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Author(s): Peter A. Abrams, Olof Leimar, Soren Nylin, Christer Wiklund

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THE EFFECT OF FLEXIBLE GROWTH RATES ON OPTIMAL SIZES AND DEVELOPMENT TIMES IN A SEASONAL ENVIRONMENT

PETER A. ABRAMS,* OLOF LEIMAR, SÖREN NYLIN, AND CHRISTER WIKLUND

Department of Zoology, Stockholm University, S 106 91 Stockholm, Sweden

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Abstract.—The interrelationships among development time, growth rate, and adult size are investigated using simple optimization models of a seasonal life history in which larger adults have greater reproductive output. Unlike most previous studies, our models assume that growth rate is an adaptively flexible character that can be increased at the expense of a greater juvenile mortality rate. Three components of fitness are considered: the cost of developing at a suboptimal time of the year, the reproductive advantage of larger adult size, and the increased mortality from rapid juvenile growth. The study focuses on the optimal responses of size, development time, and growth rate to changes in the amount of time available for completion of the life cycle. The models show that the optimal growth rate and size at maturity may respond in several different ways. Perhaps the most likely effect is that growth becomes faster and size smaller with less time available. It is also possible, however, for either growth rate or size (but not both) to stay constant; in other cases, less time available leads to slower growth or larger size. The effects of increased mortality on the juvenile stage are also explored; here, the optimal size is likely to decrease, but growth rate and development time may increase or decrease.

Adult size and the development time needed to reach this size are two of the most basic life-history variables of semelparous species. When considering adaptive variation in these variables, researchers have frequently assumed that juvenile growth is directly determined by environmental factors like food availability or temperature (see references in Roff 1992 and Stearns 1992). Such an assumption simplifies the analysis of life-history models, since a single variable, development time, is optimized, and the adult size is given by the amount of time the organism spends following the environmentally determined growth trajectory. Our aim here is to investigate the consequences of allowing adaptive variation in juvenile growth rates. We will study how the optimal growth rate and development time might vary with the conditions experienced by a growing juvenile. We focus on the effects of time constraints in a seasonal environment and the effects of mortality risk during the juvenile stage.

There are good reasons to believe that individuals would gain by being able to vary the growth rate (Case 1978; Sibly and Calow 1986), since such an ability would lead to a more efficient balancing of the cost of juvenile mortality and the benefits of large adult size or early maturation. Typically, a higher growth rate

* To whom correspondence should be sent: Department of Zoology, University of Maryland, College Park, Maryland 20742; E-mail, abrams@zool.umd.edu.

entails a fitness cost (Clutton-Brock et al. 1985), for instance, when activity levels or habitat choices producing faster growth result in greater predation (Werner 1986; Lima and Dill 1990; Ludwig and Rowe 1990; Rowe and Ludwig 1991; Fraser and Gilliam 1992; Werner and Anholt 1993). More rapid growth can entail physiological changes that increase mortality under adverse conditions (Gotthard et al. 1994). In addition to growth plasticity, one would, for similar reasons, expect genetic differences in growth strategies between populations or species having different environments.

Empirical evidence suggests that endogenously controlled variation in growth rate is common. Butterfly growth rates have been shown to vary considerably between similar individuals raised under different photoperiods, between different phenotypic classes within a species (e.g., males vs. females, first vs. second generation), and between closely related species (Wiklund et al. 1991; Nylin 1992; Nylin et al. 1993). The growth rates of individuals of a single species may also vary with the date of emergence (Nylin et al. 1989; Nylin 1992). Cushman et al. (1994) found that a lycaenid butterfly spent more time feeding and grew faster when it was protected from predators by ants, in spite of providing food to the ants. This result shows that growth rate in the absence of ants was below what was physiologically possible. Skelly and Werner (1990) and Werner (1991) have shown that larval amphibians can adjust their growth rate adaptively based on predation risk, and Wilbur (1987) and Semlitsch and Wilbur (1988) have demonstrated apparently adaptive variation in the growth rate in a larval amphibian based on the rate at which its habitat was drying up. There are other examples of flexible growth rate in such diverse taxa as mollusks (Crowl and Covich 1990) and mammals (Negus et al. 1992). Perrin and Sibly (1993) review a considerable body of work on the adaptive adjustment of growth rates in adult organisms, when there is a trade-off between growth and reproduction. Finally, a large body of literature (reviewed in Lima and Dill 1990) shows that feeding rates are varied adaptively based on foraging risks; because the growth rate is directly dependent on the food intake rate, these experiments imply plasticity in the growth rate.

In our analysis, we assume a life history in which generations are synchronized in a seasonal pattern and growth ceases at maturity. This history describes many annual species but also some that have either more or fewer than one generation per season. After suggesting a general framework for the analysis, we assume a specific class of fitness functions and investigate how a juvenile should respond to variation in the amount of time available in the season for completion of the life cycle. We also consider the response to variation in risk of mortality.

A MODEL OF OPTIMAL GROWTH RATE AND DEVELOPMENT TIME

Life-History Variables

Adult body size is determined by growth rate and development time. Here, *growth rate* refers to the proportional growth rate. Thus, the increase in body size, S , during the preadult period is described by the equation $dS/dt = G(t)S(t)$, where $G(t)$ is the instantaneous proportional growth rate. Adult body size, $S(T)$, is then proportional to $\exp(gT)$, where g is the mean proportional growth rate

(mean of $G[t]$) over the developmental period of length T . We simplify the analysis by assuming that the entire growth trajectory can be adequately characterized by the mean growth rate. If body size is measured in units of initial size, then size is equal to $\exp(gT)$; we will define s to be $S(T)$ measured in this way, so $\ln(s) = gT$. This means that we have two independent life-history variables, the average proportional growth rate g and the development time T , with the adult size s being determined by g and T .

A General Framework for the Analysis

Optimization models in which there are two adaptive variables are considerably more complex than those with a single variable, since a change in either variable can affect the optimal value of the other. General formulas for the effects of environmental parameters on optimal strategies in this case have apparently not been presented before.

We begin by considering a completely general fitness function of any two adaptive variables (which we will still label g and T) and a parameter p . This parameter represents some aspect of the environment or, more generally, any circumstance affecting fitness that the organism has knowledge of; fitness is then $F(g, T, p)$. Appendix A derives general formulas for the dependence of the optimal g and T on the parameter p , if we assume that intermediate values of both variables are optimal. It shows that the effect of the parameter on the two evolutionary variables is determined by two sets of quantities: the effects of the parameter on the gradient of the fitness function (i.e., its effect on $[\partial F/\partial g, \partial F/\partial T]$, which is described by the ordered pair $[\partial^2 F/\partial g \partial p, \partial^2 F/\partial T \partial p]$); and the three second derivatives of fitness with respect to the two evolutionary variables ($\partial^2 F/\partial g^2, \partial^2 F/\partial T^2, \partial^2 F/\partial g \partial T$), in which all derivatives are evaluated at the optimal values of g and T . If a parameter only affects one component of the fitness gradient (say p only affects $\partial F/\partial T$, so that $\partial^2 F/\partial g \partial p = 0$), then the response of the optimal T , T_0 , to p is always in the same direction as the effect of p on the fitness gradient; T_0 increases with p if and only if $\partial^2 F/\partial T \partial p$ is positive at the optimum. However, the other variable (here g) will also respond to p whenever $\partial^2 F/\partial g \partial T$ is nonzero at the optimum, and it responds in the same/opposite direction as T when $\partial^2 F/\partial g \partial T$ is positive/negative (an example of this phenomenon is shown in fig. 1). The cases in which p affects both components of the fitness gradient involve two direct and two indirect effects, and they are often difficult to deduce by intuition alone.

Analysis of a Specific Class of Fitness Functions

We now consider a class of fitness functions that are as simple as possible but still express some major trade-offs experienced by organisms in a seasonal environment. Let total fitness, W , be a product of three components: a size-dependent component of adult fitness given by $\exp(f_1[gT])$; a component expressing the fitness effects of becoming an adult at different points in time during the season, given by $\exp(-f_2[T - \tau])$, where τ is the development time resulting in adult emergence at the most favorable time in the season (i.e., maximizing the adult component of fitness for a given size); and juvenile survival given by $\exp(-d[g]T)$, where $d(g)$ is the mean juvenile mortality rate per unit time, as-

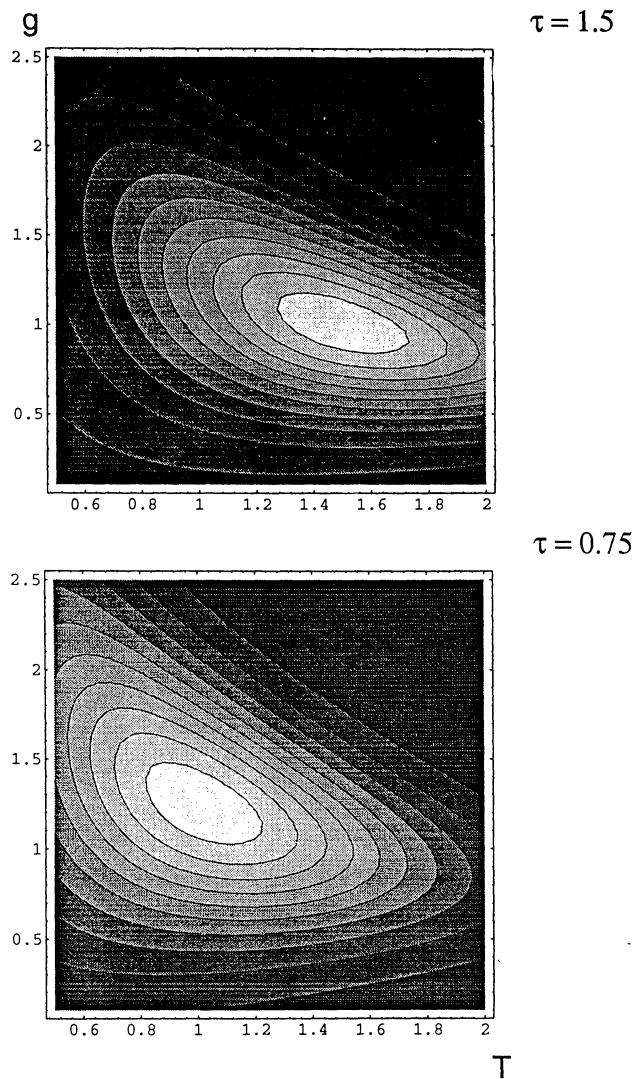


FIG. 1.—Contour plots of fitness as a function of development time, T , and growth rate, g , in a seasonal environment. Higher fitnesses are denoted by lighter colors. The two plots refer to different values of an environmental variable, τ , relating to time available for development (e.g., the smaller τ , 0.75, could apply to individuals that began development at a date halfway through a growing season of length 1.5). Thus, in the lower plot, an individual has less time available until conditions become optimal for adult life. As a consequence, the optimal development time is shorter and the optimal growth rate higher than in the top plot. The model used in this example has fitness components, $d = 1 + g^2$, $f_1 = 5gT - (gT)^2$, and $f_2 = (T - \tau)^2$.

sumed to depend only on g . The total fitness is then $W = \exp(f_1 - f_2 - dT)$, and maximizing fitness is equivalent to maximizing

$$F = \ln(W) = f_1(gT) - f_2(T - \tau) - d(g)T. \quad (1)$$

Note that the total fitness W can be interpreted as the product of juvenile survival and adult reproductive success. This is appropriate for an annual organism that overwinters in the egg stage or for one overwintering as an adult. However, with some reinterpretation, the expression for fitness may be relevant also for other types of life histories. For instance, for an insect overwintering as pupa it is critical to reach pupal diapause before winter sets in, and T could be interpreted as the time used to reach this stage. For an organism with two generations per year, the fitness of first-generation individuals may depend on the time available in the season for their offspring to grow and reproduce, but this effect can at least qualitatively be described by a seasonality component f_2 (the two generations would in general have different fitness functions).

We assume that the size-dependent component of fitness, $\exp(f_1[gT])$, is increasing ($f'_1 \equiv df_1/d[gT] > 0$) or possibly unimodal. Those components of adult fitness that have been examined (e.g., female fecundity or male mating advantage; Roff 1992) seem to increase with size. Adult fitness could be a power function of adult size; in this case, $f_1 = kgT$, where k is a constant; such an allometric relationship is often assumed for female fecundity (see, e.g., Reiss 1989). In general, reproductive success will not increase indefinitely with size, and it may even decrease for very large sizes, so f_1 is likely to be nonlinear and have a negative second derivative when gT is sufficiently large. However, f''_1 may also be positive for some ranges of gT .

For the function that measures seasonal influences on adult fitness, $\exp(-f_2[T - \tau])$, we simply assume that f_2 has a minimum of zero at $T = \tau$. This means that f_2 can be interpreted as the proportional reduction in adult fitness due to emergence at a time that is less than optimal for adults. The parameter τ expresses how an individual is positioned with respect to the season; a smaller τ means that the individual is in a "greater hurry" to complete its development. The fact that f_2 is a minimum at $T = \tau$ means that f''_2 must be positive at values of T sufficiently close to τ . If T is not close to τ , it is in principle possible for f''_2 to be negative. For completeness, we will briefly mention the consequences of this below.

The average mortality rate d will be a function only of g when the instantaneous juvenile mortality only depends on the instantaneous proportional growth rate (and not also on juvenile size or the time in the season), which at best can be regarded as an approximation. We assume that faster growth is more costly, so that $d(g)$ is increasing. In cases in which an organism can adjust the instantaneous growth rate freely to maximize juvenile survival, there is an additional property of $d(g)$ that is worth noting, namely, that it must be a convex function ($d'' \geq 0$). The reason is that if the curve $d(g)$ were potentially concave ($d'' < 0$) for some range of growth rates, an individual could achieve an average growth rate in this range at a lower cost by appropriate "switching" between the growth rates at either end of the range (the lower end could be zero growth, and the upper could be the maximal growth rate). The result of such a switching growth strategy will

TABLE 1
CHARACTERISTICS OF THE COMPONENTS OF THE FITNESS FUNCTION

Function	Definition	Shape
$f_1(gT)$	Log(adult fitness) as a function of log (size)	Increasing or unimodal; $f_1'' \leq 0$ (or > 0)*
$f_2(T - \tau)$	Reduction in log of adult fitness due to timing	Minimum of 0 at $T = \tau$; $f_2'' > 0$ (or < 0)
$d(g)$	Instantaneous mortality rate as a function of mean growth rate	Increasing; $d'' \geq 0$ (or < 0)*

* The signs given inside of parentheses are deemed to be less likely on both biological and mathematical grounds (see text).

be that $d(g)$ changes linearly with g in this range ($d'' = 0$). Such linearization of the fitness set was discussed by Levins (1968). Finally, note that, if most of the adaptive variation in growth rate is due to an irreversible choice of habitat, it is quite possible that $d(g)$ is concave ($d'' < 0$). A summary of our assumptions regarding the fitness component functions is given in table 1.

Analysis of the Life-History Model

We will apply the general analysis outlined above to the fitness function (1). Two cases will be investigated. In the first, the adult-optimal development time τ plays the role of the parameter p , and in the second we introduce a parameter related to the level of some mortality factor (e.g., predators) into the rate of mortality function $d(g)$.

If the conditions for maximum in appendix A are applied to fitness formula (1), we obtain

$$\partial F / \partial T = g f_1' - f_2' - d = 0, \quad (2a)$$

$$\partial F / \partial g = T(f_1' - d') = 0, \quad (2b)$$

$$\partial^2 F / \partial T^2 = g^2 f_1'' - f_2'' < 0, \quad (2c)$$

$$\partial^2 F / \partial g^2 = T(T f_1'' - d'') < 0, \quad (2d)$$

and

$$(\partial^2 F / \partial g \partial T)^2 - (\partial^2 F / \partial g^2)(\partial^2 F / \partial T^2) = T^2 f_1'' f_2'' + g^2 T f_1'' d'' - T f_2'' d'' < 0, \quad (2e)$$

where primes again denote derivatives (e.g., $f_1' = df_1/d[gT]$), and expressions (2c), (2d), and (2e) are evaluated at the optimal values specified by equations (2a) and (2b). Also, equation (2b) has been used to simplify inequality (2e). These formulas assume that fitness is maximized at intermediate values of the two evolutionary variables. Conditions (2c), (2d), and (2e) imply that there may be restrictions on the signs of the second derivatives of some of the component functions if there are to be optimal intermediate values of the evolutionary variables. For example, inequality (2d) prohibits the second derivative of f_1 from being positive if the second derivative of d is zero or negative (similarly, $d'' < 0$ is prohibited if $f_1'' \geq 0$).

Response to time pressure.—If, at the start of its growth, a juvenile has information about when conditions are most favorable for adult emergence (i.e., information about the adult-optimal development time τ), it should adjust its growth strategy accordingly. This information may not be difficult to obtain, since for many organisms (Rowe and Ludwig 1991), earlier is always better ($\tau \leq 0$). The general formulas in appendix A yield expressions for the derivatives of the optimal values of growth rate, g_o , development time T_o , and adult size s_o with respect to τ , and these derivatives are given in appendix B. Using inequalities (2c)–(2e), it follows that the direction of change in each trait with increasing τ is described by the following rules:

$$\partial g_o / \partial \tau \text{ has the sign of } f_1'' f_2'', \quad (3a)$$

$$\partial T_o / \partial \tau \text{ has the sign of } f_2'', \quad (3b)$$

and

$$\partial \ln(s_o) / \partial \tau \text{ has the sign of } d'' f_2'', \quad (3c)$$

where f_1'' , f_2'' , and d'' are evaluated at the optimal trait values. The previous section and table 1 discuss the signs of these second derivatives. The sign of f_2'' must be positive if T_o is close to τ . Thus, of these three responses to τ , that of T_o is closest to having a determinate sign; it is likely to increase with τ . That the optimal development time should increase when more time is available is quite intuitive.

If we assume that $f_2'' > 0$, then the optimal growth rate usually decreases with τ (negative f_1'') but may increase, especially at small sizes (where f_1'' may be positive). Size increases with τ if $d'' > 0$; this case must be true whenever growth can be adjusted instantaneously, but it need not be true when growth rate is determined by a single habitat choice. Thus, the most probable responses to a longer adult-optimal development time would seem to be increased size, decreased growth rate, and longer development. This is the type of response illustrated by the fitness surfaces shown in figure 1. However, there are at least two other possibilities. If $f_1'' > 0$ and $d'' > 0$, growth rate and size may both increase. In this case, the advantage of a unit increase in size becomes larger as size increases, which results in a positive feedback between optimal growth and optimal development time. Increasing τ relaxes the constraints on the positive feedback process, which results in larger values of both variables (and larger size). If $f_1'' < 0$ and $d'' < 0$, size and growth rate both decrease when more time is available. Conversely, when less time is available (τ is smaller), size and growth rate could both increase. These unexpected effects are again the result of the interaction of the costs and benefits of the two evolutionary variables. When T_o decreases because of a smaller τ , this situation favors an increased growth rate, because the total mortality from a given growth rate is less with a shorter development time. However, when d'' is negative, the costs of a unit increase in growth rate decrease, and the larger g becomes. Thus, the increase in growth overcompensates for the decrease in time, which results in a larger size. There are two particularly interesting special cases. First, if fitness is a power function of size (i.e., $f_1'' = 0$), the optimal growth rate is independent of τ , but size increases with

τ . Second, when d is linear ($d'' = 0$; e.g., $d = D_0 + D_1g$), the optimal size is independent of τ .

The effects of the shape of the mortality function d on optimal responses to the adult-optimal development time τ are illustrated in figure 2. All three examples in the figure use the same size advantage function (with $f_1'' < 0$) and the same seasonality function (with $\exp[-f_2]$ equal to a Gaussian curve, which may be appropriate for modeling the availability of seasonal resources). In all three cases, development time increases and growth rate decreases when more time is available, but the response of optimal size depends on whether the cost of growth function, d , is accelerating, straight (linear), or decelerating. A similar set of figures could have been produced if we had used the same d function ($d = 1 + g^2$) in the three cases and changed the size-advantage function from decelerating (e.g., $f_1 = 5gT - [gT]^2$; $f_1'' < 0$), to linear ($f_1 = 5gT$; $f_1'' = 0$), and finally to accelerating ($f_1 = 5gT + [gT]^2$; $f_1'' > 0$). The optimal development time and size would increase with available time in all three cases, but the optimal growth rate would stay constant with increasing τ when f_1 is linear and increase under an accelerating f_1 . As shown in figure 2B, g_0 decreases with τ under a decelerating f_1 .

For completeness, note that there may in principle be optima with $f_2'' < 0$ (which requires $f_1'' < 0$ and $d'' > 0$ for inequalities [2c]–[2e] to hold). This would be most likely to occur when T_0 differs greatly from τ . The surprising consequence would be that, with more time available, growth rate increases, development time decreases, and adult size decreases (which follows from the derivatives in app. B).

Response to mortality of juveniles.—Mortality factors, such as predation, can have two different types of effect on life history. If the risk of mortality is unrelated to a juvenile's foraging activity, greater mortality can be modeled by the addition of a constant to the risk function $d(g)$. Perhaps more typically, foraging is what exposes the juvenile to risk, and then an increased mortality factor increases the slope of the risk function. Either of these cases, or a combination of them, can be described by introducing a mortality parameter p that increases d and increases (or does not affect) the sensitivity of d to g . Thus, d is now a function of both g and p , with

$$\partial d / \partial p > 0 \quad (4a)$$

and

$$\partial^2 d / \partial g \partial p \geq 0. \quad (4b)$$

From the derivatives given in appendix B, we obtain the following rules for the direction of responses to changes in p :

$$\partial g_0 / \partial p \text{ has the sign of } [-g_0 f_1'' \partial d / \partial p + (g_0^2 f_1'' - f_2'')(\partial^2 d / \partial g \partial p)], \quad (5a)$$

$$\partial T_0 / \partial p \text{ has the sign of } [T_0 f_1'' (\partial d / \partial p - g_0 \partial^2 d / \partial p \partial g) - (\partial d / \partial p)(\partial^2 d / \partial g^2)], \quad (5b)$$

and

$$\partial \ln(s_0) / \partial p \text{ has the sign of } [-T_0 f_2'' (\partial^2 d / \partial g \partial p) - g_0 (\partial d / \partial p)(\partial^2 d / \partial g^2)], \quad (5c)$$

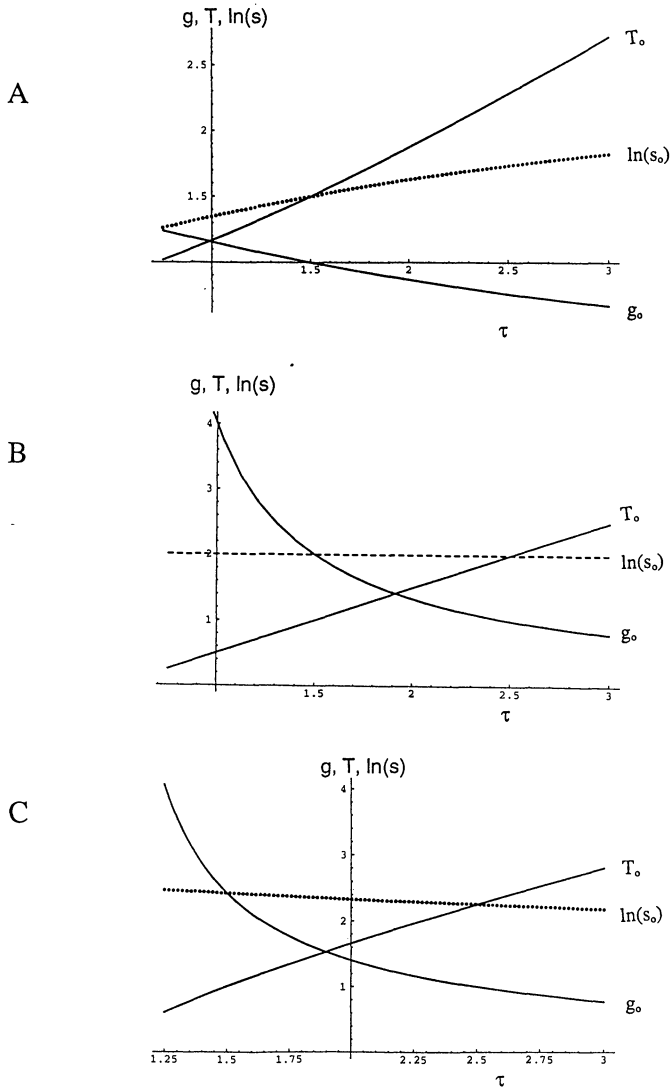


FIG. 2.—Responses of optimal development time, T_0 ; growth rate, g_0 ; and logarithm of body size, $\ln(s_0) = g_0 T_0$, to changes in the adult-optimal development time, τ . The curves are found by maximizing fitness, as illustrated in fig. 1, for several values of τ . The fitness components f_1 and f_2 are the same as in fig. 1. Fig. 2A, B, and C differ in the mortality function, d . A, Mortality is an accelerating function of growth rate ($d = 1 + g^2$; $d'' > 0$) as in fig. 1. Here, when more time is available for growth (greater τ), the optimal development time increases, growth rate decreases, and size increases. B, Mortality is linear (i.e., $d'' = 0$); $d = 1 + g$. As τ increases, the increase in T_0 is exactly compensated by the decrease in g_0 , which leads to an optimal size that is independent of τ . C, Mortality is a decelerating function of growth rate ($d = g/(1 + g)$; $d'' < 0$). As τ increases, the increase in T_0 is exceeded by the decrease in g_0 , which leads to a smaller optimal size when more time is available for growth.

where $\partial^2 d/\partial g^2$ is the derivative previously denoted d'' . In general, none of these expressions has a determinate sign. Taking into account the inequalities (2c) and (2d), we can reach a definite conclusion about the response to increasing p for some special cases. If f_1'' is nonnegative, it follows from rule (5a) that g_0 decreases (or stays constant) and from rule (5b) that T_0 decreases (or stays constant). Concerning size, if $\partial^2 d/\partial g^2$ is positive, and if (as assumed) f_2'' is positive, rule (5c) implies that s_0 decreases with p . Based on table 1, the most likely response to increased mortality risk is a smaller adult size, but for growth rate and development time no definite conclusion can be drawn.

We can get a better understanding of the response of the growth rate by considering the two types of effects mentioned above (see also Werner and Anholt 1993). When the increased risk is unrelated to foraging activity ($\partial^2 d/\partial g \partial p = 0$), intuition suggests that a juvenile should grow faster to "escape the danger," and rule (5a) shows this to be correct if $f_1'' < 0$ but otherwise not. Similarly, rule (5b) shows that development time must decrease in this case. On the other hand, if foraging gets more risky when the mortality factor increases ($\partial^2 d/\partial g \partial p > 0$), one would expect a decreased growth rate. From the last term of rule (5a), we see that there is a tendency in this direction, but because of inequality (4a) the conclusion becomes definite only for $f_1'' \geq 0$.

DISCUSSION

In studying the adaptive responses of growth rate, development time, and adult size to a change in conditions, we have used the approach here of employing the general conditions for a maximum together with assumptions about the signs of derivatives of fitness components to predict the direction of response. The class of fitness functions we have investigated has considerable generality, in that we do not assume specific forms for any of the three component functions that comprise fitness. Nevertheless, this study still represents a special case within the range of possible models of seasonal life histories. In a more general model, the fitness cost of suboptimal timing (f_2) may depend on size as well as development time. For example, if there is a constraint on the rate of egg laying, a large female with many eggs may suffer proportionately more from late development than will a small female. Another possibility is that the mortality rate depends on development time as well as mean growth rate. This result would occur if mortality factors (such as predator abundance) changed seasonally or if the size of the juvenile had a significant impact on its mortality risk. Our specific model (eq. [1]) cannot make reliable predictions about these cases. However, our main message is that growth plasticity allows a wide variety of responses to life-history variables to environmental parameters. This range of responses would be even greater in the larger class of models with plastic growth that allowed the complications mentioned above.

Nevertheless, our message is not that "anything can happen." The most likely effects of decreasing the amount of time available in the season ("greater time pressure") are a shorter development time, a higher (or unchanged) growth rate,

and a smaller (or unchanged) adult size. Similarly, increased mortality is likely to lead to smaller adult size, but growth rate and development time may either decrease or increase (of course, both cannot increase if size becomes smaller).

It is of interest to compare the above results based on adaptively flexible growth rates with a comparable analysis in which growth rates are directly determined by environmental factors. For the two types of parameters we have investigated, time pressure and mortality factors, there need be no direct or necessary influence of the environment on the process of feeding or the physiology of growth. In the absence of endogenous control of the growth rate, growth rate should not change, for example, with a change in photoperiod or predator density in laboratory experiments. A lack of the plasticity in growth implies that development time and adult size must change in the same direction. This is not the case when growth is plastic, and observations of opposite changes in size and development time should therefore not be interpreted as reflecting unknown constraints or a failure of adaptation. In our analysis, we found that growth rate should respond to time pressure, except in the special case in which adult fitness is a power function of size. Since this allometric case has frequently been assumed in previous life-history models (see references in Roff 1992 and Stearns 1992), it is worth noting that the assumption may have a qualitative effect on predictions. Concerning the response to increased mortality factors, our analysis showed that growth rate should decrease (or possibly stay constant) for the allometric case.

The introduction of this article summarized some studies showing that plasticity in growth rate is common. We know of no study in which growth plasticity has been investigated and proven to be absent. It is widely accepted by theoreticians and experimentalists that there are trade-offs between growth and reproduction in adult organisms (Perrin and Sibly 1993). Nevertheless, as indicated above, flexible growth is absent from most models of juveniles, in spite of the empirical evidence reviewed in the introduction. When growth of juveniles is plastic, we can no longer view the relationship between age and size at maturity as a reaction norm (see, e.g., Stearns and Koella 1986; Stearns 1992) because growth rate is not an environmental variable. Different environments that produce a given growth rate for different reasons (e.g., many predators or little food) will often have very different optimal development times and sizes. Plotting age versus size at maturity when growth rates are flexible would obscure the environmental effects that are of primary interest in studying reaction norms.

Some previous theoretical analyses have been made of adaptive growth in a seasonal environment. Houston et al. (1993) investigate models that assume a fixed adult size and also show that growth rate becomes faster in response to a stronger penalty of suboptimal timing. Ludwig and Rowe (1990) and Rowe and Ludwig (1991) consider the choice between two habitats, with an environmentally determined growth rate in each habitat, and Werner and Anholt (1993) study the response of foraging effort (speed of movement). The examples developed in these articles all seem to indicate that an individual, when more pressed for time, should take greater risks to achieve faster growth but still arrive at a smaller adult size. Our analysis indicates that this type of response is likely but not necessary.

Similarly, Werner and Anholt (1993) have found that when foraging is what exposes juveniles to risk, higher predation pressure should lead to slower growth. Our model predicts that the opposite response could also occur.

Going beyond our particular assumptions, it is clear that controlled experimentation, systematically varying information about time in the season or the risk of mortality, can provide a very direct test of adaptive flexibility in growth rates. Several of the studies mentioned in the introduction are in fact of this kind. Skelly and Werner (1990) have shown that the presence of (caged) predators reduced foraging activity and growth rates in larval amphibians. Others (Nylin et al. 1989; Wiklund et al. 1991; Nylin 1992) have experimentally studied the development times and growth rates of several species of butterfly larvae reared at different day lengths. Day length acts as a cue telling a larvae how it is positioned with respect to the season. In all of these studies, day lengths indicating a smaller adult-optimal development time resulted in a shorter development periods, and the shorter development periods were coupled with more rapid growth and/or development rates. Thus, the quantitative effect of photoperiod on development time was greater than the effect on size; in several cases, size was not significantly affected by photoperiod. This means that the type of response was of a kind we have suggested as being the most likely—namely, that growth variation acts to buffer changes in adult size.

Our analysis suggests that a linear relationship between proportional growth rate and mortality rate will make size very insensitive to the amount of time available for development. Perhaps the strongest test of the theory we have presented would consist of a demonstration that size was least sensitive to available time in those species for which the growth-mortality relationship was closest to linear. Such a test will require measurements of growth-mortality relationships under field conditions. Although we have evidence of a positive relationship between growth rate and mortality in at least one butterfly species (Gotthard et al. 1994) and several amphibians (Skelly and Werner 1990; Werner 1991), we do not yet have enough information to assess the linearity of these relationships.

The theory developed here could be used to help understand a variety of geographical patterns in body size and differences in sexual dimorphism between species. For example, development time decreases with increasing latitude. However, in a survey of latitudinal variation in body size among European butterflies, researchers (Nylin and Svård 1991) found several species that lacked the predicted decrease in size with higher latitudes. One potential explanation for these cases is that the growth-mortality relationships in these species were particularly close to linear. Quantification of these relationships could help settle the issue. In many insect species, competition for mates favors protandry, the earlier emergence of males. Singer (1982) suggests that the degree of sexual dimorphism should be larger in species with greater protandry because males would have comparatively less time to complete development. However, other investigators (Nylin et al. 1993) have surveyed populations of the speckled wood butterfly (*Pararge aegeria*) from a range of latitudes and failed to support this conjecture. Populations from nonseasonal (tropical) environments have no protandry because the presence of overlapping generations removes the advantage of earlier male

development. However, researchers (Nylin et al. 1993) have found that the tropical populations did not have a larger ratio of male to female size. Laboratory experiments showed that males in seasonal environments compensated for their shorter development time with a faster growth rate. If the strategies described here are responsible for this pattern, then we should again expect to find a relatively linear relationship between growth rate and mortality.

We have dealt with the effects of time constraints and mortality factors because the distinction between life histories under adaptively flexible versus environmentally determined growth rates is particularly clear in these cases. However, it is also important to consider adaptive flexibility in growth rates when modeling optimal responses to other environmental factors like food availability and temperature. Both of these factors are likely to affect the cost of growth function, d , in our model, and predictions would require detailed information on how this function is altered.

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APPENDIX A

GENERAL FORMULAS FOR RESPONSES OF EVOLUTIONARY VARIABLES

The goal is to find general formulas for the response of the evolutionary variables g , T , and s to an environmental parameter, p , when fitness is $F(g, T, p)$. The necessary conditions for g and T to maximize or minimize F are that

$$\partial F / \partial g = 0 \tag{A1a}$$

and

$$\partial F / \partial T = 0. \tag{A1b}$$

This point will be a maximum if

$$\partial^2 F / \partial T^2 < 0, \tag{A1c}$$

$$\partial^2 F / \partial g^2 < 0, \tag{A1d}$$

and

$$(\partial^2 F / \partial T \partial g)^2 - (\partial^2 F / \partial T^2)(\partial^2 F / \partial g^2) < 0. \tag{A1e}$$

Equations (A1a) and (A1b) implicitly determine the optimal g and T , denoted g_o and T_o . The effect of the parameter p can be determined by implicit differentiation of both these equations with respect to p and by solving the resulting two equations for $\partial g_o / \partial p$ and $\partial T_o / \partial p$. This yields

$$\partial g_o / \partial p = (1/Z)[-(\partial^2 F / \partial T \partial g)(\partial^2 F / \partial T \partial p) + (\partial^2 F / \partial T^2)(\partial^2 F / \partial g \partial p)] \tag{A2a}$$

and

$$\partial T_o / \partial p = (1/Z)[-(\partial^2 F / \partial T \partial g)(\partial^2 F / \partial g \partial p) + (\partial^2 F / \partial g^2)(\partial^2 F / \partial T \partial p)], \tag{A2b}$$

where Z is the left-hand side of equation (A1e). Each of these responses to the parameter can be thought of as the sum of a direct effect of the parameter on the evolutionary variable (given by the second of the two terms in each of formulas [A2a] and [A2b]) and an indirect effect, due to the parameter's effect on the other evolutionary variable (the first of the two terms in the above expressions). If the mixed derivative of fitness with respect to the two evolutionary variables is zero, there is no indirect effect, and each evolutionary variable, x , changes in the direction given by $\partial^2 F/\partial x \partial p$. More generally, the scalar product of the change in the optimal values with p , $(\partial g_o/\partial p, \partial T_o/\partial p)$, and the effect of p on the fitness gradient must be positive:

$$(\partial g_o/\partial p)(\partial^2 F/\partial g \partial p) + (\partial T_o/\partial p)(\partial^2 F/\partial T \partial p) > 0. \quad (A3)$$

This result can be seen by substituting for $\partial g_o/\partial p$ and $\partial T_o/\partial p$ from equations (A2a) and (A2b).

Because the optimal size is given by $\exp(g_o T_o)$, the effect of p on the optimal size can be measured by its effect on the logarithm of size:

$$\begin{aligned} \partial \ln(s_o)/\partial p &= T_o \partial g_o/\partial p + g_o \partial T_o/\partial p = (1/Z) \\ &\times [(\partial^2 F/\partial T \partial g)(-T_o \partial^2 F/\partial T \partial p - g_o \partial^2 F/\partial g \partial p) \\ &+ T_o(\partial^2 F/\partial T^2)(\partial^2 F/\partial g \partial p) + g_o(\partial^2 F/\partial g^2)(\partial^2 F/\partial T \partial p)]. \end{aligned} \quad (A4)$$

APPENDIX B

RESPONSES OF LIFE-HISTORY VARIABLES TO ENVIRONMENTAL PARAMETERS

A direct application of equations (A2a), (A2b), and (A4) in appendix A leads to the following formulas, where Z in all cases is the left-hand side of inequality (2e), which must be negative. In case 1, τ is used as the parameter p ; in case 2, $d = d(g, p)$. For case 2, the inequalities (4a) and (4b) are also used.

CASE 1. RESPONSES TO MORE TIME AVAILABLE

$$\begin{aligned} \partial g_o/\partial \tau &= (-g_o T_o f_1'' f_2'')/Z, \\ \partial T_o/\partial \tau &= f_2''(T^2 f_1'' - T d'')/Z, \end{aligned}$$

and

$$\partial \ln(s_o)/\partial \tau = -g_o T_o f_2'' d''/Z.$$

CASE 2. RESPONSES TO INCREASED MORTALITY

$$\begin{aligned} \partial g_o/\partial p &= [g_o T_o f_1''(\partial d/\partial p) - T_o(\partial^2 d/\partial g \partial p)(g_o^2 f_1'' - f_2'')]/Z, \\ \partial T_o/\partial p &= [-T_o(T_o f_1'' - \partial^2 d/\partial g^2)(\partial d/\partial p) + g_o T_o^2 f_1''(\partial^2 d/\partial g \partial p)]/Z, \end{aligned}$$

and

$$\partial \ln(s_o)/\partial p = [T_o^2 f_2''(\partial^2 d/\partial g \partial p) + g_o T_o(\partial d/\partial p)(\partial^2 d/\partial g^2)]/Z.$$

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