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Delayed costs of growth and compensatory growth rates

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Summary

1. Many studies recognize that growth carries with it a mortality risk that can influence an animal's growth rate.
2. Data suggest that these costs of growth act over a range of time-scales, from instantaneous to an animal's lifetime.
3. Models of adaptive growth rate have not addressed the issue of differing time-scales over which the costs of growth act. Here, we develop an adaptive growth model in which the costs of growth are delayed for a period of time, to assess optimal growth strategies in relation to delays in growth costs.
4. The optimal growth rates are calculated assuming one of two possible fitness measures: the reproductive rate, R_0 and the intrinsic population growth rate, r.
5. It is shown that if the costs of growth are felt only after maturity, then growth compensation can be an adaptive strategy, even in an unchanging environment.
6. Compensatory growth is predicted only when R_0 is the relevant fitness measure, implying that this mechanism of compensatory growth is sensitive to the processes of population regulation.
7. The effect of time-delayed costs for other life-history problems is discussed in light of these results.

Key-words: Adaptive growth rate, life history, time-delay

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Introduction

Theoretical predictions of maximal growth rate do not fit empirical data (Arendt 1997). Case (1978) reviewed evidence, in terrestrial vertebrates, for the idea that an animal need not grow at its physiological maximum rate, but may instead show submaximal growth rates, and suggested that submaximal growth rates could be adaptive. Nowadays evidence exists, over a wide range of taxa, in support of this view (for a review see Arendt 1997). A submaximal growth strategy may be rigid, in which case related individuals will have similar growth irrespective of environmental conditions; alternatively, a submaximal growth strategy may be plastic, allowing variation in the growth rate in response to an individual's environment or internal state. Evidence for growth rate plasticity exists for a range of taxa, especially in insects (for a review see Nylin & Gotthard 1998; and references therein). In fact, growth rate plasticity is common enough for Abrams *et al*. (1996) to have made the statement that they knew of 'no study in which growth plasticity has been investigated and proven to be absent'.

Submaximal growth rates appear to be adaptive from the perspective of life-history theory (Stearns 1992), provided that growth incurs a fitness cost as well as a benefit. Case (1978) perceived the cost of increased growth rate to be a mortality associated with the increase in resource acquisition effort. Evidence for resource acquisition costs, such as predation risk, have since been found (for reviews see Lima & Dill 1990; Lima 1998) and constitute an immediate cost of growth. Other costs of growth rate have also been suggested (Arendt 1997; Mangel & Stamps 2001), including trade-offs between: growth and somatic development, growth and immune response, growth and resistance to environmental stressors, and growth and competitive ability. In addition to these costs of growth rate, other growth costs exist in which growth rate does not play a role. For example, predation risk can be greater for individuals with large body sizes, and this cost need not depend upon the rate at which the individual approached its present size. These additional growth costs can be directly related to either body size (Blanckenhorn 2000) or development time (Stearns 1992; Bernardo 1993).

The growth costs listed above will have an effect over a range of time-scales (Metcalfe & Monaghan 2001).

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For example, when the cost of growth is predation, no time-delay would be expected between the cost being incurred and its effect being felt; however, if the growth cost is associated with somatic development then there may be a long time-delay until this cost is fully manifest. Delayed life-history costs are increasingly being recognized as an important demographic factor (Beckerman *et al*. 2002), and a number of recent studies are emphasizing the delayed costs of poor foetal and neonatal nutrition (e.g. Blount *et al*. 2003; Ozanne & Hales 2004).

This paper describes an optimality model which incorporates a time-delay in the cost of growth. The model is used to examine the effect of this delayed cost upon an individual's growth strategy and the response of this growth strategy to changes in the environment. In particular, the model re-examines the adaptive explanations for compensatory growth (Sibly, Calow & Nichols 1985). Compensatory (or 'catch-up') growth is a commonly observed flexible growth strategy. Experimental studies, mainly from animal science, show that *ad-libitum* access to food after a period of growth limitation can result in abnormally rapid growth relative to age (Wilson & Osbourn 1960; Donovan 1984; Ryan 1990; Metcalfe & Monaghan 2001). The mechanisms underlying compensatory growth are poorly understood, but several suggestions have been made (Wilson & Osbourn 1960; Sibly *et al*. 1985; Broekhuizen *et al*. 1994). In view of the ideas on submaximal growth, one hypothesis was that growth compensation is an adaptive response. However, theoretical studies of simple adaptive models have concluded (Sibly *et al*. 1985; Sibly & Calow 1986) that compensatory growth is unlikely to be an adaptive strategy without the environment changing over time (e.g. decreasing available resources, increasing mortality risk with time, or certain environmental conditions being better than others for reproduction). Recently, the suggestion that compensation may be adaptive has re-emerged in relation to delayed life-history effects (Metcalfe & Monaghan 2001). Compensatory growth is of general ecological interest because growth limitation can occur whenever there is a severe reduction in the availability of a resource to a growing animal (e.g. poor maternal condition, changes in temperature, seasonal changes in food availability, increased competition), suggesting that under natural conditions animals are frequently growing at submaximal rates. Here we investigate the conditions under which a time-delay in growth costs is expected to produce adaptive compensatory growth even in an unchanging environment.

The model

A life-history model was developed to look at the adaptive changes in an animal's growth rate assuming that growth incurs a fitness cost. The model is not intended to reproduce the detailed form of an animal's growth curve, but rather to explore the adaptive growth rate. For the purposes of this paper the growth curve is considered as linear, although the qualitative results are unchanged for other two parameter growth curves. A schematic of a model animal's life history is shown in Fig. 1. An animal is assumed to have reached sexual maturity when its body size is M_m, and the time taken to reach maturity is t_m. The fecundity per unit time for a mature animal is a constant, F. The life cycle of an animal starts with an initial period of growth, which lasts until time t_i. This is followed by a period of growth limitation, which lasts for a time t_L, during which body size remains constant. After this period of limitation the animal has still to grow by ΔM before it reaches maturity. To achieve this, the animal continues to grow at a rate g_2. Growth is unlimited in this period, and g_2 is a variable whose optimal value is to be determined. For a linear growth curve the growth rate is related to the maturation time by the equation $g_2 = \Delta M/(t_m - t_i - t_L)$.

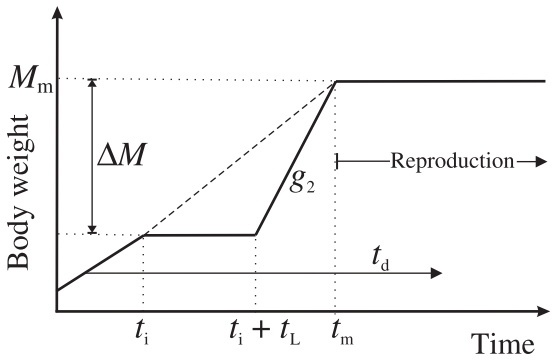

Fig. 1. The life history of a model animal described in the main text. The mature body size of an animal is fixed at M_m, while the growth rate g_2 is free to be varied. The time-delay, t_d, in the costs of growth is represented as being greater than the maturation time ($t_d > t_m$), but any time-delay can be considered. In this diagram, growth is represented as being linear, but any two parameter growth curves could be used.

Growth is assumed to carry a mortality cost. The mortality rate at time t due to growth is written as $\mu_g(t)$. All costs associated with growth are felt after a time-delay of t_d, and all costs of growth are a function of growth rate raised to the power of n (where $n > 1$ so that doubling the growth rate more than doubles the cost). One mechanism that links growth rate to mortality is considered in detail. It is assumed that the mortality rate at time $t + t_d$ is proportional to the accumulated growth cost up to time t. This type of mortality is plausible for the gradual build-up of growth-related costs, such as developmental errors, or cell damage. This form of mortality can be expressed mathematically as:

$$\mu_g(t + t_d) = \int_0^t \sigma g(t')^n dt'$$

where σ is a constant of proportionality giving the mortality rate when the growth rate is unity. In addition

to the mortality due to growth there is an extrinsic mortality rate of μ_j and μ_m for juvenile and mature individuals, respectively.

The net reproductive value (Charlesworth 1980), R (also known as the reproductive value at birth), of an animal in a large population of identical individuals can be written as:

$$R = \int_{t_m}^{\infty} FS(t)e^{-rt}dt$$

where r is the intrinsic growth rate of the population and $S(t)$ is the probability that an animal survives until time t. For $t > t_m$, the function $S(t)$ can be written as:

$$\ln\{S(t)\} = \mu_j t_m + \mu_m(t - t_m) + \int_{t_d}^{t} \mu_g(t')\,dt'$$

If the population size is stable, so that $r = 0$, then R is the net reproductive rate, commonly written as R_0. If R is set to unity then equation 2 can be numerically solved to give the intrinsic population growth rate, r (Charlesworth 1980).

Both R_0 and r are two commonly used measures of fitness out of a whole family of possibilities (Mylius & Dickmann 1995; Benton & Grant 2000; Brommer 2000; de Valpine 2000). To examine the model for different mechanisms of population regulation, both these proxies for fitness were considered (Mylius & Dickmann 1995; Benton & Grant 2000; Brommer 2000). The suitability of each fitness measure depends upon the properties of the population (Kozłowski 1999), and especially on the action of density dependence in the population (Mylius & Dickmann 1995). For example, if density dependence affects only the juvenile survival probability then R_0 is an appropriate fitness measure, while if density dependence affects the mortality rate of all age-classes equally then r is an appropriate fitness measure. The choice of fitness measure becomes more complicated when a model considers phenotypic plasticity. Firstly, the underlying genetics of the phenotypic plasticity are important in determining the evolution of phenotypic plasticity (Falconer 1952; Via & Lande 1985; de Jong & Bijima 2002). Phenotypic plasticity is the expression of different phenotypic traits in different environments, and the genetic correlation between these traits is important in determining the selection gradient on a trait (Via & Lande 1985; de Jong & Bijima 2002). In the extreme case when there is no correlation between traits selection will operate independently on each trait. In general, fitness cannot be defined separately for each environment in which an animal finds itself (Houston & McNamara 1992; Kozłowski 1992; Kawecki & Stearns 1993). Instead, all environments must be considered at the same time. However, for the model considered in this paper, the phenotypic response of a parent does not influence the state of its offspring, and in this special case phenotypic plasticity can be studied by considering each habitat individually (Houston & McNamara 1992). The optimal growth strategy is the value of g_2 that maximizes our chosen measure of fitness, either R_0 or r. The numerical solutions to the model were calculated using the optimization routines in Matlab (The Mathworks Inc., Natick, MA, USA). The model was analysed by first calculating the optimal growth rate with no growth limitation, so that $t_i = 0$, $t_L = 0$. Compensatory growth was then investigated by allowing an initial period of growth at the optimal rate for no limitation, followed by a period of growth limitation which lasts for a time t_L. The optimal growth rate, g_2, after this limitation period was then calculated. This scenario is depicted in Fig. 1, and a summary of the model's parameters and their default values is given in Table 1.

Table 1. The default parameters used for the numerical runs of the model. Unless otherwise stated all numerical runs used these parameter values. These default values give an optimal growth strategy of $t_m = 1{\cdot}58$, $g_2 = 0{\cdot}65$ when R_0 is the fitness measure and $t_m = 1{\cdot}07$, $g_2 = 0{\cdot}99$ when r is the fitness measure (figures quoted to two decimal places). The fecundity, F, was chosen so that the population's intrinsic growth rate, r, was small but positive ($r \approx 0{\cdot}04$) for the default parameters. Changing F had no qualitative effect on our results

Parameter	Value
Duration of growth before limitation, t_i	0·5
Duration of growth limitation, t_L	0·0
Time-delay of growth costs, t_d	0·0
Mortality rate of juvenile individuals, μ_j	–ln(0·9)
Mortality rate of mature individuals, μ_m	–ln(0·9)
Mortality rate due to unit growth rate, σ	0·1
Exponent linking growth rate and cost, n	1·5
Fecundity, F	0·3
Mature body size, MM	1

Results

USING R_0 AS A FITNESS MEASURE

The effect of an increasing time-delay in the cost of growth is shown in Fig. 2. A discontinuity in behaviour occurs when the time-delay is equal to the optimal maturation time ($t_d = t_m$). For time-delays that exceed the optimal maturation time, the effect of increasing the delay is to weaken the selective strength of the growth costs, producing an increase in the optimal growth rate. Other models of growth costs (discussed later in this section) were explored, and this result was found to be a robust feature of all models. For time-delays that are less than the optimal maturation time, the behaviour of the model is to decrease optimal growth rate as the time-delay increases. Even for $t_d < t_m$, there is still a tendency for increasing t_d to weaken the selection strength on growth rate; however, there is an opposing mechanism because the growth costs are felt both before and after maturation. As t_d increases, fewer of the growth costs are felt before

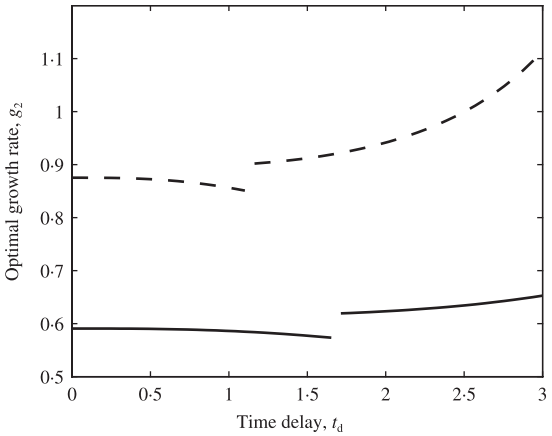

Fig. 2. The optimal growth rate as a function of the time-delay in the costs of growth. The solid and dashed lines use R_0 and r as fitness measures, respectively. The discontinuities occur when $t_m = t_d$. To the left of this discontinuity $t_m > t_d$, while to the right of this discontinuity $t_m < t_d$. For these results there was no growth limitation ($t_L = 0$) and the initial period of growth was set to zero ($t_i = 0$).

maturation. This has the same effect as decreasing the juvenile mortality and increasing the adult mortality, which acts so as to decrease the optimal growth rate. For our model this second mechanism dominates, leading to a minor decrease in optimal growth rate as the time-delay increases. Unlike the model's behaviour for large time-delays, this behaviour is not robust, so that different models of growth costs can easily change the balance between the two selective forces. As the initial period of growth, t_i, is increased, and growth limitation is considered, further discontinuities in the optimal growth rate are seen for $t_d \leq t_m$. However, the discontinuity at $t_d = t_m$ is a robust feature of this and other models.

The sensitivity of the growth rate to changes in all the parameters is shown in Table 2. Each sensitivity is the slope of the relationship between a parameter and the optimal growth rate, g_2. As the time-delay increases, the sensitivity of g_2 to all parameters generally increases. This is in keeping with the idea discussed above, where the strength of selection decreases as the costs of growth move towards later ages in an animal's life history. The sensitivity of the optimal growth rate to F can be used to assess the effect of changing F, provided that F is not functionally related to the growth strategy. Making F a function of the growth rate changes the trade-offs in our life-history model, and would require a reanalysis of the model. The problems associated with this are raised in the discussion where an adaptive mature body size is considered.

The effect of a period of growth limitation is shown in Figs 3 and 4, and by the sensitivity of g_2 to changes in t_L in Table 2. The ratio of optimal growth rates with and without limitation is used as a measure of compensatory growth. A ratio greater than 1 indicates a compensatory growth response, while a ratio less than

Table 2. Sensitivity of the optimal growth rate, g_2, to each parameter using both R_0 and r as the fitness measure and for two values of time-delay, $t_d = 0$, 3 (all values are quoted to two decimal places). Each sensitivity is the slope of the relationship between the parameter in the first column and the growth rate. Growth compensation in response to an increasing duration of growth limitation occurs when $t_d > t_m$ under a fitness measure of R_0 (shown in bold). The optimal growth strategy when $t_d = 3$ is $g_2 = 0{\cdot}74$, $t_m = 1{\cdot}41$ for a fitness measure of R_0 and $g_2 = 1{\cdot}33$, $t_m = 0{\cdot}83$ for a fitness measure of r (i.e. $t_d > t_m$ in both cases)

	Fitness measure is R_0		Fitness measure is r	
Parameter	$t_d = 0$	$t_d = 3$	$t_d = 0$	$t_d = 3$
μ_j	4·34	5·12	2·89	4·45
μ_m	3·45	5·27	−2·89	−4·45
σ	−2·08	−0·53	−9·63	−12·37
n	−1·40	−2·10	−1·64	−3·48
t_d	0·00	0·10	0·00	0·38
t_L	0·00	**0·03**	−0·20	−0·37
t_i	0·13	0·18	0·18	0·27
F	0·00	0·00	4·82	10·75
M_m	0·39	0·77	−0·58	−0·70

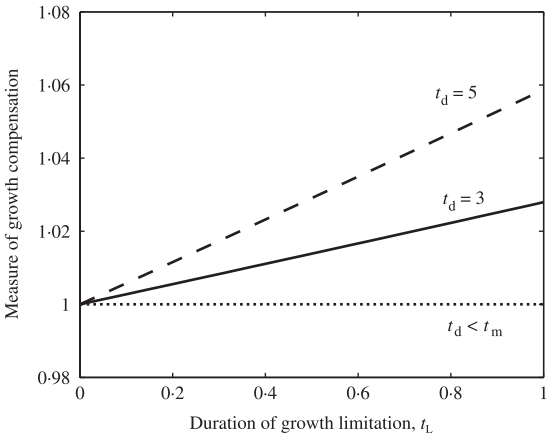

Fig. 3. Growth compensation for three time-delays as the period of growth limitation is increased (fitness measure is R_0). Growth compensation is measured as the ratio of optimal growth rates with and without limitation (compensatory growth produces a ratio greater than 1). For all time-delays less than the optimal maturation time ($t_d < t_m$) no growth compensation occurs. Growth compensation becomes stronger as the limitation becomes more severe and as the time-delay increases.

1 indicates that growth rate decreases following a period of limitation. When the time-delay is less than the optimal maturation time, growth compensation is never predicted. For these short time-delays the optimal growth rate is *independent* of the period of growth limitation, which is shown in Fig. 3 by the horizontal dotted line and in Table 2 by the zero sensitivity of g_2 to t_L when $t_d = 0$. For time-delays greater than the optimal maturation time, the model predicts compensatory growth. As the period of limitation increases the compensatory growth response becomes stronger. Even

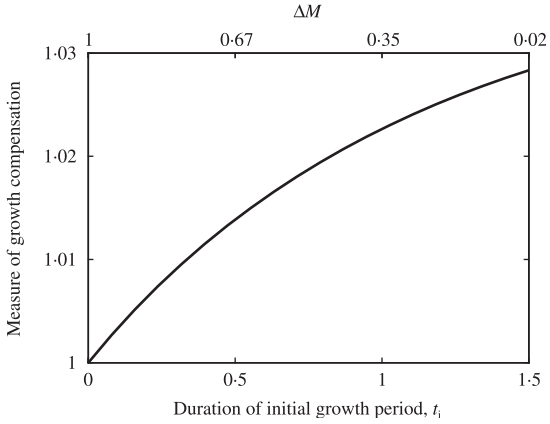

Fig. 4. Compensatory growth as a function of the time at which limitation starts (fitness measure is R_0). The time at which growth limitation starts, t_i, can be reinterpreted as a change in ΔM, and this is shown on the upper axis. The duration of the growth limitation is fixed at $t_L = 0{\cdot}5$ and the time-delay in the growth costs is $t_d = 3$.

large time-delays, where the costs of growth occur late in an animal's life history, have an impact upon the adaptive pattern of its growth. Compensatory growth also increases as the time-delay increases. The prediction of compensatory growth when $t_d > t_m$ seems to be a robust prediction which can be reproduced for several other models of growth costs. For example, changing the function linking growth rate to cost conserves the qualitative properties of the model provided that there is sufficient acceleration of damage with increasing growth rate. Letting the growth cost be a function of the maximum past growth rate also predicts adaptive compensatory growth.

Growth limitation can occur at any point during an animal's development. The effect of a growth limitation at different stages of development was investigated by varying t_i (Fig. 4). Increasing t_i has two direct effects. Firstly, it means that the animal is larger, and therefore closer to maturity when the growth limitation occurs (i.e. a smaller ΔM). Secondly, it means that the accumulated growth cost is larger when limitation occurs.

The plastic response to delaying growth limitation until later in an animal's development is a stronger growth compensation response (provided that the time-delay exceeds the maturation time). From Fig. 4 it is unclear whether this response is related to the effect of t_i on ΔM or its effect on the accumulated growth cost at limitation. Further simulations (not presented) which varied M_m while keeping t_i constant showed that decreasing M_m on its own (which decreases ΔM) decreased the compensatory growth response. This shows that it is the accumulated growth cost that is responsible for the behaviour shown in Fig. 4. Furthermore, decreasing M_m is equivalent to varying the initial size of an animal at $t = 0$. The model predicts that increasing M_m will increase optimal growth rate, so that animals that are initially small will grow faster, and the variance in body size will decrease as a cohort of equally aged animals develops.

Finally we investigated the effect of including two time-scales in the model. Growth costs were assumed to have both an immediate and a delayed effect, with both having the same mortality rate (changing the relative importance of the two time-scales had no qualitative effect). The effect of adding an immediate growth cost was to increase the optimal growth rate, in accordance with other life-history models of adaptive growth (Stearns 1992). In response to a period of growth limitation, catch-up growth was still found to be adaptive even in the presence of an immediate growth cost, but the strength of the compensation was slightly reduced.

USING *r* AS A FITNESS MEASURE

In order to gauge the importance of the fitness measure upon the results of the model, the intrinsic population growth rate, r, was also used as a proxy for fitness. Results are expected to differ from those where R_0 is used, but will the qualitative results remain?

The sensitivity of the optimal growth rate to all parameters for fitness measures of both R_0 and r are shown in Table 2. Comparing the signs and relative magnitudes of the sensitivities for the two fitness measures shows many similarities. The response of the optimal growth rate to changes in the time-delay for both fitness measures is shown in Fig. 2. The same qualitative behaviour emerges; large time-delays allow the optimal growth rate to increase, but there is a discontinuity when the time-delay is equal to the maturation time. For time-delays shorter than the maturation time, growth rate decreased with increasing t_d. However, the behaviour for $t_d < t_m$ is not robust to changes in the model linking growth rate to the growth costs. Changing the fitness measure from R_0 to r preserves many of the qualitative properties of the model.

Differences between the results for the two fitness measures are seen with the parameters μ_m, σ, t_i, F and M_m. Importantly, when r is the fitness measure, the effect of increasing the period of growth limitation is to decrease the optimal growth rate. So the prediction of compensatory growth is not robust to changes in the fitness measure. The decrease in optimal growth rate with increasing limitation becomes more pronounced as t_d increases, showing that a time-delay selects for a subnormal growth rate following limitation. The optimal intrinsic population growth rate was varied by changing the fecundity parameter F, but this had no qualitative effect upon our results.

Discussion

The results of the growth model have an intuitive explanation. The simplest result from the model is that the greater the time-delay of a cost, the less important it is in regulating an animal's optimal growth rate. This

is apparent in both the increase in the optimal growth rate, and the increase in the sensitivity of the adaptive growth rate as t_d increases. This result is not surprising, since it bears many similarities to current theories of ageing, where the later in life a cost is felt, the weaker is the selective force associated with the cost (Rose 1991). A more surprising result from the model is that a time-delay in the cost of growth can produce compensatory growth as an adaptive response to growth limitation. Sibly *et al*. (1985) point out that an adaptive strategy is determined by an animal's present state and its reproductive future, not its past. This argument suggests that compensatory growth cannot generally be an adaptive response because when growth limitation is removed, the period of limitation is in the past. For compensatory growth to be adaptive it has been argued that the environment must be time-dependent (Sibly *et al*. 1985; Sibly & Calow 1986; Ludwig & Rowe 1990; Rowe & Ludwig 1991; Abrams *et al*. 1996), such as a seasonal variation in breeding success (Abrams *et al*. 1996). Objections may be raised against this argument: the state of an animal may be changed by growth limitation, some fitness measures do not allow past and future to be simply split (e.g. intrinsic population growth rate, r), the past state of an organism may have implications for its reproductive future.

This last objection is relevant for a time-delayed cost of growth. The effect of a time-delay is to move the growth costs, which were incurred before and during the period of limitation, into an animal's reproductive future. This allows a period of growth limitation to have implications for the animal's reproductive future, which in turn permits an adaptive compensatory growth response. This mechanism appears to be fairly robust to changes in the model's formulation, although it is not expected to be completely general. An example of the model's robustness is seen with the assumption that the initial growth rate is the optimal growth rate with no limitation (which is plausible if growth limitation is a rare and unexpected event). However, the qualitative results of the model hold for any initial growth rate, provided that growth is not complete before the onset of limitation and that the initial growth rate is the same for all growth limitation scenarios (i.e. an individual cannot predict how its growth limitation will differ from the rest of the population). So if growth limitation were a regular occurrence then the initial growth rate may depend upon the *expected* growth limitation, but the qualitative results of this model will not be affected.

The robustness of our result suggests that time-delayed costs will have broad implications for life-history theory. We suggest that any adaptive trait that is constrained for a limited period can produce an adaptive response once the constraint is removed, provided that the costs associated with the trait have a delayed effect. Delayed costs, such as maternal effects, may have more implications than just their cost, since they may also entail adaptive changes in life histories. Adaptive responses to delayed costs would increase the diversity of life histories within a population. The dependence of this variation upon factors such as the typical time-scale of the delay, or the severity and frequency of the cost within the population should be goals for future research.

The compensatory growth predicted by our model was not robust to the measure of fitness, but the reason for this is not intuitively obvious. When the fitness measure is R_0, growth limitation moves an animal closer to its future growth costs without any reproductive benefit, and this favours an increase in growth rate. The same adaptive pressure also exists when the fitness measure is intrinsic population growth rate, r, but in this case there is a second factor to consider. A period of growth limitation reduces the intrinsic population growth rate, and this makes late reproduction relatively more important, therefore favouring a decrease in growth rate. The outcome between these two opposing adaptive forces will depend upon the relationship between growth rate and the costs of growth, making the outcome of using r as a fitness measure difficult to predict. Although there is no one fitness measure that is universally applicable, studies using a stochastic environment show that R_0 is generally a more reliable indicator of an adaptive traits invasion exponent (Benton & Grant 2000). While it is important to consider several fitness measures, in order to gauge the robustness of a model's predictions, the results of Benton & Grant (2000) suggest that out of R_0 and r, the results from R_0 are more likely to have general applicability.

The literature on life-history models of animal growth is extensive (e.g. Kozłowski & Wiegert 1986; Sibly & Calow 1986; Ludwig & Rowe 1990; Rowe & Ludwig 1991; Kozłowski 1992; Perrin 1992; Stearns 1992; Houston, McNamara & Hutchinson 1993; Engen & Sæther 1994; Abrams *et al*. 1996; Mangel & Stamps 2001). Previous growth models incorporating a cost of growth have considered adaptive growth rates and compensatory growth, but the topic of a time-delay to these costs of growth has not been addressed despite evidence that time-delays do exist (Metcalfe & Monaghan 2001), and that they are likely to have important consequences for population and ecosystem processes (Beckerman *et al*. 2002). Some work has looked at modelling compensatory growth. For example, Sibly *et al*. (1985) published general results on adaptive growth strategies (see also Sibly & Calow 1986), concentrating mainly upon r as their measure of fitness, and concluding that compensatory growth is not unequivocally adaptive. Abrams *et al*. (1996) followed up this work by looking at adaptive growth strategies in a seasonal environment. Their general results predict that growth rate should usually (although not always) increase as the time available to reproduce in a season decreases. Other models have considered time constraints and issues of growth (Kozłowski & Wiegert 1986; Ludwig & Rowe 1990; Rowe & Ludwig 1991; Werner & Anholt 1993), with the general conclusion being that

time constraints increase variation in growth rates, because growth strategies are generally predicted to depend upon the proximity of the time constraint as well as an animal's state. Broekhuizen *et al*. (1994) suggested a physiological model of compensatory growth that does not require a time-varying environment. Their model assumes animals partition resources between two types of tissue (tissues that can be re-mobilized and those that cannot), and that behaviour changes in response to the ratio of these two tissues. Tests of their model on data from salmonids have shown a good fit between data and model (Broekhuizen *et al*. 1994).

Comparison between our model's predictions and data show some qualitative agreement. As with other growth models, increasing the cost of growth (σ) generally reduces growth rate, as observed in insects (Nylin & Gotthard 1998), although in other animal groups the data are conflicting (Arendt 1997). An increasing extrinsic mortality risk during growth (μ_j) is predicted to increase growth rate, suggesting that any comparison with data must make a clear distinction between growth-related mortality, and extrinsic mortality. A reduced initial body size is predicted by the model to cause an increase in growth rate, which is observed in rats (McCance & Widdowson 1962), and the lack of correlation between birth or hatching weight and mature weight has been frequently pointed out (Wilson & Osbourn 1960). The time at which growth limitation occurs is also important: in cattle and sheep for example, compensatory growth tends not to be seen in animals that are growth limited either when very young or when close to maturity (Donovan 1984; Ryan 1990). The model predicts that early growth limitation (small t_i) gives little or no compensatory growth. However, the model fails to predict that compensatory growth should decrease when the period of limitation is near maturity. This could be because the model considers the mature body size as a fixed parameter, while in reality it too can show adaptive variation (Blanckenhorn 2000).

In natural systems mature body size will vary, and some of this variation may be adaptive. The question of when to stop increasing in body size is a difficult issue to model because the costs and benefits of different body sizes are not clear, and depend largely upon the system being studied (Sibly *et al*. 1985; Bernardo 1993). However, if body size is to have an adaptive explanation (Reiss 1989) our model raises some questions.

If increasing body size increases fecundity (Peters 1986; Reiss 1989) then growth rate can only be submaximal if some growth costs are felt before the end of growth. So if both body size and maturation time are adaptive, there are two possibilities: either there is one main mechanism underlying the costs of growth, which must act before maturity, and compensatory growth cannot be adaptive, or if compensatory growth is to be adaptive there must be at least two time-scales for the costs of growth, one of which must act before maturity and one after maturity. Extending our model to include immediate as well as delayed costs of growth produces no difference in qualitative behaviour. This suggests that when mature body size and time to maturation are both adaptive, compensatory growth may still occur, provided the selective gradient for body size against growth limitation is greater than that for maturation time (i.e. mature body size is relatively constant).

The number of studies observing delayed growth costs is increasing (e.g. Metcalfe & Monaghan 2001; Blount *et al*. 2003; Ozanne & Hales 2004) to such an extent that delayed costs seem more predominant than immediate costs, although an objective review of the importance of these different cost time-scales is needed. Our model of adaptive growth shows that the time-scale of growth costs has important mechanistic consequences for optimal growth rates. An increasing time-delay in growth costs allows the optimal growth rate to increase, and the selective strength of the optimum to decrease. The model highlights the maturation time as a threshold time-scale for adaptive growth strategies: only growth costs that act after an animal has reached maturity provide an adaptive explanation for compensatory growth, without any further assumptions about the environment. Furthermore, the intuitive understanding of the model suggests that time-delays in other life-history problems will be important in determining phenotypic plasticity. Delayed life-history effects are emerging as an important factor in a population's dynamics (Beckerman *et al*. 2002), and our study shows that time-delays in life-history costs can affect an animal's life-history strategy. An understanding of these effects requires data in order to assess the relevant time-scale of a cost, and to distinguish clearly between extrinsic mortality and the mortality associated with an adaptive trait.

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