

Heuristic optimization of the general life history problem: a novel approach

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Summary

The general life history problem concerns the optimal allocation of resources to growth, survival and reproduction. We analysed this problem for a perennial model organism that decides once each year to switch from growth to reproduction. As a fitness measure we used the Malthusian parameter r , which we calculated from the Euler-Lotka equation. Trade-offs were incorporated by assuming that fecundity is size dependent, so that increased fecundity could only be gained by devoting more time to growth and less time to reproduction. To calculate numerically the optimal r for different growth dynamics and mortality regimes, we used a simplified version of the simulated annealing method. The major differences among optimal life histories resulted from different accumulation patterns of intrinsic mortalities resulting from reproductive costs. If these mortalities were accumulated throughout life, i.e. if they were senescent, a bang-bang strategy was optimal, in which there was a single switch from growth to reproduction: after the age at maturity all resources were allocated to reproduction. If reproductive costs did not carry over from year to year, i.e. if they were not senescent, the optimal resource allocation resulted in a graded switch strategy and growth became indeterminate. Our numerical approach brings two major advantages for solving optimization problems in life history theory. First, its implementation is very simple, even for complex models that are analytically intractable. Such intractability emerged in our model when we introduced reproductive costs representing an intrinsic mortality. Second, it is not a backward algorithm. This means that lifespan does not have to be fixed at the beginning of the computation. Instead, lifespan itself is a trait that can evolve. We suggest that heuristic algorithms are good tools for solving complex optimality problems in life history theory, in particular questions concerning the evolution of lifespan and senescence.

Keywords: heuristic optimization; resource allocation; reproductive effort; maturation; lifespan; simulated annealing

Introduction

How should an organism optimally allocate its resources to growth, survival and reproduction? This problem, which Schaffer (1983) calls the 'general life history problem', is at the core of life history theory. It has been tackled with increasingly complex models, which Charlesworth (1990) calls 'reproductive effort models' and with progressively novel approaches to solve them (for reviews see Roff (1992) and Stearns (1992)). In this article we build on these traditions and analyse reproductive effort models with a simple numerical procedure that was originally invented to solve difficult combinatorial problems. We believe that this technique yields new insights into life history evolution.

The allocation problem is significant because many important life history traits and their evolution can be analysed in terms of resources allocated at specific ages. For example, consider an organism that can devote its resources to growth and reproduction. Given certain reproductive

trade-offs, the optimal allocation then maximizes some measure of fitness, e.g. the Malthusian parameter r . The resulting patterns of allocation can be interpreted as patterns of reproductive activity from birth to death. These patterns allow us to determine essential properties of the organism, e.g. its age at maturity, whether it should be semelparous or iteroparous, or whether its growth is determinate or indeterminate. However, some life history traits do not emerge directly from these patterns. Lifespan is one of them. Like age at maturity, lifespan is determined by a single event, namely death, but knowledge of resource allocation contains no information about this event. Rather, there is an indirect interaction between allocation patterns and lifespan. It is conventional wisdom that decisions early in life trade-off with decisions late in life and influence lifespan. Conversely, constraints on lifespan may influence allocation patterns. Therefore, lifespan should be viewed as part of an organism's life history strategy. This is not taken into consideration by optimal control theory, which is the classical tool for solving reproductive efforts models (see Schaffer (1983) and Perrin and Sibly (1993), for reviews). Optimal control theory first assumes a fixed lifespan to initialize the computation and then works successively backwards until birth, calculating the optimal allocation for each age class. This backward procedure forces us to ignore the interaction of lifespan and allocation patterns. Another drawback of optimal control theory is analytical intractability when the models become complicated. Such complications arise, for example, when fitness components such as survival depend strongly on the life history decisions of an organism. Typically, these problems can only be solved numerically. A common tool is dynamic programming (Houston *et al.*, 1988; Mangel and Clark, 1988), but the technique suffers the same pitfalls as optimal control theory where lifespan is concerned: it solves optimization problems by assuming a fixed lifespan and working its way backwards to the beginning. A general procedure for applying dynamic programming in life history theory is presented in McNamara (1991, 1993).

The purpose of this study is to apply a novel optimization technique to the general life history problem. This 'heuristic' optimization technique was introduced by Dueck and Scheuer (1990) and will be described in detail below. It has two advantages for life history optimization: it can easily be applied to complicated models, in which reproductive decisions affect survival and it is not a backward procedure, so that lifespan is free to evolve. This means that the general life history problem can be extended to questions about the co-evolution of reproductive effort with lifespan and senescence. Furthermore, the heuristic approach is distinguished by the simplicity of its algorithm and its modest requirements for input functions or data. We suggest that heuristic optimization is an appropriate tool for analysing complex reproductive effort models.

In this study we concentrate on the complications that arise when there are costs of reproduction, defined as mortalities due to reproduction, i.e. costs tied to reproductive decisions at different ages. We address the following three questions.

- (1) How is the allocation of resources to growth and reproduction affected by reproductive costs of different strengths?
- (2) How does the accumulation of reproductive costs throughout life influence the pattern of allocation?
- (3) What are the implications for the evolution of lifespan?

Heuristic optimization techniques

In 1953, Metropolis and his co-workers invented a new combinatorial technique for numerical optimization (Metropolis *et al.*, 1953). Based on this 'Metropolis algorithm', Kirkpatrick *et al.* (1983) derived the 'simulated annealing' method, named by analogy to the way metals cool down

and anneal in thermodynamics. The numerical optimization method used in this study is a simplified form of simulated annealing. It was introduced by Dueck and Scheuer (1990), who called it the 'threshold accepting' method.

Annealing methods are designed to find optimal solutions for numerical problems whose computational complexity is believed to be intractable. By definition, a problem is intractable if its computational complexity increases exponentially with the number of inputs. The intractability of many discrete problems has been conjectured but not yet proved. The most famous such problem is the travelling salesman problem (Lawler *et al.*, 1985), in which the goal is to visit X cities on the shortest possible route. If each city is to be visited only once and if the salesperson returns to his city of origin, there are $(X - 1)!/2$ possible routes. For example, if there are 800 cities on the tour, i.e. $X = 800$, one has to find the shortest route out of $799!/2$, a number whose base 10 logarithm is greater than 1973. Analytical techniques are not yet known that can tame such combinatorial explosions. The simplest but most inefficient way to find the shortest path numerically is to test systematically route by route. This procedure is not practical due to the extensive computation time required for large X . Here, annealing techniques provide a reasonable alternative: instead of looking for the optimal solution, they only find solutions that are very close to the optimal one, but they do so using a reasonably small amount of computer time (for computer coding, see Press *et al.* (1988, p. 343)). For example, for the 442 city problem, for which the exact solution is known, the threshold acceptance method finds solutions within minutes that deviate only $\sim 0.3\%$ from the shortest route (see Dueck and Scheuer, 1990). This small deviation from the best solution is the price one has to pay for reasonable computation time and, hence, the tractability of such problems.

The easiest way to understand how annealing techniques work and find (near-) optimal solutions is to imagine a fitness landscape in three dimensions. A landscape consists of valleys and mountains and the task of a mountaineer, moving on this landscape, is to find the highest peak, i.e. the global optimum. The term 'heuristic' is then best interpreted as a sort of clever wandering. The simplest rule the hiker could follow is to walk uphill only. However, in a multip peaked landscape this rule may keep one from finding the global optimum, because local optima, once ascended, represent pitfalls with no way out. Heuristic algorithms allow one to walk downwards within certain limits. The limit, described as a threshold, is wide at the beginning of the simulation, allowing almost every step uphill or downhill. As the number of iterated search steps increases, the threshold goes asymptotically toward zero, i.e. toward the simple hill climbing rule. The algorithm controlling the threshold values during the course of the computation is called the annealing schedule. It is this annealing schedule that mainly distinguishes the different annealing techniques. In contrast to the probabilistic threshold control in simulated annealing (Kirkpatrick *et al.*, 1983), Dueck and Scheuer's (1990) method is much simpler: after a certain number of iterations one multiplies the threshold by a constant number smaller than one.

Given a numerical problem, the heuristic procedure can then be summarized by the following four ingredients.

- (1) A description of all possible system configurations.
- (2) A random generator to initialize the system and rearrange these configurations.
- (3) An objective function, i.e. a fitness function containing all the trade-offs under consideration.
- (4) The annealing schedule to control the course of the simulation towards a 'freezing point', the expected optimal solution.

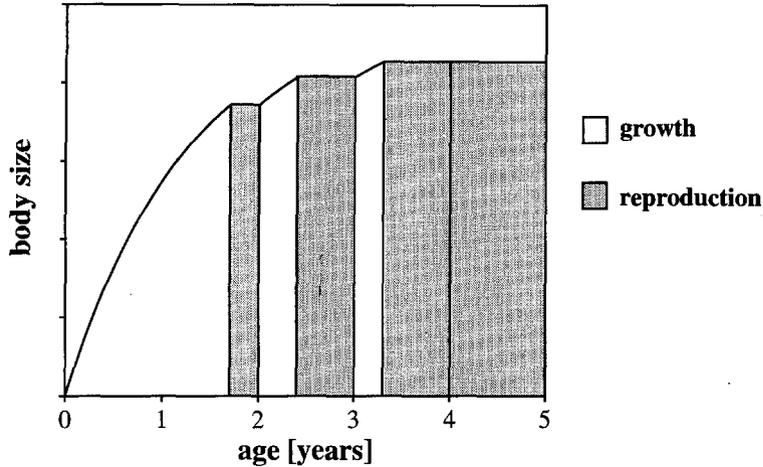


Figure 1. Representation of the lifetime energy allocation to growth and reproduction for an organism with indeterminate growth. Except for the first year there is one yearly switch from growth to reproduction. In the last year the switch occurs at the beginning of the year. Body size, and hence the size-dependent fecundity, only increase during periods of growth.

Following this recipe we applied the heuristic approach to the general life history problem as described in the next section.

The model

For our reproductive effort model we assumed an organism that lives in a constant environment for several years and devotes its resources to growth and reproduction. Within each year the organism switches once from growth to reproduction. No switch corresponds to growth during the whole year and a switch at the very beginning of a year corresponds to reproduction during the whole year. Fecundity is assumed to increase with body size. During the reproductive periods body size and hence, fecundity, remain constant (Fig. 1). This form of allocation corresponds to a Y trade-off (van Noordwijk and de Jong, 1986), where resources are exclusively divided between two vital functions. The cost of large reproductive investments is less time for growth and hence, lower fecundity. Conversely, high fecundity is achieved only at the expense of time devoted to reproduction. Using this simple trade-off, the allocation pattern of growth and reproduction is completely described by the annual decisions to switch between both vital functions. Accordingly, we defined a phenotype π to be a set of ω decisions δ_i for each year $i = 1, \dots, \omega$ where δ_i determines the moment of switch from growth to reproduction in year i :

$$\pi = \{\omega; \delta_1, \dots, \delta_\omega\} \quad (1)$$

The lifespan ω of the organism is part of the phenotype π and not initially fixed. Dividing each year i into N time intervals of equal length yields $(N + 1)$ possible values for δ_i .

$$\delta_i \in \left\{ \frac{j}{N}; j = 0, \dots, N \right\} \quad (2)$$

With $N + 1$ possible decisions in each year, there are $(N + 1)^\omega$ possible phenotypes π . For N we chose an (arbitrary) value of 40. For example, an organism living for 6 years could have more than 4.75 billion different phenotypes.

A phenotype is called optimal if it maximizes a given fitness measure. For two reasons, we chose the Malthusian parameter, i.e. the intrinsic growth rate r : first, it is the most frequently used in life history theory (Stearns, 1992; Kozłowski, 1993) and, more importantly, in contrast to the net reproductive rate R_0 , r is sensitive to the timing of reproductive decisions (see Charlesworth, 1980; Caswell, 1989). This is important because in our model a phenotype π is a set of decisions that represent the timing of reproduction. Given a phenotype π , to calculate the intrinsic growth rate one has to know the corresponding age-specific survival $l_x(\pi)$ and the age-specific fecundity $m_x(\pi)$. The growth rate is then given as the solution $r(\pi)$ of the Euler-Lotka equation:

$$1 = \sum_{x=0}^{\omega} \exp [I r(\pi) \cdot x] \cdot m_x(\pi) \cdot l_x(\pi) \quad (3)$$

Since we divided each year into $N = 40$ time steps, the age x takes on discrete values between 0 and ω with step size N^{-1} . In our model, we assumed that the age-specific fecundity m_x is a function of body size s and since growth takes place depending on the values of δ_D , size at a given age and, hence, fecundity, are determined by the phenotype π . Specifically, size s_x at age x is assumed to follow the Von Bertalanffy equation described by the function

$$s_x(\pi) = s_{\infty} \cdot (1 - \exp [-k \cdot \sigma_x(\pi)]) \quad (4)$$

where $\sigma_x(\pi)$ is the time devoted to growth up to age x for phenotype π and k denotes the growth rate of body size. For simplicity, the limiting size s_{∞} was set to 1 (or, equivalently, to 100%). Given the size $s_x(\pi)$, the fecundity of phenotype π at age x was determined as

$$m_x(\pi) = \begin{cases} [s_x(\pi)]^{\gamma} & \text{if } x - (i + 1) > \delta_i \\ 0 & \text{if } x - (i + 1) \leq \delta_i \end{cases} \quad (5)$$

The fecundity is zero during periods of growth and during periods of reproduction it is determined by the size at the end of the previous growth period using the allometric parameter γ . We assumed a cubic, fish-like relationship between body size and fecundity, i.e. $\gamma = 3$.

Age-specific survival is the second component of fitness in the Euler-Lotka equation (Equation 3). Following Charlesworth (1980, p. 12) survival from birth until age x is given by

$$l_x(\pi) = \exp \left[- \int_0^x \mu_s(\pi) ds \right] \quad (6)$$

where $\mu_x(\pi)$ is the instantaneous mortality of phenotype π at age x . We distinguished two sources of mortality, an extrinsic and an intrinsic source, which add to yield the total mortality $\mu_x(\pi)$. By definition, extrinsic sources of mortality are not sensitive to changes in reproductive decisions (Medawar, 1952). In our model we used an extrinsic, phenotype-independent mortality μ_x^e of the form

$$\mu_x^e = a \cdot \exp [b \cdot x] \quad (7)$$

with $a > 0$. This is a general form for mortalities that are either constant ($b = 0$) or increasing with age ($b > 0$). Other components of extrinsic mortality such as juvenile mortality could be introduced by adding a second exponential term of the form $a' \cdot \exp[-b' \cdot x]$ with $a', b' > 0$ (see Siler, 1979). To avoid too many case distinctions, we only used Equation 7 with a positive $b > 0$. While using constant mortalities ($b = 0$) or incorporating juvenile mortality would have changed particular results quantitatively, the basic trends in our results remained the same, as a

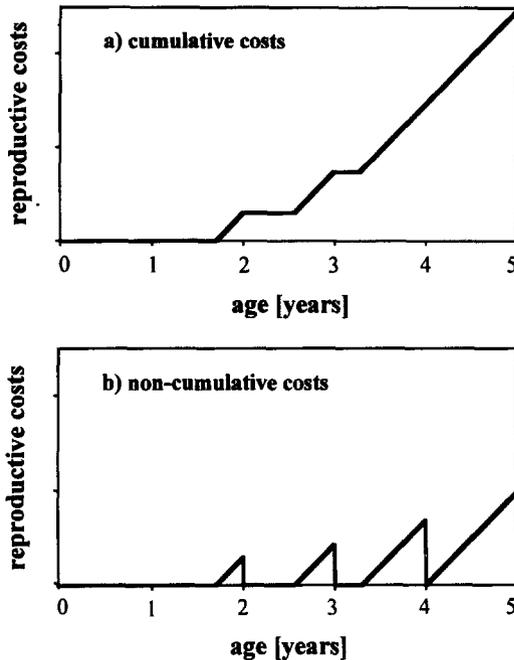


Figure 2. The two ways in which reproductive costs accumulate. (a) The intrinsic mortality caused by reproductive investments accumulates throughout life. (b) The reproductive costs only accumulate within the yearly reproductive periods, but they are not added to the intrinsic mortality of previous years. Instead, they are reset to zero at the beginning of the next year. We call these non-cumulative reproductive costs.

few selected simulations showed. In particular, the same mechanisms caused the qualitative transition from bang-bang strategies to graded switches that becomes the centre of attention below.

In contrast, an intrinsic source of mortality depends on the reproductive decisions and therefore on the phenotype π . We defined the intrinsic mortality as a linearly increasing mortality that occurs during the periods of reproduction determined by π . Thus, the intrinsic source of mortality is a cost of reproduction. The intrinsic mortality is denoted by μ_x^i and is determined as follows. For a given age x and a given phenotype π let $\rho_x(\pi)$ be either (1) the time devoted to reproduction from age 0 to age x or (2) the time devoted to reproduction from the beginning of the year in which x occurs up to age x . Then

$$\mu_x^i(\pi) = c + d \cdot \rho_x(\pi) \quad (8)$$

The two cases (1) and (2) above correspond to whether reproductive costs accumulate or not. Figure 2 shows the difference between the two cases. In Fig. 2(a), the increase of the mortality rate due to reproduction in one year is carried over to the next year, in which reproduction further increases the intrinsic mortality and so on. This corresponds to an organism in which reproductive costs at a certain age affect all future ages. The alternative is an organism whose reproductive costs only accumulate within a year: at the start of the next season the organism has recovered. This is shown in Fig. 2(b), where intrinsic mortality is reset to the initial value at the beginning of each year. In the sequel, the slope d in Equation 8 is called the strength of the reproductive costs.

The mortalities $\mu_x^e(\pi)$ and $\mu_x^i(\pi)$ (Equations 7 and 8), determine the total mortality $\mu_x(\pi)$ and, hence, the survival $l_x(\pi)$ by Equation 6. From this and from the fecundity $m_x(\pi)$ (Equation 5), the fitness $r(\pi)$ of various phenotypes π can now be calculated by solving the Euler-Lotka equation (Equation 3).

However, a problem remains concerning the lifespan ω that is part of the phenotype π (Equation 1). Using the principle for maximizing the intrinsic rate of growth r , an infinitely long lifespan is the best solution: since survival as defined in Equation 6 never becomes zero, r increases if the lifespan ω is increased and if there is some reproduction during the added time. But the increase in r becomes infinitesimally small with increasing age, both because the survival becomes smaller (Equation 6) and because of the age discounting factor in the Euler-Lotka equation (Equation 3). To define a finite lifespan, one can find the age after which the prolongation of life returns a fitness increase that is ‘small’ and does not affect previous life history decisions. For this purpose we used an age-specific measure of fitness sensitivity introduced by Hamilton (1966) and discussed in the context of senescence by Abrams (1991, 1993). This fitness sensitivity measures the change in the intrinsic growth rate r for a given phenotype π caused by an increase in mortality at age x that persists through all subsequent ages. More precisely

$$\frac{\partial r_\pi}{\partial \mu_{xs}} = - \sum_{j=x+\frac{1}{N}}^{\omega} (j-x) \cdot \exp[-r(\pi) \cdot j] \cdot l_j(\pi) \cdot m_j(\pi) \div \left[\sum_{j=\frac{1}{N}}^{\omega} j \cdot \exp[-r(\pi) \cdot j] \cdot l_j(\pi) \cdot m_j(\pi) \right] \quad (9)$$

It is assumed that the increase in mortality affects the remainder of an organism’s life, as would be expected from senescent effects. Therefore, the notation μ_{xs} is used instead of μ_x in Equation 9. At birth, when age $x = 0$, the fitness sensitivity equals 1. With increasing age the fitness sensitivity decreases, converging to zero at very late stages in life. Assuming a critical value, ϵ , for the fitness sensitivity, a limiting age x_{crit} was determined at which the fitness sensitivity falls below this critical value ϵ (we set $\epsilon = 0.00001$). Lifespan was then defined as the year in which ϵ is reached. For example, in a phenotype with $\omega = 8$ decisions and the x_{crit} at 5.75 years, lifespan was cut to 6 years. Short-lived phenotypes whose fitness sensitivity never falls below ϵ were not affected by the cutting procedure. Thus, only those phenotypes were constrained whose lifespan was unrealistically large. It follows from Equation 9 that the reduction of lifespan to the year at which x_{crit} appears implies at most a fitness loss of the order of ϵ (Abrams, 1991), so that using this equation to restrict phenotypes to realistic lifespans is appropriate.

Having thus set the range of possible phenotypes, we used the numerical method described in the last section to find phenotypes with maximal fitness $r(\pi)$ for various regimes of mortalities and bodily growth. The implementation of the heuristic optimization technique is summarized by the following steps.

(1) Initialize the system with a threshold T that determines the annealing schedule (T was set to 0.01) and with a random phenotype π according to Equation 1. Compute the corresponding fitness according to Equation 3.

(2) Create a new phenotype: random variables were used to change the lifespan and the decisions δ_i from the previous phenotype; the direction and the amount of change, within the defined range for δ_i (Equation 2), also depended on uniform distributed random variables; lifespan ω could maximally change 2 years (up- or downwards) and the allocation decisions maximally $10/N$ time units.

(3) Calculate the fitness sensitivity according to Equation 9 and determine x_{crit} , adjust the lifespan of the new phenotype accordingly and compute the fitness using Equation 3 for the new phenotype π .

(4) Accept the new phenotype if the difference between the fitness of the previous phenotype and the fitness of the new phenotype is smaller than the threshold T .

(5) Anneal the system: multiply (and hence decrease) the threshold T by a number smaller than one (we used the value 0.9) if either of the following two conditions are satisfied for the actual threshold T : k new phenotypes have been accepted according to step (4) or l new phenotypes have been created according to step (2). Throughout all our simulations we set $k = 10$ and $l = 400$.

(6) Repeat steps (2)–(5) until no more phenotypes are accepted and the second condition of step (5) is satisfied.

These iterative steps were applied to different types of growth and different sources of mortality. The parameters a and b used to define the extrinsic mortality in Equation 7 remained constant for all scenarios considered in this study ($a = 0.01$ and $b = 1.1$). We modelled a slow-growing organism with a growth rate $k = 0.2$ and a fast-growing organism with $k = 0.8$.

To gain confidence in our results we repeated the heuristic procedure, described by the five iterative steps above, for each scenario, until the resulting phenotypes and their maximized fitness values appeared at least ten times.

Results

The results describe which set of decisions δ_i maximizes the intrinsic rate of growth r for various types of mortalities. The basic models, in which no reproductive costs occur and the organisms only suffer from extrinsic mortality, serve as a reference to compare phenotypes that suffer from additional intrinsic sources of mortality. In Figs 3 and 4, this reference is always given as scenario A.

For both the slow and the fast growth patterns, the optimal phenotype in the basic models follows a life history strategy called a ‘bang-bang’ or ‘on-off’ strategy: growth occurs until a certain age, the age at maturity, followed by an exclusive allocation of the resources to reproduction until the end of life (Schaffer *et al.*, 1982). A bang-bang phenotype shows determinate growth, since body size does not increase after the age at maturity. The differences between slow and fast growth in the basic models are consistent with previous theoretical work: age at maturity increases as the bodily growth rate decreases and slow-growing organisms mature at smaller body sizes (Roff, 1984; Stearns and Koella, 1986; Berrigan and Koella, 1994). The lifespans differed for the two basic models: the slow-growing organism reached its critical fitness sensitivity in the sixth year of life, whereas the fast-growing organism only lived for 5 years (Fig. 3(A), upper and lower panel).

The effects of reproductive costs, i.e. of phenotype-dependent mortalities, on these basic allocation patterns were then investigated. We first considered the case where reproductive costs accumulate throughout life (cf. Fig. 2a). The results are shown in Fig. 3 for the two types of growth dynamics. Without exception the optimal phenotypes retained determinate growth and displayed a bang-bang strategy. Increasing the strength of reproductive costs, i.e. the value of the slope d in Equation 8, affects reproduction in two ways: age at maturity is delayed and lifespan is reduced. Hence, the combination of both effects restricts the reproductive output to shorter periods. As expected, the delay of age at maturity is much more pronounced if body growth is slow. For very strong reproductive costs this finally leads to the semelparous life history depicted in Fig. 3(D) (upper panel), where age at maturity is delayed until the last year of life.

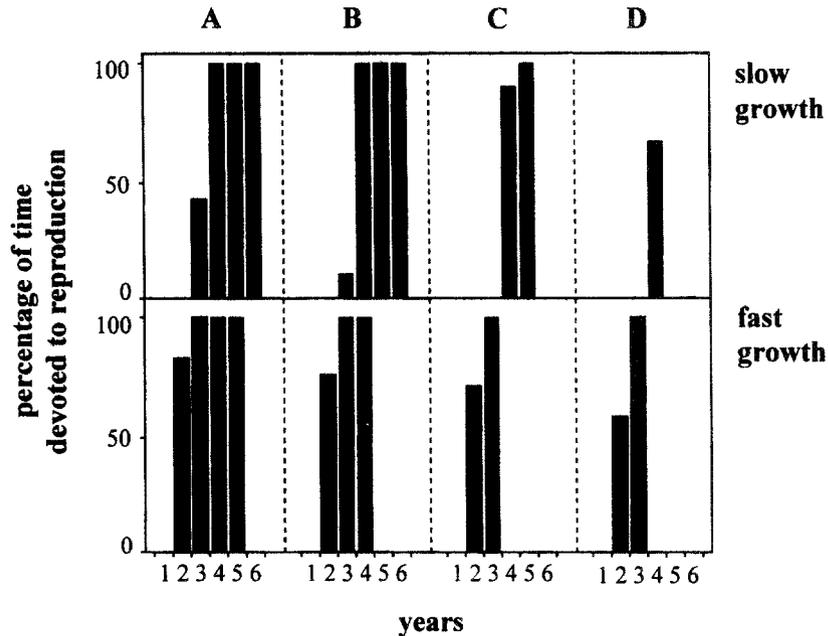


Figure 3. The optimal resource allocations of organisms with cumulative reproductive costs for two different growth rates. In the upper panel the growth rate k was set to 0.2, representing slow growth, whereas the lower panel with $k = 0.8$ represents fast growth. The four scenarios (A)–(D) exhibit different strengths of reproductive costs. The diagrams depict the yearly fraction of time devoted to reproduction throughout life. Time devoted to growth is given by the complementary fraction. (A) The basic model with only extrinsic mortality (see text). (B)–(D) Cumulative intrinsic mortalities are included and the corresponding strengths of the reproductive costs in Equation 8 are $d = 0.5$, $d = 2.0$ and $d = 6.0$ for the (B), (C) and (D), respectively. The constant parameter c in Equation 8 is set to 0 for all cases. For both growth rates the bang-bang strategy is optimal in all scenarios. The effect of accumulated intrinsic mortality is 2-fold: age at maturity is delayed (more in the slow-growth model than in the fast-growth model) and lifespan is shortened. In the most extreme case (D, upper panel), this leads to semelparity.

Combined with fast body growth, the same strengths of reproductive costs delayed age at maturity to a much smaller extent (Fig. 3, lower panel). Reproduction started earlier in life and the lifespan was shorter. With fast growth, increasing the strength of cumulative reproductive costs thus yielded optimal life histories that are best summarized as ‘living fast and dying young’ (Jones, 1990).

If reproductive costs only accumulated within years but not between years, i.e. if they were reset to 0 at the beginning of each year (cf. Fig. 2b), optimal life histories could change drastically. This is shown in Fig. 4, where the scenarios denoted by (A) again represent the basic model with extrinsic mortality only. If non-cumulative reproductive costs of sufficient strength were added to this basic model, the optimal patterns of resource allocation resulted in graded switches to reproduction and growth therefore became indeterminate. Thus, after a first period of resource allocation to reproduction, the organisms switched back to growth and so forth. The transition from a bang-bang to a graded switch did not occur abruptly but began with small growth investments in the year following maturation. For slow body growth (Fig. 4, upper panel) and for small reproductive costs (scenario B), the organism still allocated its resources according

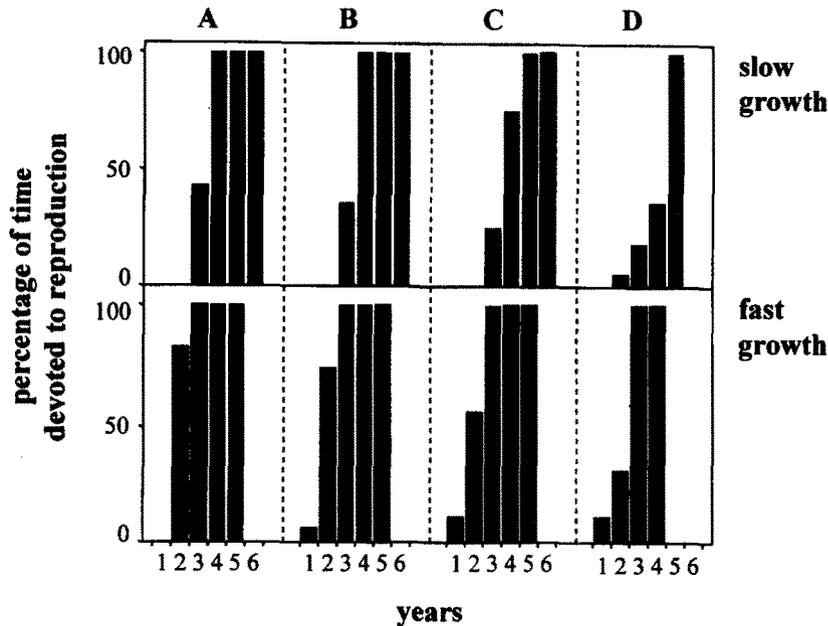


Figure 4. The optimal resource allocation of organisms with non-cumulative reproductive costs for two different growth rates (slow growth, $k = 0.2$, upper panel; fast growth, $k = 0.8$, lower panel). (A)–(D) represent different strengths of reproductive costs. The panels depict the yearly fraction of time devoted to reproduction (A) The basic model with only extrinsic mortality. (B)–(D) Non-cumulative intrinsic mortalities are included and the corresponding strengths of reproductive costs in Equation 8 are $d = 0.3$, $d = 1.0$ and $d = 4.0$, respectively. Non-cumulative costs yield graded switch strategies if these costs are sufficiently high. For small reproductive costs and slow growth, age at maturity is delayed and a bang-bang strategy is optimal (B, upper panel). In contrast, sufficiently high costs induce a graded switch and decrease the age at maturity (D, upper panel). For the fast-growth model these tendencies are more pronounced. Even small intrinsic mortalities cause a graded switch to be optimal and lead to a decrease in age at maturity. Note that lifespan for both growth rates is not affected much if the reproductive costs are non-cumulative.

to the bang-bang strategy. The transition to the graded switch depended on the strength of the reproductive costs, i.e. on the slope d in Equation 8: graded switches were only optimal when d was large enough. The strength of reproductive costs is associated with the concavity of survival curves that correspond to the intrinsic mortality. In Fig. 5 three types of linear mortality functions are shown: a constant mortality with $d = 0$ and $c > 0$ in Equation 8 and two mortality functions with different slopes of $d > 0$. Using Equation 6 one can determine the corresponding ‘intrinsic’ survival curves, depicted in Fig. 5(b). The constant mortality, i.e. $d = 0$, always yields a convex survival curve (curve A), whereas positive slopes of d result in an initially concave decrease of survival (curves B and C). The concavity becomes more pronounced for larger d , as indicated by the arrows in Fig. 5. Only values of d yielding sufficiently concave curves (e.g. curve C) lead to optimality of graded switches. Therefore we can correlate the concavity of the survival curve with the emergence of graded switches: a graded switch is optimal if reproductive costs are not accumulated and if these costs cause mortalities that result in sufficiently concave survival curves.

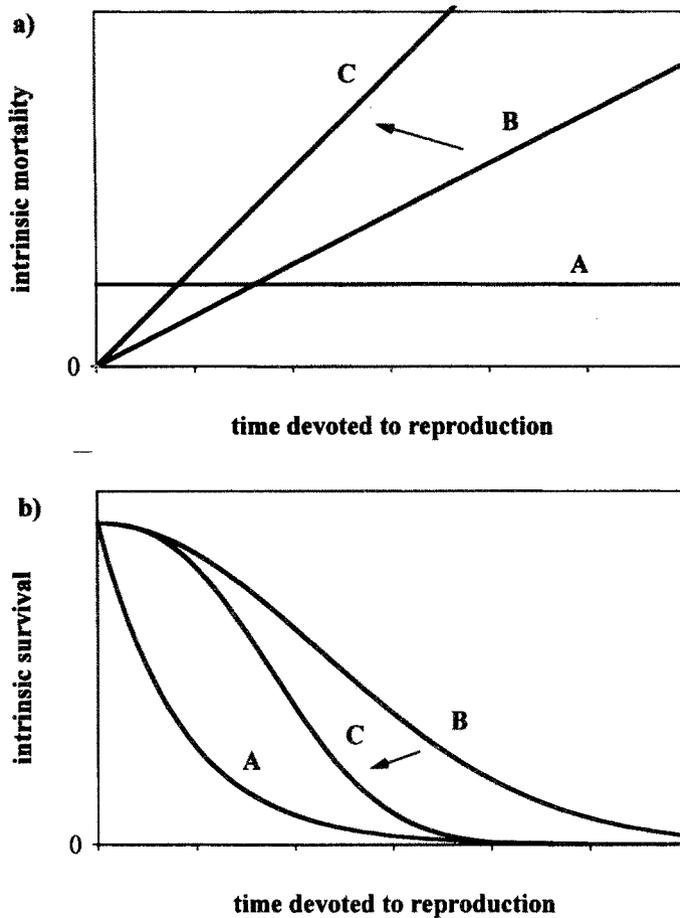


Figure 5. The decrease in survival due to yearly reproductive costs. (a) Intrinsic mortality curves are shown for three different strengths of reproductive costs defined as d in Equation 8. Curve A represents a constant mortality with $d = 0$, and a positive constant value c . Curves B and C result from a positive slope d (larger in C; the constant c is set to zero). The corresponding intrinsic survival curves are shown in (b). The constant mortality (with $c > 0$ and $d = 0$) yields a convex survival curve (curve A). Mortalities that increase with slope $d > 0$ yield a survival curve with an initially concave part (curves B and C). This concavity becomes more prominent as the slope d increases (indicated by the arrow). Only larger values of d , i.e. sufficiently concave survival curves, yield a graded switch strategy. Note that even greater concavities than shown in Fig. 7(b) would result if mortality increases exponentially.

In contrast to the cases where reproductive costs accumulate, the delay of age at maturity when costs do not accumulate was not linear: with increasing strength of reproductive costs, age at maturity was first delayed (Fig. 4(B) and (C) upper panel), but this trend was reversed when sufficient strength of reproductive costs induced the graded switch strategy and maturity started 1 year earlier in life (Fig. 4(D) upper panel). The fast-growing organisms were even more susceptible to this transition: their switches became graded and the age at maturity was decreased already with small reproductive costs (Fig. 4(B), lower panel); since the reproductive costs are restored at the beginning of each year, i.e. the organisms are not senescent, it is profitable to mature earlier in life even if the reproductive investments are small.

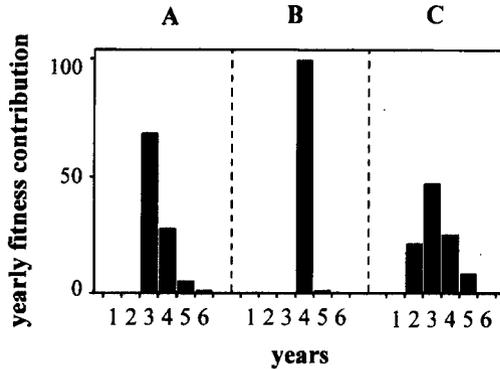


Figure 6. The yearly contribution to fitness for different life history strategies. Solving the Euler-Lotka equation (Equation 3) iteratively for each year yields decreasing values of the fitness measure r (see text). Since these values can be negative we used their exponentials ($\exp(r)$). This transformation allows us to describe the yearly fitness contribution as a proportion of the total fitness, i.e. the fitness computed from birth to death. The first scenario denoted by (A) represents the fitness contributions of the reference model with slow growth (see Fig. 3A). The biggest contribution comes from age at maturity. The pattern of contribution in (B) corresponds to the bang-bang strategy displayed in Fig. 3(C). Again the biggest contribution is from age at maturity, but contributions of later years are much smaller than in the reference model (A). Finally, in (C) the fitness contribution of a graded strategy, that of Fig. 5(D), is shown. Here the fitness contributions have a bell-shaped distribution with the biggest portion occurring clearly after the age at maturity: contributions from later years than that of age at maturity remain important.

Whereas lifespan was reduced more markedly by cumulative reproductive costs (Fig. 3), it seems to be less variable in phenotypes with graded resource allocation. For both growth rates in the non-cumulative case, lifespan was reduced by only 1 year when the strength of reproductive costs increased to its maximal value (Figs. 4D). The corresponding difference in the sensitivity of fitness can be explained by looking at the importance of different years for the total fitness of an organism. To do this, we define a measure of yearly fitness contributions as follows. Given a phenotype with lifespan ω , we calculated the ‘fitness’ values $r_\omega, r_{\omega-1}, \dots, r_2, r_1$ by setting the upper summation boundary in the Euler – Lotka equation (Equation 3) to $\omega, \omega - 1, \dots, 2, 1$, respectively and solving for r . Thus r_ω is just the usual fitness of a phenotype. The difference between two successive values r_i and r_{i-1} , divided by the total fitness r_ω , then represents a measure of the fitness contribution of year i . In Fig. 6, this yearly fitness contribution is shown for the basic model, for a model with cumulative reproductive costs and for a model with non-cumulative reproductive costs. In the first two cases growth is determinate and in both cases the year of age at maturity makes the biggest fitness contribution (Fig. 6A and B). However, the tendency to concentrate all the fitness in this year is greater with cumulative reproductive costs (Fig. 6B), whereas fitness contributions in later years are smaller than in the basic model. Thus later years are less important, which leads to a reduction in lifespan as compared to the basic model. In contrast, the yearly fitness contributions in the third case, in which reproductive costs do not accumulate and for which a graded switch strategy is optimal, result in a bell-shaped distribution that peaks at an age older than the age at maturity (Fig. 6C). The decline in fitness contribution occurs late and is less abrupt for phenotypes with a graded allocation pattern. Consequently, for these phenotypes older age classes continue to make significant contributions to fitness and the lifespan is not reduced by reproductive costs.

Discussion

Determinate and indeterminate growth, iteroparity and semelparity are fundamental distinctions in life histories and one would like to know the general mechanisms that trigger the transitions between these different patterns. The first purpose of this study was to show that such transitions could be connected to the way intrinsic mortalities due to reproduction are accumulated throughout life. For this we studied reproductive effort models that are not analytically tractable. Our second purpose was to apply to life history theory a novel numerical procedure with which such complicated optimality models can be solved. The method we used was introduced by Dueck and Scheuer (1990) and is based on the 'simulated annealing technique' of Kirkpatrick *et al.* (1983). It consists of exploring fitness landscapes in a clever and economic way. Compared to other numerical techniques such as dynamic programming, one advantage of our method is that it is not a backwards procedure. For reproductive effort models, this means that lifespan can be treated as a trait of a phenotype, rather than a fixed quantity. Thus, the interaction of lifespan with allocation patterns can be studied, and questions concerning the optimal lifespan can be addressed.

Bang-bang or graded switch strategies?

In our model, resources can be allocated either to growth or to reproduction. The constraint is that fecundity is size dependent. In addition, there can be costs of reproduction. Our main result is that these costs can induce the transition from bang-bang strategies, in which there is one global switch from growth to reproduction, to graded switch strategies, in which the organisms continue to grow after their first reproductive investment. If intrinsic mortality due to reproduction is accumulated throughout life (senescent mortality), then the optimal phenotype is a bang-bang strategist (Fig. 3). If the costs of reproduction accumulate only within one year, but are reset to zero at the beginning of the next season, then a graded switch tends to be optimal. Thus, whether an organism should have determinate or indeterminate growth may depend on how early reproductive investments affect survival at late stages. If mortality due to reproduction is senescent, a bang-bang strategy is favoured, but if damage due to reproduction can in some way be repaired, a graded switch should result.

Concerning the optimality of graded switches, our results differ from those of Kozłowski and Uchmanski (1987). Those authors found a graded switch to be optimal under the same basic assumptions concerning the trade-off between growth and reproduction, but with only extrinsic strategy-independent sources of mortality. In contrast, we found the bang-bang strategy to be optimal when there was only extrinsic mortality. This did not depend on the particular form of the extrinsic mortality, i.e. on whether it was constant or increasing with age. The fact that we optimized the growth rate r while Kozłowski and Uchmanski (1987) optimized life time fecundity R_0 cannot be the reason for this difference: due to the simplicity of the algorithm we used, it is very easy to optimize R_0 instead of r in our model and we still obtained a bang-bang strategy as the optimal solution when we changed the fitness definition to R_0 . Instead, the reason for the difference lies in how the loss in survival due to extrinsic mortality was defined. While our assumptions (Equation 6) resulted in a continuously decreasing survival, Kozłowski and Uchmanski (1987) used a step function, so that survival was constant throughout each year, but was decreased exponentially between years (Fig. 7). This would correspond to a mortality that has the form of a strong but very brief impulse and only acts at the beginning of each year. We feel that our assumptions are more realistic.

What actually causes the different outcomes seems to be a rather subtle detail: while in both models decisions do not affect the age-specific survival when mortality is only extrinsic, in our model decisions do affect survival up to the onset of reproduction in each year. Because survival

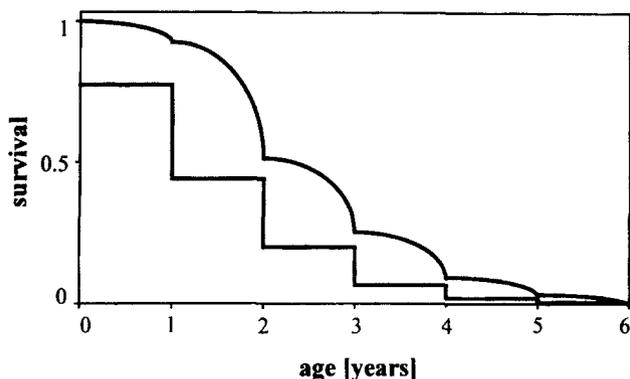


Figure 7. Reproductive costs that do not accumulate throughout life yield a survival curve (containing extrinsic and intrinsic sources of mortality) that shows alternating concave and convex regions of decrease. With increasing strength of reproductive costs this curve looks more and more like the step function for survival used in the model of Kozłowski and Uchmanski (1987). In both cases the alternating convex and concave parts of the survival curve induce the graded switch strategy.

is continuously decreasing, survival up to the start of reproduction is higher if reproduction starts early in the year. In contrast, in Kozłowski and Uchmanski's (1987) model, survival is constant throughout the year, so that survival to the onset of reproduction does not depend on whether reproduction starts early or late in each year. This shows that whether bang-bang or graded switch strategies are optimal can depend on small differences. On the other hand, there are also some clear tendencies. With non-cumulative intrinsic mortality, the transition from bang-bang to a graded switch occurs when the strength of the reproductive costs reaches a certain threshold (Fig. 4). This happens when the yearly survival curves that are calculated from this intrinsic mortality are concave 'enough' (Fig. 5). Thus, the graded switch is associated with the concavity of intrinsic survival curves. To get the overall age-specific survival, one has to multiply the extrinsic survival with the non-cumulative intrinsic survival, and the result is a curve with alternative concave and convex regions (Fig. 7). With increasing concavity of the intrinsic survival, the overall survival looks more and more like the step function used by Kozłowski and Uchmanski (1987). This again explains why concavity of intrinsic yearly survival leads to a graded switch.

The evolution of lifespan

Using optimal control theory or any other backward algorithm to optimize the resource allocation problem demands a fixed lifespan to initialize the computation (McNamara, 1991). However, the choice of the initial lifespan can critically change the optimal life history. Consider, for example, the phenotype following the graded switch scheme in Fig. 4(C) (upper panel). By limiting its lifespan to 5 years instead of the 6 years that result from our model, the strategy that maximizes fitness changes to bang-bang. On the other hand, if the lifespan is very large, the life history may not change qualitatively but lifespan may be unrealistic. For example, in the model of Kozłowski and Uchmanski (1987) the organisms live for 10 years. In some scenarios they assumed a constant yearly survival of 0.4, which yields an unrealistically low survival probability of 0.00013 in year 10. The question is then, how should lifespan be bounded from above without influencing the optimal life history pattern? In our study, lifespan was defined as part of a phenotype and not initially fixed. We then used a fitness sensitivity measure that depended on the yearly decisions

to calculate an upper bound for the lifespan. Accordingly, lifespan was truncated at a value such that no qualitative change in the life history would result from additional lifetime. Using this definition for lifespan yielded a significant difference between life histories with determinate and indeterminate growth. Determinate growth resulted in a rapid decrease of the fitness sensitivity, the major determinant of lifespan, after the age at maturity. In contrast, organisms with indeterminate growth showed prolonged periods after the age of first reproductive investments in which they remained sensitive to changes in (senescent) mortality and therefore longer lifespans are essential to them. This shows that considering lifespan as part of the phenotype can be important and heuristic optimization is an appropriate tool to study corresponding evolutionary models.

Other costs and benefits of heuristic optimization

Another advantage of the heuristic optimization technique is that one needs no initial knowledge about the correlations between particular traits. It suffices to know all theoretically possible values for the traits under consideration, which is achieved by discretizing the problem, i.e. by allowing only discrete values for each of the traits. The step size of the discretization will be a compromise between refinement and computer time. At the beginning of each simulation trial the initial discrete values (the initial phenotypes) are chosen randomly. The correlation between the traits then emerges from the heuristic optimization procedure. However, the causal relationships between correlated traits can only be inferred by systematically changing the basic assumptions of the model. This is the price one has to pay for abandoning analytical models with their high explanatory power. On the other hand, life history models very soon become complex and analytically intractable and the fast and economic heuristic approach then provides an excellent alternative. Moreover, the heuristic algorithm makes no demands on the input functions, which do not have to be continuous or differentiable as for analytical optimization models. Even experimental data as input functions are conceivable and one could then turn the problem around: given some data and assuming that some fitness measure is optimized under certain selection pressures, one could use the heuristic approach to investigate the shape of trade-off curves that lead to the optimal life history.

Besides not giving analytical results, a problem with heuristic algorithms is that good annealing schedules have to be found by trial and error. No general methods are available to determine the best compromise between being able to escape from local optima and converging to global optima. To find such methods is a field of active research. Recently, two other simplifications of simulated annealing have been introduced by Dueck (1993). They differ from the threshold accepting method used in the present paper by their annealing schedules. Which methods work best for which problems remains to be seen, but overall, we believe that heuristic algorithms provide a simple and efficient tool for studying a multitude of complex optimality problems in life history theory.

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