

## **A note on the timing of tradeoffs in discrete life history models**

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### **Abstract**

We discuss the timing of tradeoffs in discrete life history models. With a simple mathematical example we show that different assumptions about the temporal order of costs and benefits resulting from a reproductive effort can lead to qualitatively different predictions. We examine two models taken from the literature, in which an implicit assumption is that benefits from reproductive efforts are received before the corresponding costs are paid. We show that the reverse assumptions would have led to very different results. Since there is no biological basis for a bias towards a particular set of assumptions, we conclude that a more flexible approach should be used when studying optimality problems that are based on discrete life histories.

### **Introduction**

Applications of the theory of natural selection hinge upon the definition of fitness measures. For many practical purposes, the definition of such measures is based on discrete time. The basic reproductive rate  $R$ , describing the mean number of offspring produced per individual during its life, and the intrinsic rate of increase  $r$ , describing the exponential growth or decline of a population, are examples of fitness measures that are often used in their discrete form. To calculate them, one has to know the survival probabilities and fecundities of individuals at discrete points in time.

In this note we argue that the designation of the points in time at which survival probabilities and fecundities are determined is crucial, and that different assumptions about the discretization can lead to qualitatively very different biological results. This happens when fitness measures are used to study optimality models with tradeoffs between reproduction, survival, and growth. It then becomes important whether the cost of the reproductive effort in a particular year is paid before

or after the benefit from the effort is received. Different assumptions about the cost-benefit timing lead to models with potentially very different solutions of the corresponding optimality problem. Below we illustrate this with a simple mathematical example. Since the usual notation in discrete life history models almost automatically induces a bias towards one particular set of assumptions about the cost-benefit timing, existing results about optimizing reproductive effort may also be biased. We discuss two examples from the literature and show how the results change when different assumptions are made about the timing of reproductive tradeoffs. Only few authors, among them Sibly and Calow (1984) and Caswell (1989), have called attention to the importance of cost-benefit timing, and in general the pertaining problems do not seem to be well recognized. It is our aim in this note to advocate a more careful use of discrete equations in evolutionary life history theory.

### Formulation of the problem and a simple example

In the sequel, we use the basic reproductive rate  $R$  as fitness measure. It can be defined as follows (Stearns, 1992). "Breeding events" are numbered from 1 to  $n$  and designate the points in the life of an organism at which the fecundity payoff from the reproductive effort in a particular year is received. For example, for most birds a breeding event would be the point at which the nestlings leave the nest and become independent of their parents. Then the payoff is the number of nestlings that survived to leave the nest. On the other hand, for many fishes the breeding event is the point at which eggs are released into the water, in which case the payoff is the number of eggs released. We denote by  $m_x$  the payoff received at breeding event  $x$ , and by  $l_x$  the probability to survive from "birth" to breeding event  $x$ , where "birth" corresponds to the breeding event from the viewpoint of the offspring, e.g. the instant when leaving the nest as a young bird or when being released as an egg into the water. The quantity  $l_x m_x$  is the payoff from breeding event  $x$  weighted by the probability to receive this payoff. The survival  $l_x$  is partitioned into period survivals:

$$l_x = J \cdot p_1 \cdot \dots \cdot p_{x-1}. \quad (1)$$

$J$  is the juvenile survival rate, i.e. the probability to survive from birth to the first breeding event. The  $p_i$ ,  $i = 1, \dots, x-1$ , are the probabilities of survival from breeding event  $i$  to breeding event  $i+1$ . Thus, the lifetime survival and fecundity schedule of an individual is given by two sets of numbers  $\{J, p_1, \dots, p_n\}$  and  $\{m_1, \dots, m_n\}$ , where  $n$  denotes the last breeding event and can be interpreted as the lifespan of the individuals. The basic reproductive rate is now defined as:

$$R = \sum_{x=1}^n l_x m_x, \quad (2)$$

where the  $l_x$  are given by (1). In an evolutionary context the question is, given certain constraints, what is the survival and the fecundity schedule that maximizes  $R$ ?

Constraints are often given by tradeoffs between reproduction and survival, a pattern believed to be common in natural populations (Roff, 1992; Stearns, 1992). If there is a tradeoff between reproductive effort and period survival, the payoff  $m_x$  at breeding event  $x$  is proportional to reproductive effort, and a higher  $m_x$  can only be obtained at the expense of a lower period survival. However, there is an ambiguity as to which period survival is sacrificed for higher fecundity. The index notation used so far suggests that the tradeoff should be between  $m_x$  and  $p_x$ , and indeed this is what is usually assumed when studying this type of model (Gadgil and Bossert, 1970; Schaffer, 1974; Charlesworth and Léon, 1974; Pianka and Parker, 1975; Schaffer and Rosenzweig, 1977; Taylor, 1986; Roff, 1992; Stearns, 1992; Charlesworth, 1994). One assumes a relationship

$$p_x = g_x(m_x), \quad x = 1, \dots, n, \quad (3)$$

where the functions  $g_x$  determine the form of the tradeoff, and the index  $x$  in these functions indicates that the tradeoff may be different in different years. A reproductive strategy then consists of a set of numbers  $\{m_1, \dots, m_n\}$  that determine the reproductive effort for each breeding event (for simplicity, we have equaled reproductive effort and fecundity, which constitutes no loss of generality if we assume that fecundity is proportional to reproductive effort).

Because we assumed that there are only  $n$  breeding events, the period survival  $p_n$  does not affect  $R$  (see eqs. (1) and (2)). Therefore, reproduction in the last breeding event has no cost, so that the last reproductive effort will always be maximal in an optimal reproductive strategy. In fact, this reflects the general bias in the formulation of the problem that we want to point out. Assuming that  $m_x$  trades off with  $p_x$  is equivalent to assuming that the benefit of the reproductive effort for a particular breeding event is always received *before* the cost in form of lower survival is paid: since  $p_x$  is the survival probability from the breeding event  $x$  to breeding event  $x+1$ , it does not appear in the expression (1) for  $l_x$ , which means that the weighting factor for the payoff  $m_x$ , i.e., the probability of survival from birth up to receiving the payoff, does not depend on the investment made for the payoff. This may sometimes be realistic, but often it is not. For example, the reproductive effort of birds with parental care consists not only of producing and incubating the eggs, but also of caring for the nestlings over an extended period after hatching. Such care typically involves great expenditure of energy while searching for food, and may also incur other costs, e.g. in form of exposure to predation. The payoff is the number of fledglings that leave the nest, and is only received after an extended period during which the parents have risked their lives in order to receive the payoff. Not only will there be no future reproduction if the parents die due to the reproductive effort in a particular year, but the payoff from that year will also be zero. Such a situation is more accurately modeled by assuming a tradeoff between  $m_x$  and  $p_{x-1}$ . Then the reproductive effort to obtain the payoff from breeding event

$x$  affects the probability of survival up to the instant the payoff is received. In the model, one would then replace eq. (3) by

$$p_{x-1} = g_x(m_x), \quad x = 1, \dots, n. \quad (4)$$

There is now a period of survival  $p_0$  that determines the probability of receiving the payoff from the first breeding event, and which is in general  $< 1$  due to the effort made to receive this payoff. Thus  $l_x$  has now the form

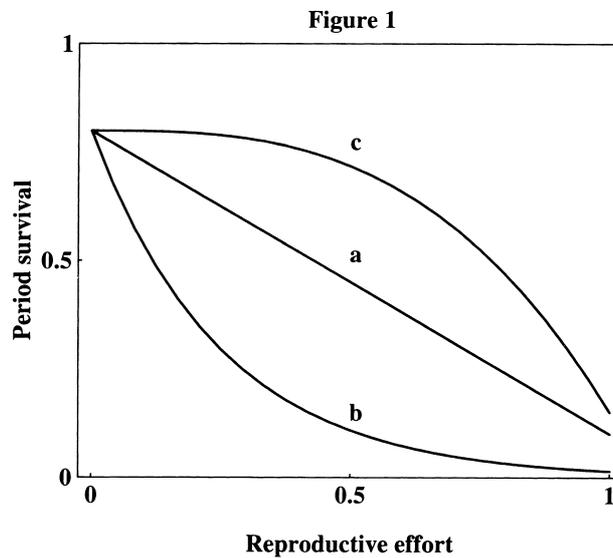
$$l_x = J \cdot p_0 \cdot p_1 \cdot \dots \cdot p_{x-1}. \quad (5)$$

As before, a reproductive strategy consists of a set of reproductive decisions  $\{m_1, \dots, m_n\}$ , which lead to period survivals  $p_0, p_1, \dots, p_{n-1}$  by applying eq. (4). Using eq. (5) one can then calculate the reproductive rate  $R$  that is associated with the reproductive strategy.

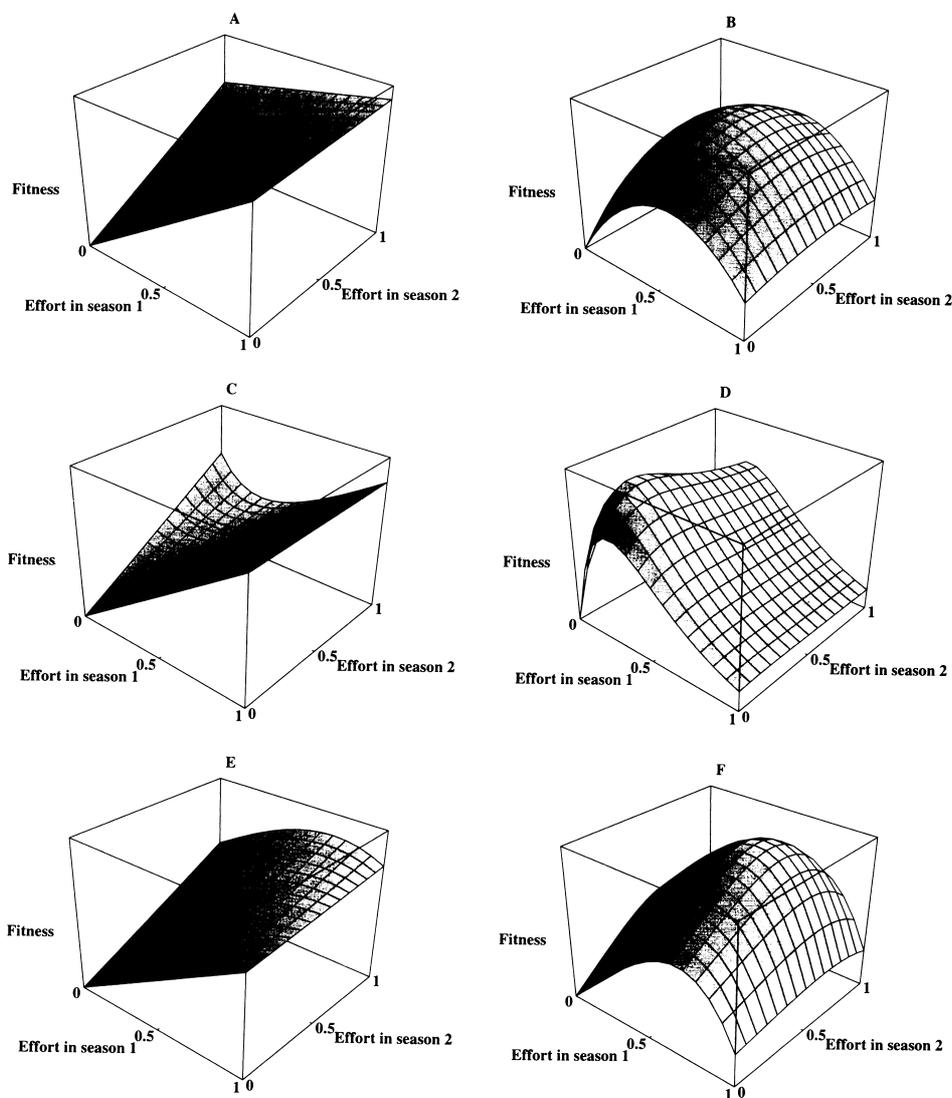
Whereas the first model corresponds to receiving the benefit of an effort before the cost is paid, in the second model the cost is paid first, and then the benefit received. Here is a simple arithmetic example showing that the two models can lead to quite different results. We consider two breeding events with a linear tradeoff function that does not change with age (Fig. 1a). Therefore, in the first model

$$p_x = a \cdot m_x + b, \quad x = 1, 2, \quad (6)$$

while



**Fig. 1.** Three different reproductive tradeoffs. The curves determine period survival as a function of reproductive effort  $m_x$ , which is scaled to values between 0 and 1. The decline in survival is linear in case a, convex in case b and concave in case c. The curves are given as follows:  $g(m_x) = a \cdot m_x + b$  for the linear tradeoff, with  $a = -0.7$  and  $b = 0.8$ ;  $g(m_x) = c \cdot \exp(-d \cdot m_x)$  with  $c = 0.8$  and  $d = 4.0$  for the convex curve;  $g(m_x) = e - f \cdot m_x^3$  with  $e = 0.8$  and  $f = 0.65$  for the concave tradeoff.



**Fig. 2.** Fitness landscapes for the tradeoffs in Fig. 1. 2A and 2B: linear tradeoff (Fig. 1a); if payoffs are received before costs are paid (2A), the maximum is at the vertex (1, 1). If payoffs are received after costs are paid (2B), the intermediate strategy ( $m_1^* = 0.457$ ,  $m_2^* = 0.571$ ) is optimal. 2C and 2D: convex tradeoff (Fig. 1b); if payoffs are received before costs are paid (2C), the maximum is at the vertex (1, 1). Note that there is also a local optimum at the vertex (0, 1). If payoffs are received after costs are paid (2D), the intermediate strategy ( $m_1^* = 0.176$ ,  $m_2^* = 0.250$ ) is optimal. 2E and 2F: concave tradeoff (Fig. 1c); if payoffs are received before costs are paid (2E), an intermediate value  $m_1^* = 0.716$  for the reproductive effort in the first season and a maximal reproductive effort in the second season is optimal. The optimum changes to ( $m_1^* = 0.588$ ,  $m_2^* = 0.675$ ) if payoffs are received after costs have been paid (2F). In all cases, the effect of breeding on survival in the first season is much less severe in the second model than in the first.

$$p_{x-1} = a \cdot m_x + b, \quad x = 1, 2 \quad (7)$$

in the second model. We assume that the reproductive effort  $m_x$  can take on values between 0 and 1, corresponding to 0% and 100% of the available resources allocated to reproduction. Thus the parameter  $b$ , which is the period survival in the absence of reproduction, must lie between 0 and 1. The parameter  $a$  determines the severity of the reproductive costs. It is negative with  $|a| < b$  in order to avoid negative values for  $m_x$ . Finally, we assume that juvenile survival is 1. Since juvenile survival occurs in all expressions  $l_x$ ,  $x \geq 1$ , and hence in all summands of eq. (2), this assumption does not affect the results from optimality calculations. In the first model we now have

$$\begin{aligned} l_1 &= 1 \\ l_2 &= am_1 + b, \end{aligned} \quad (8)$$

and the corresponding expression for  $R$  is

$$R = m_1 + (am_1 + b) \cdot m_2. \quad (9)$$

Thus  $R$  is linear in both  $m_1$  and  $m_2$ , and the corresponding fitness landscape is shown in Fig. 2A. It is clear that in the set of all possible strategies, i.e. in the unit square  $[0, 1] \times [0, 1]$ , the strategy corresponding to the vertex (1, 1) confers the highest fitness. Thus it is optimal to always reproduce with maximal effort. If the costs of reproduction are high, i.e. if the parameter  $a$  in the tradeoff (6) has absolute value close to  $b$ , such a strategy would correspond to semelparity in the simple scenario considered here.

In the second model, the survival values for a given strategy are

$$\begin{aligned} l_1 &= am_1 + b \\ l_2 &= (am_1 + b) \cdot (am_2 + b), \end{aligned} \quad (10)$$

which leads to

$$R = (am_1 + b) \cdot m_1 + (am_1 + b) \cdot (am_2 + b) \cdot m_2. \quad (11)$$

$R$  is now quadratic in both  $m_1$  and  $m_2$ , and the corresponding fitness landscape is shown in Figure 2B. Typically, there is an intermediate optimum, which can be calculated using the derivatives of eq. (11) with respect to  $m_1$  and  $m_2$ . For example, when reproductive costs are high ( $|a|$  is close to  $b$ ), then the optimal  $m_1$  is less than 0.5 and also less than the optimal  $m_2$ , and the resulting “iteroparous” strategy is qualitatively different from the optimal strategy in the first model. Therefore, even in this very simple scenario, the two models, “benefit received before cost is paid” and “cost paid before benefit is received”, lead to quite different results.

The above is but a simple arithmetic example to illustrate the point that different assumptions about the timing of tradeoffs in discrete life history models can lead to qualitatively different outcomes. Using various analytical and numerical techniques, a similar analysis can be performed for more complicated scenarios. For example,

similar phenomena as for linear tradeoffs can be observed for non-linear tradeoff functions in eqs. (3) respectively (4) (Fig. 1b and 1c). This is also illustrated in Fig. 2, both for convex and concave tradeoffs. In addition, the analysis can be extended to more than two breeding seasons, and in Blarer et al. (1995) we have described a method how one can deal with potentially infinite lifespans. If we apply this method to the example discussed above, we obtain the same qualitative results. Other fitness measures, such as the intrinsic rate of population increase calculated from the Euler-Lotka equation, are also sensitive to the cost-benefit timing. For example, results with this fitness measure for two breeding seasons with a tradeoff between survival and reproduction as in the examples above would look very similar to those shown in Fig. 2. Based on these examples and on the results from the next section, we predict that in many discrete life history models the optimal reproductive strategy will depend strongly on the assumptions about the cost-benefit timing of tradeoffs.

### Two examples from the literature

In most discrete time models that use reproductive tradeoffs to determine optimal life histories, the implicit assumption is that benefits from reproductive efforts are received before the corresponding costs are. Therefore, it is interesting to see how the results from such models change when this assumption is reversed, and we now examine two examples from the literature.

The first is a model which Schaffer (1974) and Schaffer and Rosenzweig (1977) used to study the evolution of semelparity and the existence of alternative life histories. Their basic model describes organisms without age structure and with a potentially infinite lifespan. It uses the discrete Euler-Lotka equation to determine the fitness from the following data. For a given yearly reproductive effort  $E$ ,  $b(E)$  is the fertility at age at maturity;  $g(E)$  is the rate at which fertility increases with age due to growth of the organism; and  $p(E)$  is the yearly survival probability, with  $p(1) = 0$ , i.e. 100% reproduction leads to death. The Euler-Lotka equation then has the form

$$1 = \sum_{x=1}^{\infty} b(E) \cdot g(E)^{x-1} \cdot p(E)^{x-1} \cdot \exp(-rx). \quad (12)$$

In the terminology of the last section,  $b(E)g(E)^{x-1}$  is the fecundity of an  $x$ -year old and corresponds to the quantity  $m_x$ , while  $p(E)^{x-1} = l_x$  is the survival probability to breeding event  $x$ . Thus there are only  $x-1$  factors  $p(E)$  occurring in  $l_x$ , and since  $p(E)$  is the yearly survival (independent of  $x$ ), this implies that  $p_x$  is not a factor of  $l_x$ , i.e. that costs are paid after benefits are received. (Note that in this model the juvenile mortality  $J$  is incorporated in the quantity  $b$ .) Given a reproductive effort  $E$ , the corresponding intrinsic rate of increase  $r$  is given by eq. (12). In fact, it is easy to see (s. Schaffer, 1974, p. 293) that maximizing  $r$  is equivalent to maximizing the sum

$$b(E) + p(E) \cdot g(E). \quad (13)$$

It follows that the optimal reproductive effort depends on the shape of the curves  $b(E)$  and  $p(E)g(E)$ . Schaffer (1974) discusses various cases, and in particular analyzes when  $E = 1$ , leading to death after the first reproductive event and hence to semelparity, is optimal. He also extended the model to organisms with age structure, for which the task is to optimize in each year a quantity that is related to (13), namely

$$b_x(E) + p_x(E) \cdot g_x(E) \cdot \frac{v_x}{v_0}. \quad (14)$$

Here the  $v_x$ ,  $x = 1, 2, \dots$  are the reproductive values at age  $x$ , scaled to the size of the organism. For a detailed discussion of eq. (14) see Taylor (1986). Schaffer (1974) and Schaffer and Rosenzweig (1977) discuss several cases in which optimization of (14) leads to semelparous life histories.

How do these formulas change when the assumption “benefits received before costs are paid” is reversed? As we argued in the last section, this would correspond to including the survival probability  $p_x$  as a factor in the expression for  $l_x$ , hence to assuming  $l_x = p(E)^x$ . The Euler-Lotka equation (12) then becomes

$$1 = \sum_{x=1}^{\infty} b(E) \cdot g(E)^{x-1} \cdot p(E)^x \cdot \exp(-rx), \quad (15)$$

and using similar arguments as in Schaffer (1974), it is again easy to see that the optimal reproductive effort  $E$  now maximizes the quantity

$$p(E) \cdot b(E) + p(E) \cdot g(E). \quad (16)$$

Similarly, one can check that in the age-structured case, in each year the quantity

$$p_x(E) \cdot b_x(E) + p_x(E) \cdot g_x(E) \cdot \frac{v_x}{v_0} \quad (17)$$

must be maximized. Thus, the effect of changing the timing of the tradeoff is multiplication of the fertility  $b$  by the yearly survival  $p$  in the formulas determining the optimal reproductive effort. This is intuitively clear, and we do not want to go into the details of how the various predictions of Schaffer and Rosenzweig are affected. But one thing is obvious: since  $p(1) = 0$  by assumption, expressions (16) and (17) will both be 0 for a reproductive effort of 100%, and hence semelparity will never be optimal, irrespective of the shapes of the various curves involved! Thus, the assumption “benefits received *after* costs are paid” has a significant qualitative effect on the conclusions drawn from this model.

Our second example is again an allocation model and concerns the problem of whether somatic growth and reproduction should be separated in time. If resources can be allocated to either growth or reproduction, many models predict so-called bang-bang strategies to be optimal, in which all resources are allocated to growth during a first part of the life, and after a single and complete switch all resources are allocated to reproduction during the remainder of life. In contrast, Kozlowski and Uchmanski (1987) devised an elegant model yielding an optimal strategy

consisting of a gradual switch from growth to reproduction: in successive years a bigger and bigger proportion of the available resources is allocated to reproduction, and there is a range of years in which resources are divided between growth and reproduction. In their model, the resource can be regarded as time, and in each of a finite number of years a fraction  $f$  of the year is devoted to reproduction, while a fraction  $1-f$  is allocated to growth. A tradeoff is incorporated by assuming that the rate of producing offspring is size dependent. Thus, allocating time to growth increases future fecundity at the cost of time allocated to reproduction in the present year. For a given size  $w$ , the rate of offspring production is  $aw^b$ , where  $a$  and  $b$  are parameters describing this allometric relationship. If reproduction in a given year starts when size is equal to  $w$ , then the fecundity, i.e. the number of offspring, in that year is therefore  $f \cdot aw^b$ . It is further assumed that size  $w = s(t)$  is an increasing, polynomial function of the total time  $t$  allocated to growth (Kozłowski and Uchmanski, 1987).

In this model, a reproductive strategy is given by a set of numbers  $f_1, \dots, f_\omega$ , where  $\omega$  is the lifespan. Kozłowski and Uchmanski (1987) use the basic reproductive rate  $R$ , eq. (2), as fitness measure. To determine the survival probabilities, they assume that mortality only occurs in the winter, so that survival is constant throughout the time of growth and reproduction. Thus they assume that the period survival is strategy-independent and equal to a constant  $p$ , and that  $l_x = p^{x-1}$ . The fecundities  $m_x$ ,  $x = 1, \dots, \omega$ , are determined by the reproductive strategy through

$$m_x = f_x \cdot aw_x^b. \quad (18)$$

Here  $w_x$  is the size of the organism when it starts to reproduce in year  $x$ . It is in determining this size that the timing of the tradeoff is crucial for the results.

Kozłowski and Uchmanski (1987) assumed that in each year, growth occurs before reproduction. Thus, before the onset of reproduction in year  $x$ , the organism has allocated a total of  $t_x = (1-f_1) + (1-f_2) + \dots + (1-f_x)$  years to growth, and accordingly, its size at reproduction is

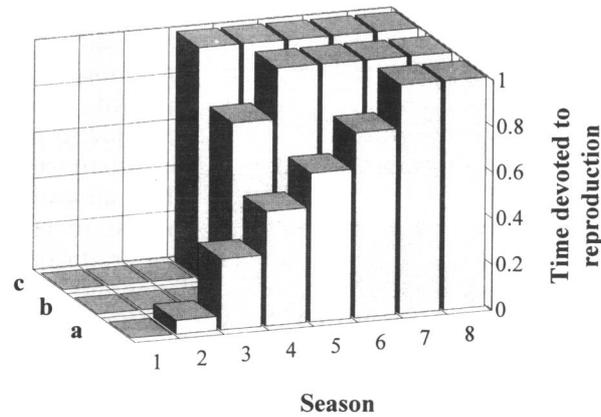
$$w_x = s(t_x). \quad (19)$$

With these assumptions, Kozłowski and Uchmanski found that the strategy resulting in the highest value of  $R$  is typically a gradual switch strategy. To solve the optimality problem they used the techniques of optimal control theory. In contrast, we used the numerical technique described in Blarer and Doebeli (1996) to find the optimal strategy. The results are the same: a gradual switch is optimal. A typical example is shown in Fig. 3a.

In terms of timing, however, an alternative possibility is to assume that growth occurs *after* reproduction in each year. Then, before the onset of reproduction in year  $x$ , the organism has only devoted a total of  $t_{x-1} = (1-f_1) + (1-f_2) + \dots + (1-f_{x-1})$  years to growth, and its size at reproduction in year  $x$  is

$$w_x = s(t_{x-1}). \quad (20)$$

While in Kozłowski and Uchmanski's model (19) the benefits of growth in form of increased reproductive rates are received before the costs in form of less time



**Fig. 3.** Optimal allocation of resources to growth and reproduction for a species with a lifespan of 8 seasons. The bars indicate the optimal percentage of time devoted to reproduction in each season. In Kozłowski and Uchmanski's model, the optimal strategy results in a pattern of "graded switches". This is shown in the first row of columns in the figure (row a). If the assumption about timing of growth and reproduction is reversed, then the set of optimal reproductive decisions yields the "bang-bang strategy" shown in the last row c. An intermediate scenario is obtained with the assumption that half of the growth period occurs before and the other half after reproduction in each season (see discussion). With these assumptions, the strategy shown in row b is optimal. The strategy is more similar to c than to a. For all graphs, we used the relation  $w(t) = (1 + t)^4$  to model the growth dynamics, where  $w(t)$  is the body size after having devoted  $t$  time units (here: seasons) to growth. The rate of production is given by the allometric relationship  $a \cdot w^b$ , with  $a = 0.05$  and  $b = 0.75$ . The period survival  $p_x$  was set to  $p_x = 0.5$  for each of the eight seasons.

devoted to reproduction are paid, the converse is true with assumption (20), for which time devoted to growth in a particular year only pays off in subsequent years. Surprisingly, with this assumption the results are radically different, and the optimal strategy is typically a bang-bang strategy with a single global switch from growth to reproduction. This is illustrated in Fig. 3c. Thus, the cost-benefit timing again has a strong effect on the results of the model. It seems that for both assumptions there are examples in nature, and the lesson is again that the timing of different events in discrete life histories is very crucial.

## Discussion

In life history optimization models that involve tradeoffs whose effects are measured at discrete points in time, the outcome strongly depends on the assumptions about the cost-benefit timing. Even simple examples with a tradeoff between reproductive effort and period survival show that two qualitatively different life histories emerge as optimal solutions, depending on whether the benefit of the reproductive effort in a particular year is received before or after the corresponding

cost is paid (Fig. 2). The results generalize to more complicated settings with non-linear tradeoffs, many breeding seasons and technically more difficult fitness measures that use survival and fecundity values given at discrete points in an organism's life. For example, Schaffer's (1974) model uses the Euler-Lotka equation to calculate the fitness of organisms with a potentially infinite lifespan. Using the implicit assumption that costs are paid after benefits have been received, he concluded that whether semelparity is an optimal life history depends on the shape of the tradeoff curves. But, as shown above, in the same model semelparity is never optimal with the reverse assumption about the cost-benefit timing.

That the timing of different events in discrete-time life history models is crucial has been pointed out by Caswell (1989), who also discussed the difficulty of defining period survival in such models, but not in the context of tradeoffs between survival and reproduction. One of the few papers that deal explicitly with cost-benefit timings of tradeoffs in optimality models is Sibly and Calow (1984). These authors also concluded that the timing can affect optimal reproductive strategies, but in their particular model different timings led to different shapes of the tradeoff curves. Here we argue that even if reproductive costs are the same, individuals with different timing should often have different life history strategies.

Unfortunately, the usual notation for discrete fitness measures implies a bias towards assuming that the cost of the reproductive effort in a particular year is only paid after the benefit is received. This is so because the natural way to formulate the model is to assume a tradeoff between reproductive effort  $m_x$  and the period survival  $p_x$  with the same index. However,  $p_x$  usually denotes survival from breeding event  $x$  to breeding event  $x + 1$ , so that this year's effort does not affect last year's payoff and is only paid in form of a reduced probability to get next year's payoff. This notational bias is independent of the numbering used for the different life stages and exists in various alternative formulations of discrete fitness measures (see Charlesworth, 1994 and David et al., 1995 for discussions of notational problems in the Euler-Lotka equation). The bias towards assuming that costs are paid after benefits are received is apparent in earlier work on life history evolution (Gadgil and Bossert, 1970; Schaffer, 1974; Charlesworth and Léon, 1974; Pianka and Parker, 1975; Schaffer and Rosenzweig, 1977; Taylor, 1986; Charlesworth, 1994). Only in models that effectively describe only one breeding event is it necessary to implicitly assume that costs are paid in advance (e.g. Abrams, 1991), because otherwise there is no optimality criterion. In general, however, deviations from the traditional assumptions that benefits are received in advance were most often thought to be of marginal importance and not discussed in detail (e.g. Schaffer, 1979; Caswell, 1980; Yodzis, 1981). In contrast, we think that taking account of the timing of tradeoffs in life history models can give useful insights.

Sometimes, specific timing assumptions are so implicit that they are buried by other, seemingly harmless and obvious ingredients of a model. This is the case in the second example discussed in the previous section, where a particular cost-benefit order follows from the assumption that growth occurs before reproduction in each year of the organisms' life. If this assumption is reversed, then so is the cost-benefit timing, and the results change rather drastically from gradual switch strategies to

bang-bang strategies as the optimal life history. This illustrates again that one has to be very careful when formulating discrete models.

Of course, the biological question behind model sensitivity to cost-benefit timing is, which scenario should we expect in natural populations? Concerning energy allocation to growth and reproduction, the two cases, growth before and growth after reproduction in each year, both seem to be abundant in nature, since they often just refer to whether reproduction occurs early or late in the year. Concerning an explicit tradeoff between reproductive effort and survival, it may often be the case that the reproductive effort occurs over a relatively short period, say production of eggs over a few days, during which survival probability does not decrease significantly. The payoff is received after this short period as the amount of eggs released, and the cost of reproduction is paid later, e.g. by having to recuperate physiologically from the reproductive effort, which may affect survival to the next breeding event. On the other hand, it may also happen that survival up to the point where the payoff is received depends on the reproductive effort made for the payoff. This is typically the case with parental care: the benefit from the care is only obtained after having been exposed to greater risk due to the effort.

The two cases, “benefit received before cost is paid” and “costs paid before benefit is received”, are two extremes. In reality, there will be a mixture of the two, so that part of the costs are paid before and part after receiving the benefit. Thus, a bird which experiences greater risk during parental care may also incur costs due to physical exhaustion after the nestlings have fledged. In the model of section 2, such a situation should be described by assuming that the reproductive effort  $m_x$  trades off with both period survivals  $p_{x-1}$  and  $p_x$ . This can be done such that the total cost remains the same as in the extreme cases. For example, instead of assuming tradeoffs (3) or (4), one could assume tradeoffs of the form

$$\begin{aligned} p_0 &= \sqrt{g_1(m_1)} \\ p_{x-1} &= \sqrt{g_{x-1}(m_{x-1})} \cdot \sqrt{g_x(m_x)}, \quad x = 2, \dots, n. \end{aligned} \quad (21)$$

This would correspond to the total cost of one year being paid in two equal parts, one before and one after the payoff is obtained. If this model is applied to the scenarios with two breeding events and the tradeoffs from Fig. 1, then the fitness landscapes are very similar to the ones resulting when all costs are paid before benefits are received (Fig. 2B, D, F), and intermediate strategies are optimal in all cases. This implies that even if only part of the costs are paid in advance, the results may differ substantially from the case where the whole benefit is received in advance.

A similar result is obtained with the allocation model of Kozłowski and Uchmanski. Here, an intermediate case between the two alternatives already discussed (Figs. 3a and 3c) is to assume that growth occurs partly before and partly after reproduction in each season, e.g. by assuming that the total time devoted to growth before reproduction starts in season  $x$  is  $t_{x-1/2} = (1-f_1) + \dots + (1-f_{x-1}) + (1-f_x)/2$ , instead of  $t_x$  used in eq. (19) for the original model or  $t_{x-1}$  used in

eq. (20) for the non-standard model leading to a bang-bang strategy. If this is done for the same parameter values as in Fig. 3a and 3c, the strategy shown in Fig. 3b yields the highest fitness. For this strategy, there is a single season in which both growth and reproduction occur, and the optimal strategy is very similar to the one resulting from the non-standard model in which reproduction precedes growth in each season.

In general, some temporal overlap between costs and benefits from reproductive efforts seems ubiquitous in nature. These overlaps might span more than one season, which could change optimal life histories even more drastically than in our simple models. Therefore, the timing of costs and benefits should be taken explicitly into account when studying tradeoffs in optimality models that are based on discrete life histories.

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