

Unexpected discontinuities in life-history evolution under size-dependent mortality

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In many organisms survival depends on body size. We investigate the implications of size-selective mortality on life-history evolution by introducing and analysing a new and particularly flexible life-history model with the following key features: the lengths of growth and reproductive periods in successive reproductive cycles can vary evolutionarily, the model does not constrain evolution to patterns of either determinate or indeterminate growth, and lifetime number and sizes of broods are the outcomes of evolutionarily optimal life-history decisions. We find that small changes in environmental conditions can lead to abrupt transitions in optimal life histories when size-dependent mortality is sufficiently strong. Such discontinuous switching results from antagonistic selection pressures and occurs between strategies of early maturation with short reproductive periods and late maturation with long reproductive cycles. When mortality is size-selective and the size-independent component is not too high, selection favours prolonged juvenile growth, thereby allowing individuals to reach a mortality refuge at large body size before the onset of reproduction. When either component of mortality is then increased, the mortality refuge first becomes unattractive and eventually closes up altogether, resulting in short juvenile growth and frequent reproduction. Our results suggest a new mechanism for the evolution of life-history dimorphisms.

Keywords: life-history model; size-dependent mortality; growth; time allocation; state-dependent decisions; bifurcation

1. INTRODUCTION

Body size strongly influences survival in many organisms. Predation risk and over-winter survival, for example, may critically depend on body size (e.g. Sogard 1997). Yet, life-history evolution under size-dependent mortality is still not fully understood. Body size results from an ontogenetic growth process that, in turn, is influenced by size-dependent life-history decisions and ecological conditions (reviewed by Roff 1992). Size-dependent production rates are a key assumption of theoretical studies focusing on evolutionarily optimal patterns of energy allocation (reviewed by Kozłowski (1992) and Perrin *et al.* (1993)). Consequently, body size has been identified as an important factor determining life-history decisions in many organisms (e.g. Roff 1992). However, size-dependent mortality rates have received surprisingly little attention in general models of life-history evolution. Even though some earlier investigations considered size-dependent mortality (Sibly *et al.* 1985; Kozłowski & Wiegert 1987; Vance 1992a,b; Perrin *et al.* 1993; Heino & Kaitala 1996), its general implications for evolutionarily stable patterns of growth and reproduction have not yet been systematically explored.

In this paper, we introduce a flexible life-history model to investigate evolutionary patterns of growth and reproduction when both mortality and production rates can

vary with body size. The model divides the lifetime of an individual into reproductive cycles, with each cycle comprising a period of somatic growth followed by a period devoted to reproduction. To avoid confounding interferences between evolving life-history patterns and those imposed by external influences, we consider non-seasonal environments. The model presented here is unusually versatile in that it allows the length of growth and reproduction periods to vary evolutionarily in all reproductive cycles. This flexibility allows us to encompass potential patterns of determinate and indeterminate growth in a single model. In addition, the expected number and size of broods can vary in the course of life-history evolution. Such generality has not been considered in earlier models, even though considerable variation in inter-brood periods is well documented in nature (e.g. Reznick & Endler 1982).

We elucidate the dependence of optimal life-history decisions on the variation of three ecological factors, the growth potential of the environment, and the magnitude of the size-independent and size-dependent components of mortality. According to results by Sibly *et al.* (1985), Kozłowski & Wiegert (1987), Vance (1992a,b) and Perrin *et al.* (1993), gradual variation of these three factors is expected to translate into continuous changes in evolutionarily optimal life histories. Surprisingly, however, our model shows that environmental changes of small magnitude may induce large and abrupt shifts in optimal life histories. Such shifts are associated with transitions from early maturation and short inter-brood intervals to late maturation and long reproductive cycles. Although simi-

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larly abrupt transitions are well known to occur in many nonlinear dynamical systems (where they are referred to as catastrophic bifurcations; e.g. Abraham & Shaw 1992), it would appear that the potential for such discontinuities prominently to affect life-history evolution has previously been overlooked.

2. MODEL DESCRIPTION

(a) *Life-history model*

We focus on life histories that can be divided into alternating, non-overlapping periods of growth and reproduction. Surplus energy (i.e. energy in excess of maintenance needs) is fully allocated either to somatic growth or to energy accrual for a clutch. At the end of each bout of growth and reproduction (hereafter termed 'reproductive cycle'), energy invested in reproduction is fully released in the form of offspring. The lengths of the time periods devoted to growth and reproduction are the evolving life-history variables in our model. No limit was imposed on the duration of these periods. The life-history 'decisions' depend on the individual state that is given by body size.

(i) *Growth and reproduction*

For simplicity, we assume that size at birth is zero. Size is measured as length and is denoted by s . The weight w of individuals is assumed to depend on their length according to a general allometric relation,

$$w = \alpha s^\gamma, \quad (2.1)$$

where α is a scaling constant and γ is the allometric exponent. Unless otherwise stated, we assume a cubic relationship between weight and length ($\gamma = 3$). We assume that growth is linear and occurs with a rate g throughout growth periods. Thus, during a growth period of length T_g , an individual increases its length by gT_g . This simple linear growth model implies that the size-specific weight production rate is $g\alpha\gamma s^{\gamma-1}$. Fecundity, F , is the product of this rate and the time T_a invested into energy accrual before release of a clutch, divided by the weight w_0 of an egg or newborn

$$F(s, T_a) = \frac{g\alpha\gamma}{w_0} s^{\gamma-1} T_a. \quad (2.2)$$

(ii) *Survival*

We assume that mortality rate depends on body length s according to

$$m(s) = m_i + m_d \exp\left(-\frac{s}{s_0}\right), \quad (2.3)$$

and is composed of a size-independent component, m_i , and a size-dependent component. The magnitude of the latter is determined by m_d , while the parameter s_0 characterizes at which length the size-dependent component of mortality drops to $1/e = 36.8\%$, relative to its value at size $s = 0$. The general shape considered for $m(s)$ is applicable to a variety of empirically determined dependences of mortality on size (see § 4). The survival probability p over a period of time from t_0 to t_1 is now given by

$$p = \exp\left(-\int_{t_0}^{t_1} m(s(t)) dt\right). \quad (2.4)$$

This equation can be simplified because size increments are constant during growth periods, and no growth occurs during reproductive periods. Thus, survival can be conveniently expressed in terms of size s at the beginning of a reproductive cycle and the durations T_g and T_a allocated to growth and reproduction, respectively

$$p(s, T_g, T_a) = \exp\left(-\int_0^{T_g} m(s + gt) dt\right) \exp(-m(s + gT_g)T_a), \quad (2.5)$$

where the two factors describe survival during growth and reproductive periods, respectively. Based on the chosen function, m , the remaining integral can be solved analytically. We allow for an additional instantaneous cost of reproduction M , which can be envisaged as the probability of females dying immediately after releasing their offspring.

(b) *Evolutionarily optimal life histories*

We assume that density dependence acts multiplicatively on reproductive success. Under that assumption, the density of conspecifics does not influence the optimal life-history decisions of individuals, and the optimal reproductive strategy (corresponding to an evolutionarily stable strategy, or ESS) maximizes expected lifetime reproductive success (Mylius & Diekmann 1995).

The expected lifetime reproductive success R_0 is the sum of reproductive output from all reproductive cycles c , with the latter being given by the product of fecundity F_c in cycle c and survival probability p_c up to that cycle

$$R_0 = \sum_{c=1}^{\infty} F_c p_c \quad (2.6)$$

with $F_c = F(s_c + gT_{g,c}T_{a,c})$ and

$$p_c = (1 - M)^{c-1} \prod_{c'=1}^c P(s_{c'}, T_{g,c'}, T_{a,c'}), \quad (2.7)$$

where s_c is the expected size at the onset of reproductive cycle c , and $T_{g,c}$ and $T_{a,c}$ are the life-history decisions in cycle c .

The optimization algorithm used to find the ESS ($T_{g,1}^*$, $T_{a,1}^*$, $T_{g,2}^*$, $T_{a,2}^*$, ...) based on this expression is described in Appendix A.

(c) *Model reduction*

At first sight, the model described in § 2a,b comprises eight free parameters: α , γ , w_0 , g , m_i , m_d , s_0 and M . To simplify the further analysis, we extract the model's essential dimensionless parameters.

We first observe that two of the model parameters have no influence on the ESS: α and w_0 influence lifetime reproductive success only multiplicatively, and thus do not affect the qualitative dependence of R_0 on the evolving life-history variables. Without influencing the evolutionary analysis we can thus assume that $\alpha/w_0 = 1$.

Four model parameters specify mortality and growth rates and have the dimensions of size (s_0), time⁻¹ (m_i and m_d), and size \times time⁻¹ (g). Without any loss of generality, these four parameters can be combined into two dimensionless ratios

$$r_i = m_i \frac{s_0}{g} \quad \text{and} \quad r_d = m_d \frac{s_0}{g}. \quad (2.8)$$

By choosing convenient units for size (s_0) and time (s_0/g), we can now remove two out of the four parameters: in the chosen units, both s_0 and s_0/g assume the value 1. Hence, increases in r_i can result from a strengthening of the size-independent component of mortality, from a shallower decrease of mortality with size, and/or from a decrease in growth potential. Analogously, increasing values of r_d result from a strengthening of the size-dependent component of mortality, from a shallower decrease of mortality with size, and/or from a decrease in growth potential.

Thus, by varying only three dimensionless parameters (r_i , r_d and M) the model's full range of possible environmental settings can be explored. In addition, the allometric exponent γ can be altered. For reasons that will become evident in the course of the further analysis, we refer to r_i and r_d as the model's primary parameters, and to M and γ as the model's secondary parameters.

3. RESULTS

(a) Common features of optimal life histories

Our analysis shows that, in all model environments, optimal life histories share several qualitative features. First and most importantly, in any given environment an optimal size is always reached at the end of one continuous growth period in the first reproductive cycle before the onset of reproduction. Afterwards no further growth occurs. Optimal size is the same for all reproductive cycles during an individual's life because decisions depend on size, but not on age *per se*. Hence, all optimal life histories in our model follow a pattern of determinate growth, even though we did not *a priori* constrain the mode of growth in any way.

Second, the initial growth period is followed by multiple reproductive periods, resulting in iteroparous reproduction. Again, the mode of reproduction was not constrained *a priori*. Within an individual's life, the optimal time spent on the acquisition of energy for reproduction is the same for all reproductive cycles because reproductive investment always starts out from the same optimal size.

According to these two qualitative features of optimal life histories, the life cycles of individuals are always divided into (i) a pre-reproductive or immature period during which the optimal size is reached, and (ii) a reproductive or mature period, consisting of reproductive bouts of equal lengths, during which the lifetime reproductive success is accrued. We can thus describe optimal life histories with only two life-history variables: the duration T_g^* of the first growth period ($T_{g,1}^* = T_g^*$, $T_{g,2}^* = T_{g,3}^* = \dots = 0$) and the duration T_a^* of the first and all subsequent reproductive periods ($T_{a,1}^* = T_{a,2}^* = \dots = T_a^*$).

Based on this result, the calculation of lifetime reproductive success can be greatly simplified. Survival to the end of the first growth period is $p_g = p(0, T_g, 0)$, survival over one reproductive cycle is $p_a = p(gT_g, 0, T_a)$, and fecundity in each cycle is $F_a = F(gT_g, T_a)$. The lifetime reproductive success of any candidate life history (T_g, T_a) can hence be evaluated as

$$R_0 = \frac{p_g p_a F_a}{1 - (1 - M)p_a}$$

The previously arduous optimization task (see Appendix A) is thus reduced to a two-dimensional problem. Optimal

life histories can now be found easily, for example, by applying Powell's method (Press *et al.* 1992, pp. 309–317). The following results are based on this simplified algorithm. We first focus on cases in which the cost of reproduction, M , is small and the allometric exponent, γ , is set to its most likely value at $\gamma = 3$.

(b) Influence of primary model parameters on optimal life histories

For small r_i , variation of r_d affects optimal strategies only weakly (figure 1*a,b*). Increasing r_i leads to a shortening of growth and reproductive periods. For larger r_i , both periods become shorter with increasing r_i and r_d , with the effect of r_i being weaker than that of r_d .

For low r_d values, increasing r_i leads to a continuous change from life histories with long growth periods and late maturation towards life histories with short growth periods and early maturation. For higher r_d values, however, increasing r_i results in an unexpected abrupt transition between life histories with long and with short periods of growth and reproduction. This discontinuous switch of life-history strategies is accompanied by a kink in the fitness surface (figure 1*c*, black line). Figure 1*d* summarizes the established optimal life histories schematically.

A closer look at the fitness of possible decisions in different sample environments illustrates what happens at the life-history switch. While for small r_d only a single fitness maximum exists (figure 2*a,b*), two local fitness maxima are present for larger r_d . At the life-history switch (i.e. along the black curve in figure 1*d*), these maxima are of equal height. Above the black curve, for slightly larger r_i and/or r_d , life histories with short periods of growth and reproduction are globally optimal (figure 2*c*), whereas below this curve this applies to long periods of growth and reproduction (figure 2*d*).

The so-called cusp bifurcation underlying all discontinuities described in this paper is shown in figure 3*a*. The resultant projection in figure 3*b* highlights the mortality conditions that allow for two locally optimal life histories (conditions within the grey wedge). Natural populations may achieve a switch between the alternative optimal strategies in two scenarios.

- (i) If there are sufficient candidate life histories present in a population that is situated between the two local optima, or if feasible mutational steps are large enough, we expect that evolution can always attain the global optimum since it 'samples' both fitness maxima. Rapid switches to the highest maximum are expected at environmental conditions for which the fitness functions corresponding to the two local optima intersect (figure 3*c*).
- (ii) If mutational steps are small, a population could track the globally optimal life history only when passing through a fitness minimum (grey line in figure 3*d*). Such populations will rather adhere to a locally optimal life history (stippled lines in figure 3*d*) until, through ongoing environmental change, the tracked local fitness maximum disappears (by colliding, in one dimension, with the local fitness minimum, or, in two dimensions, with a fitness saddle). The remaining single fitness maximum can then be attained through directional selection. Slow

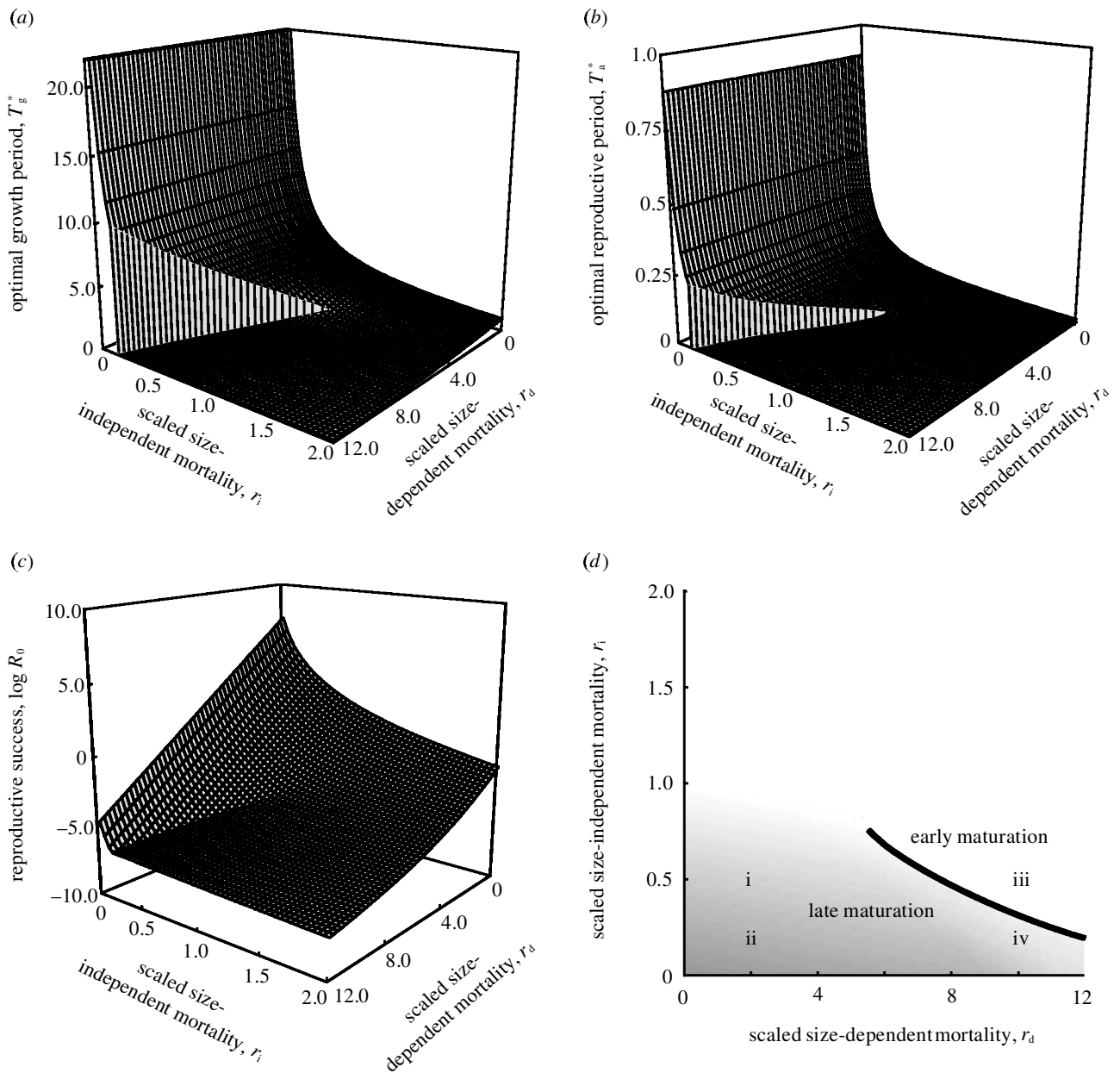


Figure 1. Influence of the environmental parameters r_d and r_i on the evolutionarily optimal (a) time invested in growth, T_g^* , and (b) time invested in the accrual of energy for reproduction, T_a^* . (c) Resultant lifetime reproductive success R_0 . The black curve highlights the kink corresponding to the discontinuities in optimal life histories. (d) Schematic overview of life-history regimes. The black curve shows the location of discontinuous transitions of optimal life-history strategies T_g^* and T_a^* , while the numbers i–iv indicate the parameter combinations for which fitness landscapes are illustrated in figure 2. Other parameters: $M = 0.001$ and $\gamma = 3$.

environmental change may thus drive a population's life history from one fitness maximum to another. If this occurs repeatedly through environmental fluctuations, the optimal life history exhibits a hysteresis.

(c) Influence of secondary model parameters on optimal life histories

In § 3b, the effects of environmental parameters r_d and r_i were explored for fixed values of M (the instantaneous costs of reproduction) and γ (the allometric exponent in the size–fecundity relationship). The response of optimal life histories towards variation of r_d and r_i remains qualitatively the same when M and γ are varied.

Quantitatively, a reduction of the cost M results in reduction of the time invested in reproduction. At the limit in which the cost approaches zero, reproductive cycles become infinitely short, i.e. reproduction becomes continuous. Importantly, however, variation of M leaves the position of the cusp in the r_d – r_i diagram (figure 1 and figure 3a,b) essentially unaffected.

When decreasing the exponent γ , the tendency of evolutionarily optimal growth and reproductive periods to increase with r_d becomes more pronounced. For γ equal to 1, the cusp leaves the r_d – r_i diagram (figure 1 and figure 3a,b) at $r_d = 0$. The general importance of the life-history switches highlighted in this paper is underscored by the fact that even for γ values smaller than 1, the dependence

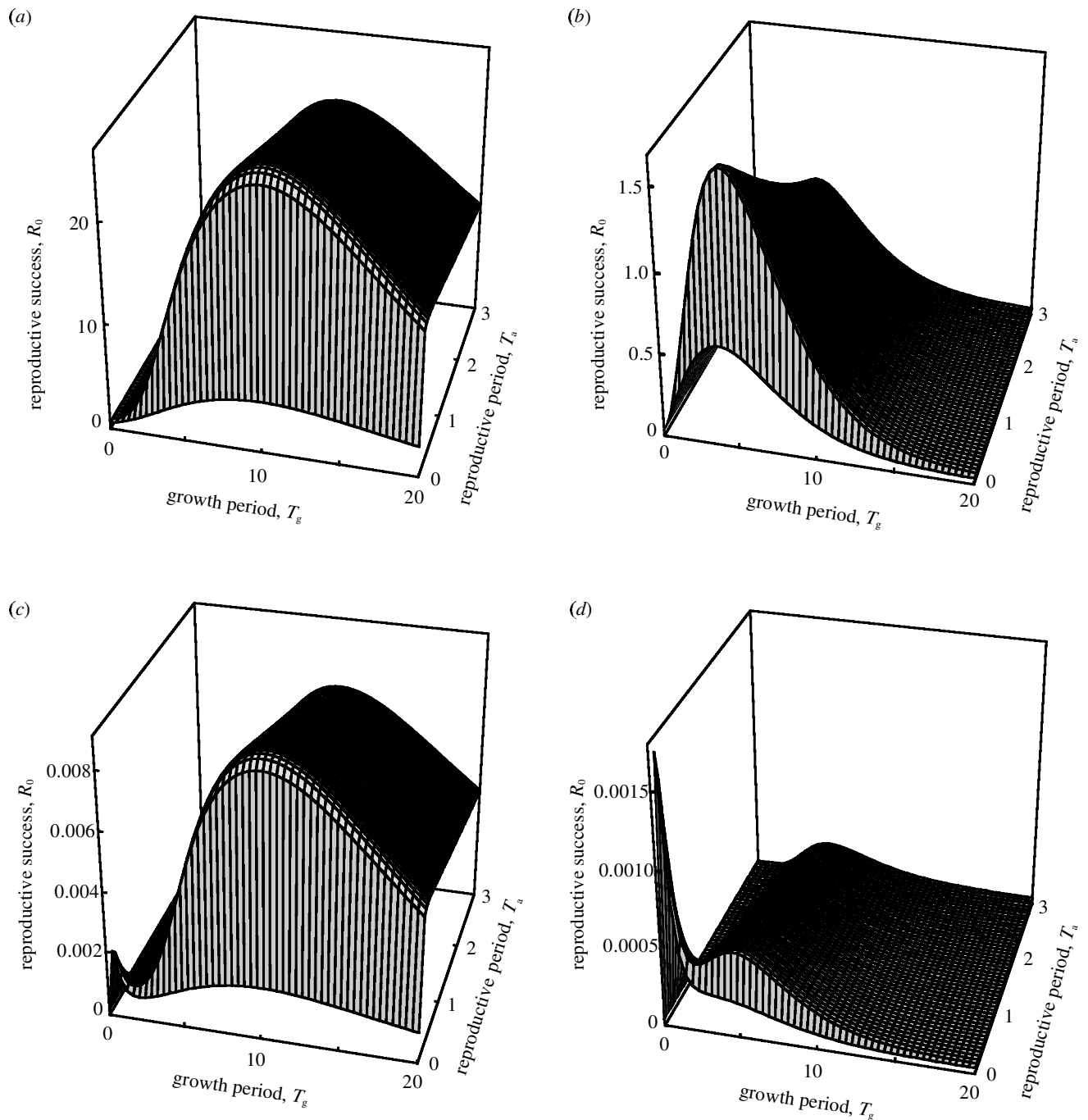


Figure 2. Lifetime reproductive success of all possible life-history strategies with $0.001 < T_g^* < 20$ and $0.001 < T_a^* < 3$ for (a) $r_d = 2$, $r_i = 0.5$; (b) $r_d = 2$, $r_i = 0.2$; (c) $r_d = 10$, $r_i = 0.5$; and (d) $r_d = 10$, $r_i = 0.2$. Note the drastic change in the relative magnitude of the two local maxima between (c) and (d) that straddle the life-history discontinuity in figure 1d. Other parameters: $M = 0.001$ and $\gamma = 3$.

of life-history decisions on the model's primary parameters remains discontinuous.

4. DISCUSSION

Our model predicts discontinuous transitions between dissimilar life histories. We expect such discontinuities for a wide range of environmental conditions in which size-dependent components of mortality are sufficiently large and not dominated by size-independent components. They can occur both for locally adapting populations along environmental gradients in space and in evolving

single populations through environmental change over time. In the course of transitions, life histories change abruptly from early maturation with frequent reproduction to late maturation with long reproductive cycles.

Qualitative jumps of life-history strategies along gradients in non-fluctuating environments were not observed in previous models of life-history evolution. Outside of the range of environmental conditions that lead to discontinuous transitions, in particular when size-dependent mortality is absent or weak, our model agrees with earlier findings by Kozłowski & Wiegeert (1986) in that increasing size-independent mortality leads to a continuous decrease

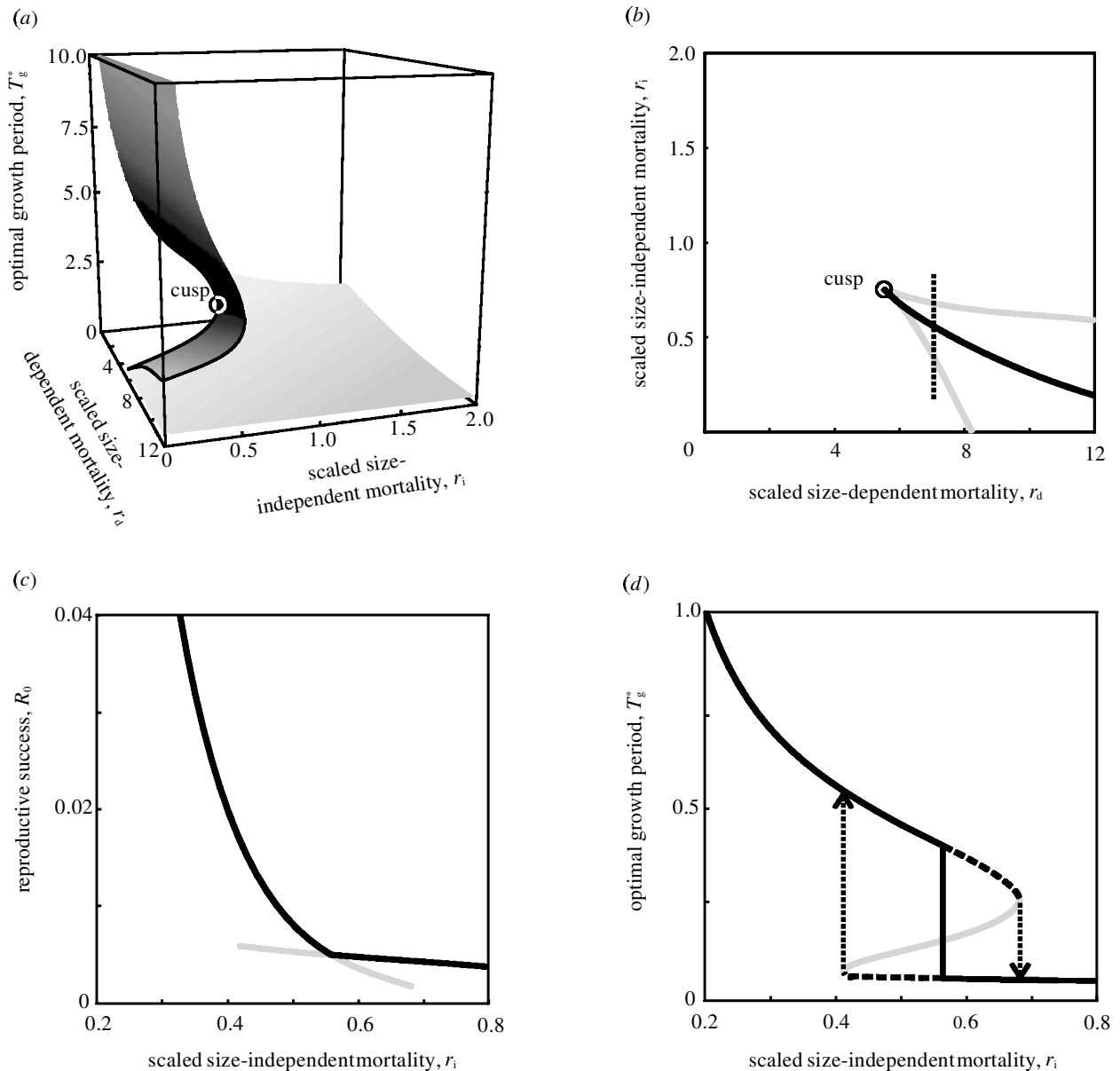


Figure 3. (a) The cusp bifurcation. The folded surface shows the variation of T_g^* with r_i and r_d . For some values of r_i and r_d , evolutionary equilibria are reached at three values of T_g . In these cases, the inner value corresponds to an unstable equilibrium (saddle; corresponding parts of surface are outlined in black), whereas the outer values correspond to alternative evolutionary attractors at local fitness maxima (see also (b)). (b) Overview of evolutionary bifurcation curves. The black curve indicates the environmental conditions for which the two local fitness maxima swap rank. The grey curves describe the conditions that lead to the disappearance of one of the two local maxima through collision with the intermediate fitness saddle. As indicated by these bifurcation curves, the discontinuity found in our model represents a cusp bifurcation. The dashed line highlights the position of the cross-section illustrated in the subsequent panels. (c) Cross-section of figure 1c: variation of R_0 with r_i at $r_d = 7.0$ for the two local fitness maxima. The values R_0^* at the global fitness maximum are shown in black, and those of the alternative local maximum in grey. (d) The cross-section of figure 1a: variation of T_g^* with r_i at $r_d = 7.0$, showing the resulting discontinuous life-history switches. The continuous black curve highlights the position of global fitness maxima, and the grey curve that of fitness minima. The dashed curves describe the position of local fitness maxima that are not global fitness maxima. The vertical dotted lines indicate abrupt evolutionary transitions that result from the disappearance of a local fitness maximum. Other parameters: $M = 0.001$ and $\gamma = 3$.

of immature growth and reproductive periods. Orzack & Tuljapurkar (2001) found bimodal fitness landscapes to occur in life-history evolution under high stochastic environmental variability, but the local optima were not observed to switch ranks in this study. Evolutionary bifurcations were observed in reaction norms for morphological traits by Van Dooren (2001), but in dynamic environments with temporal oscillations in the fitness optimum,

and with a time lag between life-history decisions and their fitness consequences. To our knowledge, models of life-history evolution allowing for a level of flexibility in life histories similar to the model introduced here, with reproductive periods of arbitrary length, have not been analysed before. We have shown that, despite this flexibility, our model comprises only two salient environmental parameters and only two salient life-history variables, which

provides an attractive compromise between generality and tractability.

The discontinuity predicted by our model may be interpreted biologically as the outcome of two antagonistic selection pressures. Negative size-selective mortality may select for phenotypes reaching a 'mortality refuge' by growing quickly to a large body size, i.e. without any delay incurred by reproduction. For example, some bivalve species start to reproduce only after growing to a refuge size at which they are safe from their major predator (Nakaoka 1998). Increasing levels of size-dependent mortality select for a prolongation of the initial growth period. At high mortality, however, long initial growth periods result in very low probabilities of survival to first reproduction. Eventually, an alternative life-history strategy with short periods of growth and reproduction becomes optimal. Especially size-unselective mortality strongly selects for shorter immature growth periods and smaller sizes at maturation (Roff 1992; Reznick *et al.* 1996). Environments with sufficiently high size-dependent mortality and relatively low size-independent mortality may thus create a mortality refuge that vanishes abruptly when mortality increases.

Evolutionarily optimal life histories such as those found in our model may be expressed by different genotypes, each adapted to a different environment, or by a single genotype exhibiting a reaction norm in response to the conditions of mortality and growth that it actually experiences. In both cases, populations with a bimodal distribution of life-history strategies are likely to exist under certain environmental conditions. In a number of species, adult size and life history differ markedly within a local area, ranging from normal forms to 'dwarfs' with stunted growth (reviewed in Roff 1992). Usually, dwarfs mature earlier and live for a shorter time than individuals with normal growth (Roff 1992). In some populations of fish (e.g. smelts *Osmerus* spp. (Taylor & Bentzen 1993); Arctic charr *Salvelinus alpinus* (Parker *et al.* 2001); lake whitefish *Coregonus clupeaformis* (Trudel *et al.* 2001)) and invertebrates (e.g. red-sea urchin *Strongylocentrotus franciscanus* (Botsford *et al.* 1994)), the extremes at both ends of this size spectrum coexist sympatrically, with a truly bimodal distribution of adult size and corresponding life histories. Such coexisting life-history morphs can lie anywhere on a spectrum between ecological polymorphisms (through phenotypic plasticity) and genetically distinct groups without gene flow (Taylor & Bentzen 1993; evidence reviewed in Parker *et al.* (2001)).

Even though we did not prescribe the growth pattern in our model in any way, optimal phenotypes exhibit determinate growth across all modelled environments. Previous life-history models found indeterminate growth to be optimal only under restrictive environmental conditions (e.g. unpredictable season length), physiological or morphological constraints, or age-dependent mortality (reviewed in Cichon (1999) and Heino & Kaitala (1999)). The universal occurrence of determinate growth in our model was therefore not unexpected, as we did not include such specific assumptions.

Below we critically review the assumptions included in our analysis. Empirical relevance and checks of robustness are considered where possible, and alternative approaches are briefly discussed.

- (i) Our results are presented for a mortality function consisting of a constant level and an exponential function of size. Such a relation has provided excellent fits to empirical data in species with size-dependent mortality (Hutchings 1993; F. Bashey, personal communication). Alternatively, size-dependent mortality can be modelled as a hyperbolic function, $m(s) = m_i + m_d/(1 + s/s_0)^\beta$. Owing to the additional parameter β , a hyperbolic model allows more flexibility when fitting it to data. Assuming a hyperbolic function does not qualitatively alter the results presented here. For $\beta > 1$, two local fitness maxima and discontinuities in the global optimum always occur and, across all model environments, we find optimal life-history patterns with determinate growth.
- (ii) We assumed that the environmentally determined growth potential is constant, resulting in a linear increase in size during growth periods. This assumption may appear simplistic. However, many ectotherms show linear growth of structural size early in life, sometimes even until maturation (e.g. American plaice *Hippoglossoides platessoides* (Roff 1983); cod *Gadus morhua* (Jørgensen 1992); fire salamander *Salamandra salamandra* (Alcobendas & Castanet 2000); freshwater clam *Anodonta grandis* (Hanson *et al.* 1988)). We chose linear growth to avoid the impact of a predefined growth model on optimal life-history decisions. Any growth model depending on length or weight would inevitably influence size-dependent life-history decisions (Czarnoleski & Kozłowski 1998).
- (iii) There is ample evidence that reproductive activities may reduce survival. For example, mating itself may reduce female survival, conspicuous reproductive behaviours may increase predation risk, or a lowered body condition may enhance the susceptibility to stress and diseases (reviewed in Roff 1992). In the model, we expressed costs of reproduction in a very general way, as instantaneous costs affecting survival after the release of offspring. Costs of reproduction did not influence any model results qualitatively, but when approaching zero, led to infinitely short reproductive periods.
- (iv) We assumed that fecundity was proportional to weight production rate (which is a power function of size (e.g. Roff 1983)) and not limited by physiological or morphological constraints. When testing the robustness of the results to these two assumptions we found no qualitative change when (1) the allometric exponent of the size-weight relationship was varied, as long as it exceeded 1, and (2) an upper bound for clutch weight was introduced that increased with maternal weight.

In summary, our assumptions about size-dependent mortality, growth mode, reproductive costs and the nature of the fecundity-size relationship did not critically influence the model results. In particular the reported discontinuities in optimal patterns of growth and reproduction appear to be a very robust feature of life-history evolution under size-dependent mortality.

To conclude, our results show that in spatially heterogeneous or temporally varying environments small changes in mortality and/or growth conditions can induce drastic changes in optimal life histories. A generalist may perform poorly under such conditions. The divergent selection pressures near the discontinuity may facilitate the emergence of distinct ecotypes, even when environmental conditions vary gradually. Our results could therefore offer a new mechanism for the emergence of ecological polymorphisms—which, in turn, may lead to genetic differentiation and eventually even to sympatric speciation.

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APPENDIX A: OPTIMIZATION ALGORITHM

We use a dynamic optimization algorithm (see Houston & McNamara 1999; Clark & Mangel 2000) to determine optimal life histories. In our model, the optimal life-history decisions during a given reproductive cycle depend only on the size of an individual at the onset of the cycle (size is the only state variable, since there is no explicit age dependence of demographic rates) and on the fitness consequences of the decisions in the current cycle. The latter can be decomposed into (i) the fitness gain from the current cycle (i.e. the product of the survival probability to the end of the cycle and the fecundity realized then), and (ii) the fitness contributions from future reproductive cycles (given by the product of the survival probability to the end of the cycle and the reproductive value at that stage).

Reproductive values thus depend on all life-history decisions in an individual's future. Therefore, they are initially unknown and have to be found through a process of backward iteration. The general procedure can be summarized as follows. First, reproductive values for all relevant sizes are set to zero. Second, optimal decisions are determined for all relevant sizes, given the current estimates of size-specific reproductive values. Third, the estimates are updated with the reproductive values obtained as the result of the optimal decisions. Fourth, the second and third steps are repeated until convergence is achieved, that is, until reproductive values do not significantly change any more. From this, optimal decisions at all relevant sizes are determined.

More precisely, the following optimization algorithm has been used in this study.

- (i) Initialize the optimization procedure by setting to zero the reproductive values $R(s)$ for each of n evenly spaced sizes between $s = 0$ and $s = s_{\max}$.

- (ii) For each size s , search for the life-history decisions $T_g(s)$ and $T_a(s)$ that confer the highest reproductive value

$$(T_g(s), T_a(s)) = \arg \max_{(T_g, T_a)} R'(s, T_g, T_a), \quad (\text{A } 1)$$

given the current size-specific reproductive values $R(s)$,

$$R'(s, T_g, T_a) = p(s, T_g, T_a) [F(s + gT_g, T_a) + R(s + gT_g)]. \quad (\text{A } 2)$$

- (iii) For each size s , replace $R(s)$ with $R'(s, T_g(s), T_a(s))$.
- (iv) Repeat steps 2 and 3 until the convergence criterion

$$\frac{1}{n} \sum_{s=0}^{s_{\max}} \left[\frac{R(s) - R'(s, T_g(s), T_a(s))}{R(s)} \right]^2 < c \quad (\text{A } 3)$$

is met.

After convergence has been achieved, for each size s at the beginning of a reproductive cycle we obtained the optimal life-history decisions $T_g^*(s)$ and $T_a^*(s)$, together with the corresponding reproductive values $R^*(s)$. The optimal life history is then determined by forward iteration: starting at age and size zero at the onset of the first reproductive cycle, individuals grow and reproduce according to the obtained optimal life-history decisions.

To ensure that the global optimum has been identified in step 2 instead of a local one, we utilized a combination of exhaustive and simplex search (Press *et al.* 1992, pp. 305–309). The exhaustive search is used initially for searching for local maxima on a pre-defined grid of values (T_g, T_a) ; a subsequent simplex search is then used for fine-tuning the coarsely established globally optimal life-history decisions through local search. We used $n = 100$ size classes, with s_{\max} (the largest size considered) re-set iteratively, when necessary, such that the maximum size corresponding to the optimal life history is within the range of 20–80% of s_{\max} . Quadratic interpolation was employed to obtain reproductive values for sizes falling between size bins, and a value of $c = 10^{-6}$ was used in the convergence criterion.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.