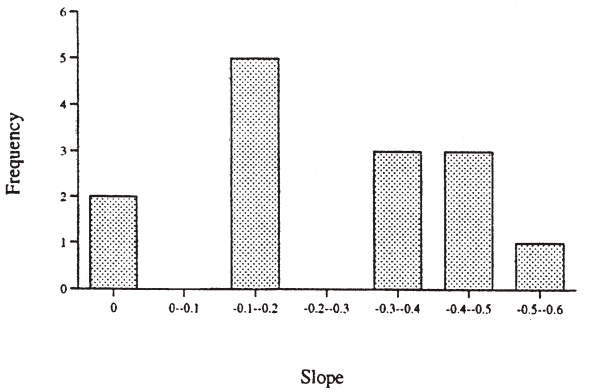

Fig. 2. Histogram of the slopes of major axis regressions relating A and k for fourteen populations of fish. The data were obtained from Pauly (1978) and included estimates of A and k for 6 to 14 year classes from 14 populations. We chose to use functional i.e., major axis regression because both A and k are measured with error. The two studies with a slope of zero showed no significant relationship. For the 12 populations with significant ($p < 0.05$) correlations between A and k, all were negative (Mean = –0.30, S.D. = 0.13). The 14 studies included data from two populations of *Clupea harengus*, one population of *Sardinops caerula*, and five populations of *Brevoortia tyrannus*, all in the family Clupeidae. It also included data from 6 populations of *Merlangius merlangus* in the family Gadidae. These species are all economically important fish which is why A and k were estimated for 6–14 successive years in these populations.

nately, the shapes of the growth trajectories for *Drosophila* reared at different temperatures have not been measured. **Case 3**: Dome-shaped reaction norms can also occur if juvenile mortality increases more than linearly with growth rate (Berrigan and Koella 1994). However, this result requires very strong correlations between growth and juvenile mortality rates. In his extensive review of the effects of temperature on age and size at maturity in ectotherms, Atkinson (1994) found no consistent correlations between temperature and mortality rate. **Case 4**: Kindlmann and Dixon (1992) predict delayed maturity at a larger size when growth is slowed by reduced temperature if the gonadal growth rate is constrained to be lower than the somatic growth rate and if gonadal growth rate increases with temperature. Their model was designed to address life history evolution in aphids and it is not clear whether it is applicable to other animals.

A detailed analysis of models for age and size at maturity in the face of temporal and spatial heterogeneity in the opportunities for growth has reached conclusions similar to the four cases discussed above (Sibly and Atkinson 1994): it is difficult to predict delayed maturity at larger size when immature growth is slowed.

The fact that diverse ectotherms respond to reduced temperature by maturing later at a larger size but respond to reductions in food quality by maturing later at a smaller size leads us to suspect that there might be some general explanation for this pattern. In the remainder of this commentary we show how differential expression of a tradeoff between growth rate and asymptotic size results in predictions consistent with the observed responses of ectotherms to variation in temperature and food quality. Theory for the evolution of reaction norms for age and size at maturity has often assumed that growth can be modeled as a Bertalanffy curve with a fixed asymptotic size (e.g., Stearns and Koella 1986). The Bertalanffy equation for length is: $l_x = A(1\text{-}Be^{-kx})$, where l_x is the length at age x, B is the ratio of length at birth to the asymptotic length (A), and k is the growth coefficient. If B and A are fixed, then k, the growth coefficient, is proportional to growth rate for small values of x.

Consider the two cases illustrated in Fig. 1. In both cases prereproductive growth rate declines as we move from left to right. In case I, however, the change in prereproductive growth is not associated with a change in the asymptotic size (A). The change in the growth curve occurs solely through a reduction in k. In case II the decline in growth occurs because of changes in both A and k. A and k are negatively correlated and their correlation is given by an equation in the form $A \approx k^{-h}$, with h between 0 and 1 (Charnov 1993: 77). These two cases represent distinct ways in which we may observe reduction in the opportunity for immature growth. Here we argue that the two cases may account for the differences in ectotherm responses to variable opportunities for growth imposed by temperature versus reductions in food quality (Fig. 1). With a fixed asymptotic size, simple models for age and size at maturity predict delayed maturity at *smaller* size when juvenile growth is reduced. In contrast, if A is negatively related to k (and size at birth is constant), otherwise identical models predict delayed maturity at a *larger* size when juvenile growth is reduced.

The models used to calculate the results illustrated in Fig. 1 are among the simplest possible for age and size at maturity. In these models we assume that selection acts only on the age at maturity (α) and fitness is defined as the net reproductive rate (R_0). The *only* benefit of delayed maturity is increased fecundity caused by an assumed linear relationship between size and fecundity and the *only* cost to delayed maturity is an increased risk of death prior to maturity caused by a constant juvenile mortality rate. The appendix gives the details of this approach (Berrigan and Koella 1994).

The two cases discussed above both consider the consequences of reduced immature growth. If slower growth caused by reductions in food quality does not alter the asymptotic size while slower growth caused by reduced temperature does alter it, then this could account for the typical life history response of ectotherms to reduced temperature versus reduced food quality. What evidence is there that temperature effects on growth are associated with negative correlations between A and k? Recent work on fish and some invertebrates suggests that there may often be a negative correlation between A and k (Beverton and Holt 1959, Longhurst and Pauly 1987: 312, Charnov and Berrigan 1991, Charnov 1993). Comparisons

among species and among populations within a species have shown that A and k are inversely related and that their relationship can be described by the formula $A \approx k^{-h}$ with h between 0.25 and 0.75. Here we extend these results by examining the relationship between k and A within populations between year classes. Unfortunately, few studies report data on the growth of individuals over their entire lives. Pauly (1978) reviews the literature on over 1500 studies of fish growth rates. From this data set we were able to extract the results of 14 studies on four species in two families that included estimates of A and k for at least six year classes within a population. Twelve of these studies had significant and negative relationships between A and k. Fig. 2 summarizes these results. Note that the average slope of the line relating A and k is −0.3, significantly lower than 0.

In this commentary we are proposing a potential explanation for a general characteristic of ectotherm responses to food and temperature variation. This explanation could be tested by comparing growth curves. Unfortunately, comparisons of growth curves are confounded by the fact that the organisms begin to reproduce, diverting resources away from growth. It would be interesting to compare the growth curves under various temperature and food regimes of an animal with indeterminate growth that had been experimentally manipulated to prevent the onset of reproduction. Hormonal or surgical procedures might be suitable tools for these manipulations of reproductive effort.

More elaborate models should be analyzed involving other fitness measures and allowing for selection on the growth curve itself. For example, Charnov and Berrigan (1991) develop a model for the evolution of age and size at maturity where selection acts on both age at maturity (α) and on k, the growth coefficient of the Bertalanffy equation. Ideally, a model for the evolution of life histories should explain both when an animal should mature and what its growth trajectory looks like before and after maturation. However, analytically tractable models such as the ones considered here are still useful because they can give clues about what a more general life history model might have to include.

If the tradeoff between A and k is real, then a major puzzle for evolutionary and developmental biology is why this tradeoff exists.

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Appendix

The results in Fig. 1 are obtained by considering the following model. Fitness is defined as

$$R_0 = \int_{\alpha}^{\infty} l(x)m(x)dx \qquad (1)$$

where x denotes age, α denotes age at maturity, $l(x)$ denotes survival up to age x, and $m(x)$ denotes fecundity at age x. To determine the optimal age at maturity we further assume 1) that growth is determinate and that 2) adult and juvenile mortality rates are independent of age and size. With these assumptions eq. (1) is reduced to

$$R_0 = \frac{l(\alpha)\, m(\alpha)}{a} = \frac{e^{-j\alpha}\, m(\alpha)}{a} \qquad (2)$$

where a denotes adult and j denotes juvenile mortality rate. To find the age at maturity that maximizes fitness, R_0, we differentiate eq. (2) with respect to α and set the resulting equation to 0 to get

$$\frac{dm}{d\alpha} = \frac{dmds}{ds\, d\alpha} = j\, m(\alpha) \qquad (3)$$

where s denotes size.

To make quantitative predictions about the location and shape of the reaction norms, we define functions for growth, fecundity, and mortality. Specifically, in addition to the assumptions mentioned above, we assume 1) that growth can be described by a saturating growth equation, 2) that fecundity increases linearly with size, and 3) that juvenile mortality is a fixed constant. We also assume that no genetic or physiological constraints prevent reaching the local optima for age and size at maturity. These assumptions are required so that selection can lead to the spread of the predicted trait.

For example with Von Bertalanffy growth,

$$s(x) = \begin{cases} A(1\text{-}Be^{-kx}) & \text{for } x<\alpha \\ A(1\text{-}Be^{-k\alpha}) & \text{for } x\geq\alpha \end{cases}$$

and size dependent fecundity

$$m(x) = Fs(\alpha) - H, \text{ for } x\geq\alpha \text{ and } s(\alpha)>H/F,\ 0, \text{ otherwise}$$

We solve eq. (3) for the α that maximizes R_0 to get the optimal age at maturity

$$\alpha^* = \frac{\ln\left(\frac{FAB(K+j)}{(FA-H)j}\right)}{k}$$

Optimal size at maturity, s^*, is then calculated with the equation

$$s^* = A(1\text{-}Be^{-k\alpha^*})$$

To obtain the results in Fig. 1 (I) we set $F=212$, $A=4.58$, $B=0.934$, $j=0.1$, and $H=358$ and then calculate α^* and $s(\alpha)$ for several values of k. To obtain the results in Fig. 1 (II) we assumed that $A \approx k^{-0.5}$ and that size at birth is constrained to be 0.3 as in Fig. 1 (I).