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# DYNAMIC MODELS OF ENERGY ALLOCATION AND INVESTMENT

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## *Abstract*

In dynamic models of energy allocation, assimilated energy is allocated to reproduction, somatic growth, maintenance or storage, and the allocation pattern can change with age. The expected evolutionary outcome is an optimal allocation pattern, but this depends on the environment experienced during the evolutionary process and on the fitness costs and benefits incurred by allocating resources in different ways. Here we review existing treatments which encompass some of the possibilities as regards constant or variable environments and their predictability or unpredictability, and the ways in which production rates and mortality rates depend on body size and composition and age and on the pattern of energy allocation. The optimal policy is to allocate resources where selection pressures are highest, and simultaneous allocation to several body subsystems and reproduction can be optimal if these pressures are equal. This may explain balanced growth commonly observed during ontogeny. Growth ceases at maturity in many models; factors favouring growth after maturity include non-linear trade-offs, variable season length,

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and production and mortality rates both increasing (or decreasing) functions of body size. We cannot yet say whether these are sufficient to account for the many known cases of growth after maturity and not all reasonable models have yet been explored. Factors favouring storage are also reviewed.

## INTRODUCTION

### *Historical Review*

“It would be instructive to know not only by what physiological mechanism a just apportionment is made between the nutriment devoted to the gonads and that devoted to the rest of the parental organism, but also what circumstances in the life history and environment would render profitable the diversion of a greater or lesser share of the available resources towards reproduction.” This often-quoted statement by Fisher (21) shows clearly the central place occupied, right from the beginning, by optimal resource allocation in the evolutionary synthesis. Fisher’s remark delineates a major research program, with both empirical and theoretical implications.

This program, however, took several decades to implement. As far as the theoretical side is concerned, the main reason for the delay lay in technical difficulties: The optimal allocation is that which maximizes fitness, which (as also shown by Fisher—21) is best measured by the organism’s per capita rate of increase, expressed by the Euler-Lotka equation as an implicit function of its life-time schedules of survival and reproduction. For several decades, no analytical technique was available for biologists to cope with the dynamic problem in which the optimal allocation is allowed to vary with age. This had to await not only the development by mathematicians of dynamic-optimization techniques, but also the formalization by biologists of the problem in a way that would open it to the analytical weaponry of dynamic optimization.

Accordingly, the first analytical inroads relied on simplifying the Euler-Lotka equation (e.g. assuming constant mortality and fecundity rates), thus in effect dropping the dynamic aspect from the problem. Following the key paper by Cole (18), questions of semelparity versus iteroparity, and optimal age at first reproduction were addressed in this way (e.g. 5, 13, 25, 63, 66). Another way to circumvent analytical difficulties was to use a numerical approach and computer simulations (e.g. 20, 23, 47). This approach gives insight into more complex and realistic situations, but with the obvious problem of lack of generality.

A proper analytical approach incorporating age structure stemmed from a seminal comment by Williams (87), who suggested that a perennial organism should maximize in any year its reproductive value, which is made of two

components: current reproduction and residual reproductive value. By explicitly defining age-specific trade-offs and the way to solve them, this comment paved the way to an analytical approach. A series of papers were subsequently devoted to the question of optimal age-specific reproductive effort in a discrete-time setting (e.g. 11, 12, 27, 64, 68).

Meanwhile, dynamic optimization techniques in a continuous-time setting were developed in mathematics. The so-called optimal control theory, including in particular Pontryagin's maximum principle (PMP; 57), was rapidly adopted in engineering science. The application of optimal control to resource-allocation problems in biology was made possible by a reformalization of the biological problem by Taylor et al (79), which included a definition of fitness as an explicit function of life-history schedules. Since then, PMP has emerged as the most convenient technique to tackle allocation problems in continuous time (e.g. 26, 44, 65), thereby to implement the theoretical aspects of Fisher's research program.

### *Scope and Outline of Chapter*

In the section on *Models*, we review the most significant published dynamic models of energy allocation using a common mathematical formulation involving PMP. The variety of models that exists is well illustrated by their schematic depiction in Figure 2. We have organized our review according to the seasonality or otherwise of the environment, starting with a nonseasonal (constant) environment because this is the simplest case. We focus on four important areas of prediction: the timing of maturity and the circumstances under which various patterns of indeterminate growth, storage, and allometry, are favored by natural selection.

Growth is here said to be *determinate* if it stops at first reproduction (maturity); otherwise, if the organism continues to grow after maturity, it has *indeterminate growth*. In the former, resources go first to growth, then to reproduction (a "bang-bang" strategy with a single switch). In the latter, either resource allocation is "intermediate" or multiple switches occur. In this context it may be useful to remember that indeterminate growth is a necessary consequence of intermediate strategy, and this in turn is often a consequence (as will appear) of singular arcs. In early analyses, determinate growth appeared optimal in most situations (e.g. 76), but this is paradoxical given the ubiquity of indeterminate growth in nature (e.g. 61). The models reviewed here throw further light on this important problem.

Before tackling the analysis we introduce mathematical tools common to most of the models, and we attempt to provide some insight into some of the mathematics, since some quantities at first sight formal and abstract turn out to have rich and deep biological meaning.

## BIOLOGICAL FORMULATION AND MATHEMATICAL TOOLS

### *Dynamic Optimization*

The models discussed in the next section are models of dynamic allocation, in which resources must be divided among competing demands in such a way as to maximize fitness. Fitness is the net contribution to the next generation and a dynamic allocation pattern reflects the possibility that the optimal allocation of resources, i.e. the allocation that maximizes fitness, will change during the organism's lifetime. The competing demands for that allocation include growth, reproduction, storage, or maintenance, depending upon the specific problem under consideration. In general terms we refer to these competing demands as *subsystems* of the organism. A particular pattern of allocation to the subsystems is represented by the *proportion of resources allocated* to each subsystem. The total resource amount available at time  $t$  is denoted as  $P(t)$ , and the proportion allocated to subsystem  $i$  at time  $t$  is called the *control variable*  $u_i(t)$ . The collection of these variables for all subsystems is called the *control vector*  $\mathbf{u}(t)$ .

As resources are incorporated into each subsystem the state of that subsystem changes. The size or state of subsystem  $i$  at time  $t$  is denoted by a *state variable*  $\mathbf{x}_i(t)$ , and the collection of these variables is denoted as the *state vector*  $\mathbf{x}(t)$ . The simplest model we might envision (Figure 2a) has two state variables, with an amount of resource  $P(t)u_1(t)$  being devoted to subsystem 1 at time  $t$  and an amount  $P(t)u_2(t)$  being devoted to subsystem 2 (of course with only two subsystems  $u_2 = 1 - u_1$ ).

The driving force of the problem is the collection of constraints on what is possible and the collection of rules that translate the attributes of the state variables into fitness. The simplest constraints are that allocations cannot be negative, that allocation to a subsystem must change the state of that subsystem, and that allocations are exclusive, i.e. resources allocated to one subsystem are not available to the other subsystems. The rules of translation describe how the state variables contribute to fitness. The description of these rules begins with the *survival state variable*. This is denoted as  $l(t)$ , the probability of surviving from birth until age  $t$ . The change of survivorship with time,  $dl(t)/dt$ , will depend upon the time-dependence of the mortality rate,  $\mu$ , which in turn can be a function of one or more of the state variables. It will usually be more revealing to discount survival rate by the function  $e^{-r^*t}$ , where  $r^*$  is defined as the maximum possible fitness (see below). This discounted survival rate will be denoted by  $L(t) = l(t) \exp(-r^*t)$ , and the time derivative of this state variable is given by  $dL(t)/dt = -(r^* + \mu)L(t)$  or  $-mL(t)$  if we allow  $m = r^* + \mu$ .

The problem then is to find the  $\mathbf{u}(t)$  at each time so that fitness is maximized, given the constraints and the translation of state variables to fitness. Fitness in this context refers to the rate of increase of the alleles producing the allocation pattern. Optimal allocation patterns are the expected outcomes of evolution (72), and presumably allelic variation at many loci combines with selection to produce these allocations. Fitness as defined here is a function of the life history in a specific environment, and more appropriate specific definitions of fitness for various types of environments are outlined in the next section.

The dynamic allocation problem can be solved using mathematical techniques collectively known as “Optimal Control Theory” (e.g. 3, 7, 8, 10, 15, 29, 43). If all the constraints are binding and continuous, the problem can be solved by classical methods developed in the nineteenth century (e.g. Calculus of Variations, Lagrangian Mechanics). However, if some constraints are not necessarily binding (e.g.  $0 \leq u \leq 1$ ) or are discontinuous, these methods cannot be readily applied. To cope with this, Pontryagin et al (57) developed new methods based on a quantity called the “Hamiltonian”  $H$ , which is a function of the control and state variables (see Appendix for detailed definitions). Pontryagin et al showed that the solution to the optimality problem corresponds to choosing  $u$  to maximize  $H$  at each moment in time (this is known as “Pontryagin’s Maximum Principle”). This appears to translate the dynamic problem into a simple static problem at each moment in time (see below).

Of course there has to be a snag with a powerful theorem of this kind, and the fly in this ointment is that  $H$  depends not only on the state and control variables, but also on some new variables, called *costate variables*,  $\mathbf{y}(t)$ , which are rather difficult to calculate. There is one costate variable  $y_i(t)$  for each state variable  $x_i(t)$ , and the costate variables usually have to be found by integrating backward from the known final value of the costate variable. Obviously this is not going to be easy. For one thing we need to know the optimal strategy in the future, but that involves solving the static optimization problem at all future times.

The problem may still appear intractable, yet despite these difficulties the method often can be applied in practice. The Hamiltonian usually has the form:

$$H(t) = I(t) + \sum_i y_i \dot{x}_i, \quad 1.$$

where  $\dot{x}_i$  is the time derivative of the state variable  $x_i$ . In the problems discussed here,  $I(t)$  is derived from the fitness measure and may itself be a function of  $\mathbf{u}$ , while  $\dot{x}$  always is.

### *Interpretation of Costate Variables*

To understand the meaning behind the maximization of the Hamiltonian, consider the simplest type of problem: choose  $u(t)$  to maximize  $H(t) = y_1\dot{x}_1 + y_2\dot{x}_2$ . The time derivatives of the state variables ( $\dot{x}_i$ ) indicate the changes in those variables achieved by a suitable choice of the  $u(t)$ ; the costate variables,  $y_1$  and  $y_2$ , can be taken to indicate the priority to be assigned to changing state variable  $i$ . A high value for  $y_1(t)$  will give a high priority to changing  $x_1$  at time  $t$  and force a high value for  $u_1(t)$ . Our biological intuition suggests that this priority  $y_1(t)$  ought to be related to the fitness effects of changing  $x_1$  at this time. As the age-specific effects of the state variables on fitness change, so should the priorities for allocation of resources to those variables, and so therefore should the optimal allocation change. Intuition is here correct; each costate variable is indeed proportional to the marginal value of its state variable in fitness units (44),  $y_i(t) \propto \partial(\text{fitness})/\partial x_i(t)$ .

The costate variables then indicate the sensitivity of fitness to a small change in the value of the corresponding state variable at time  $t$ . Sensitivities of this type are used in many evolutionary models and are often called partial selection pressures or selection gradients. In the present context  $y_i(t)$  represents the selection gradient or partial selection pressure on  $x_i$  at time  $t$ , and in the optimal strategy the priority given to an allocation to subsystem  $i$  will reflect the instantaneous selection pressure acting on that subsystem.

While the selection gradients on subsystems such as growth or storage can be understood readily in this fashion, there must also be a selection gradient for the discounted survival state variable,  $L(t)$ . This in fact is Fisher's reproductive value (52) and gives the value of immediate self-preservation in relation to immediate reproduction: The value of self at time  $t$  in relation to the value of offspring at time  $t$ . Thus resources should be allocated to self-preservation if reproductive value is high, but otherwise to reproduction. In a similar way the costate variables for other subsystems can be thought of as indicating their value (from the gene's point of view) in terms of birth-equivalents. In other words if the survival costate variable is reproductive value, then the other costate variables represent the reproductive value of allocating resources to subsystem  $i$  (74).

### *Types of Solutions*

The solution to the optimal control problem will involve maximizing the Hamiltonian at each point in time. The Hamiltonian is a function of (i) the appropriate fitness measure (which will differ in different environmental circumstances), (ii) the selection pressures on the subsystems (including reproductive value), and (iii) the effects of an allocation change on the state of each subsystem. At any point in time the Hamiltonian may take one of a

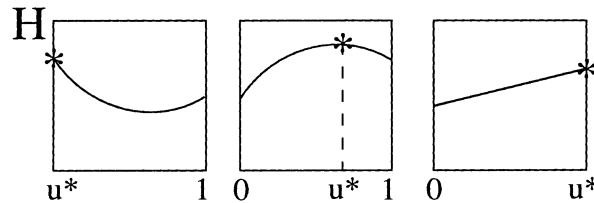


Figure 1 The Hamiltonian ( $H$ ) may be (a) a concave, (b) a convex, or (c) a linear function of the control variable  $u$ . In the first case, the optimal control is a boundary ( $u^* = 0$  in the figure). In the second case, it may be interior ( $0 < u^* < 1$ ). In the third case, it may be either boundary (as represented), or interior (if the slope = 0). A singular arc arises if the slope = 0 over a nonzero period of time.

few simple forms. If  $H(u)$  is a concave function of the  $u_i$  (Figure 1a) then the optimal values for the control variables (designated as  $u^*$ ), i.e. the optimal allocation for that moment in time, will be boundary values. That is, all allocation will go to one of the subsystems. If  $H(u)$  is convex, then the optimal allocation may be an intermediate one that is found by setting  $dH/du = 0$  (Figure 1b). In many biologically interesting cases the Hamiltonian will be a linear function (Figure 1c) with slope given by  $dH/du$ , which produces the optimal solution as a boundary value. In many cases the shape of this function will change over time, and as it does the optimal allocation will switch. This is especially dramatic when a linear function changes from a positive slope to a negative one, which causes the optimal allocation to change from a total allocation to one subsystem to a total allocation to another. The switch occurs when the function  $dH/du$  vanishes. For this reason  $dH/du$  is called the *switching function*.

In some situations the switching function may vanish over a nonzero period of time which means that  $H$  becomes independent of  $u$ . When this occurs a *singular arc* is said to exist (6). In these cases the optimal strategy can often be found by setting both the switching function and its time-derivative equal to zero; this often, but not always, produces an intermediate strategy for that time period. The time course of the Hamiltonian and the switching function can produce a diversity of dynamic allocation patterns, from abrupt changes and all or nothing patterns (bang-bang) to gradual and continuous shifts in allocation.

## MODELS

In this section we review a series of models in a logical (not historical) order, starting from the simplest situation (constant environment) and extending in the several directions that have been worked out until now.



### Constant Environment

We first disregard any temporal structure in the environment, so that returns from investments do not depend on *external* time (even though they may depend on state variables that vary with age). The time horizon  $T$  is infinite, which does not mean that the organisms do not die, but simply that there is no maximal longevity (such as season end, for instance, would impose on univoltine organisms). Fitness is measured by  $r$  in the Euler-Lotka equation

$$1 = \int_0^{\infty} e^{-rt} l(t) b(t) dt \text{ and can be maximized directly (as in 55).}$$

Let  $r^*$  be this maximum value. Most workers have taken advantage of a theorem due to Taylor et al (79) which shows that the optimal strategy maximizing  $r$  also maximizes  $\int_0^{\infty} e^{-r^*t} l(t) b(t) dt$  keeping  $r^*$  constant. Such analyses obtain some insights without finding the value of  $r^*$  but for a complete analysis this must of course be obtained. The Hamiltonian in this case is:

$$H = L(t)b(t) + \sum_i y_i \dot{x}_i \quad 2.$$

(see Appendix).

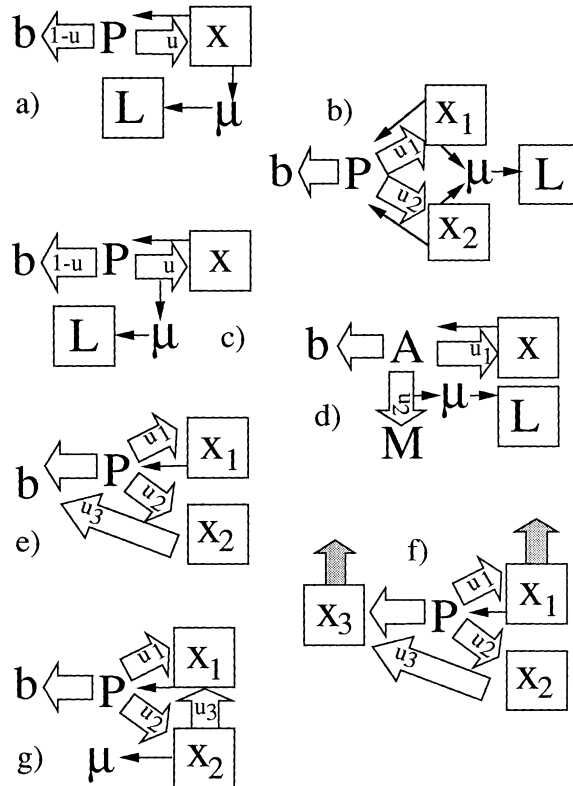
This kind of model may apply to organisms living in constant environments (equatorial ecosystems, deep seas, etc) or to multivoltine organisms such as planktonic algae or invertebrates, if generation time is much shorter than season length. It may also apply to perennial organisms in a discrete-time formulation if the time unit for allocation decisions is one year.

**STATE-DEPENDENT RATES** We consider first the case in which the only trade-off is between somatic investment and reproduction. That is, we assume that metabolic needs are met from assimilated energy, and we consider the allocation of the remaining energy. We also assume that production and mortality rates depend only on somatic state variables (Figure 2a). Variations of these assumptions will be discussed later.

In the most basic model (Figure 2a) there is only one somatic state variable—body mass, and the problem is one of optimal growth vs reproduction (76, 79). The other state variable is discounted survival,  $L$ , with costate variable Fisher's reproductive value, which we here write  $v$ . As shown above,  $\dot{L} = -mL$ . A somewhat detailed analysis will be given for this simple case, in order to illustrate the mathematical technique. From equation (2) the Hamiltonian is written:

$$H = Lb + y\dot{x} - mLv. \quad 3.$$

The only control variable,  $u$ , is the proportion of production ( $P$ ) that is invested into growth ( $\dot{x}$ ), as opposed to reproduction (see Figure 2a for details).



**Figure 2** Some of the basic allocation models investigated. Symbols in squares represent state variables, and the others are rates. Wide arrows are energy transfers, either under control (open), or not (shaded). Thin arrows represent other relationships. (a)  $x$  is a state variable, here body size.  $P$  indicates “production”, i.e. the rate at which energy can be channelled into reproduction ( $b$ ) or growth ( $\dot{x}$ ). Allocation between  $b$  and  $\dot{x}$  is determined by the control variable  $u$  so that  $\dot{x} = uP$  and reproductive allocation  $= (1 - u)P$ . How fecundity depends on reproductive allocation is discussed in the text.  $\mu$  = mortality rate and  $L$  is “discounted survival.” (b)  $x_1$  and  $x_2$  are state variables for subsystems 1 and 2. (c) Here the control variable affects  $\mu$  and  $x$ . (d)  $P$  has been replaced by  $A$ —assimilated energy—some of which goes to maintenance  $M$ , thereby reducing mortality. (e) Introduces the possibility of storage in subsystem 2 by allowing energy transfer from subsystem 2 to reproduction. (f) Energy losses (shaded arrows) occur from subsystems 1 (vegetative mass) and 3 (seed mass) because of grazing and seed mortality respectively. (g) Energy stored in  $x_2$  can be reallocated to vegetative mass  $x_1$ , and affects winter survival.

The way reproductive allocation translates into fecundity ( $b$ ) determines the trade-off  $b(\dot{x})$  between fecundity and growth. The analysis consists in substituting this trade-off in (3), then inspecting  $H$  for a maximum.

If  $b(\dot{x})$  is linear (which would result if fecundity was proportional to

reproductive allocation) then  $H$  is linear in  $\dot{x}$  (i.e. in  $u$ ). Let the inverse of offspring biomass,  $1/x_0$ , be the coefficient for transforming reproductive allocation into offspring. Then:

$$H = L(1 - u)\frac{P}{x_0} + yuP - mLv \quad 4.$$

so that the switching function is given by

$$\frac{dH}{du} = P(y - \frac{L}{x_0}) \quad 5.$$

Because Equation 4 is linear in  $u$ , this switching function does not depend on  $u$ : It is positive or negative depending on whether  $y$  is larger or smaller than  $L/x_0$ . In the first case,  $H$  is maximized by maximum  $u$ , i.e. by investing all energy in growth (as occurs early in life); in the latter case, all energy must go to reproduction (as often occurs late in life). The switch from growth to reproduction occurs when  $y = L/x_0$ . This kind of solution, characterized by an instantaneous switch from one boundary to the other, is often called *bang-bang*.

The biological interpretation is as follows:  $y$  is a measure of the value of investing in more soma at age  $t$ , whereas  $L/x_0$  represents the value of immediate reproduction. Equation 5 simply indicates that energy should go where the returns are higher, and that the shift should occur when these returns equalize.

For further quantitative analyses,  $y$  has to be calculated explicitly using the methods outlined in the Appendix. Then the condition for maturity ( $y = L/x_0$ ) turns out to be:

$$\frac{\partial \frac{P}{m}}{\partial x} = 1. \quad 6.$$

Here  $P/m$  is the ratio of production to “discounted mortality”  $m$ . Immediately after birth, mortality rate is high (high  $m$ ) and production is relatively low (in most organisms, because they are then relatively small), so  $P/m$  is low. As the organism grows,  $P$  increases and  $m$  may decline, so the ratio  $P/m$  is likely to increase initially, though not indefinitely (Figure 3a) because  $P$  must eventually be limited, if by nothing else then by the availability of resources. Thus  $P/m$  increases, but subject to a diminishing law of returns. By delaying reproduction, an organism can therefore increase the eventual level of offspring production—but there is a cost. If it dies before reproduction, all is wasted. So when should it switch from growth to reproduction—i.e. when should it “mature”? Equation 6 tells us it should wait until the slope of  $P/m$  has declined to 1 (Figure 3a).

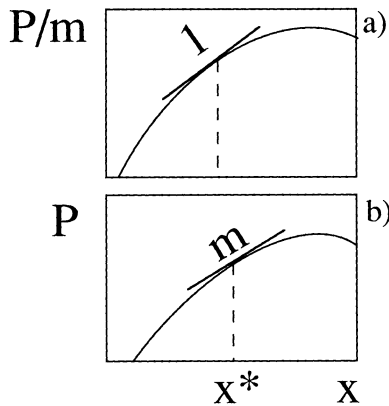


Figure 3 (a)  $P/m$  as a function of body mass  $x$ . The optimal strategy is to grow as long as the pay-off from increased size (increased  $P/m$ ) exceeds its cost (slope  $> 1$ ). (b) If mortality does not depend on body mass, then the optimal strategy is to grow as long as the increase in  $P$  exceeds  $m$ . The optimal adult size is  $x^*$ .

This result, reached originally by Taylor et al (79), can be interpreted as follows: Investing in soma is beneficial as long as this improves the organism's prospective reproduction, either by increasing its productivity or by decreasing its mortality. The way  $P/m$  increases with soma can be seen as a *marginal value* of somatic investments (Figure 3a). It is worth noting that  $P/m$  has the same units as soma (energy, say), so that this marginal value is dimensionless. Thus, Equation 6 means that organisms should stop investing in soma when the marginal value of increased size equals the cost of the increase (Figure 3a) [see also Taylor & Williams (80) for an independent derivation of the same result].

A further interesting biological insight is the following: At maturity, the reproductive value  $v$  is given by the product of fecundity ( $b$ ) and discounted life expectancy ( $\frac{1}{m}$ ):  $v = b/m$ , i.e.  $P/mx_0$ . Thus Equation 6 may be written  $\partial v/\partial x = 1/x_0$ , which is the coefficient for transforming reproductive investment into offspring. The optimal strategy maximizes the organism's reproductive value at each age, provided decisions at one age affect the subsequent but not the earlier life history (70, 88). It follows that reproduction should occur when the reproductive value is no longer better increased by somatic investment than by immediate reproduction.

In the special case where mortality does not depend on body mass, then Equation 6 becomes  $\partial P/\partial x = m$ : Maturity occurs when the gain in productivity obtained by growing further is exactly compensated by the costs of postponing

reproduction (in terms of discounted mortality) (39, 89). It is worth emphasizing that this optimal adult size does not correspond to a maximum in productivity (Figure 3b) unless we also assume that  $m = 0$  (i.e. population stable and mortality nonexistent); this means that there are no costs in postponing reproduction (see models of Sebens—69; Bloom et al—9). This last assumption does not fit the facts. In cladocerans, for instance, reproduction is known to start long before the maximum in production is reached (e.g. 22, 54, 77).

Fecundity is not necessarily linearly proportional to reproductive allocation. There might be fixed costs prior to reproduction (e.g. building the reproductive structures), making  $b(\dot{x})$  concave, in which case bang-bang reproduction is optimal (76). In contrast an intermediate strategy, with simultaneous growth and reproduction (i.e. indeterminate growth), may result if  $b(\dot{x})$  is convex (Figure 4). In this case, the optimal growth strategy is given by  $\partial H/\partial u = 0$  (Figure 1b), i.e. from Equation 3:

$$y = -L \frac{\partial b}{\partial \dot{x}}, \quad 7.$$

which means that, during the period of balanced allocation, the returns from growth and reproduction equalize (note that Equation 7 is equivalent to the condition determining the switching point in the linear case). Such a convexity, resulting in an intermediate strategy, may arise if the energy required for producing one offspring is an increasing function of offspring number (1). It may also stem from constraints on maximal investments in growth and/or reproduction. Kozłowski & Ziolkowski (41) develop such a model where the maximum rate of reproduction is limited, so that energy in excess of reproduction goes to growth. Consequently the optimal strategy is intermediate. Perrin (51, 54) discusses the possibility that such a constraint

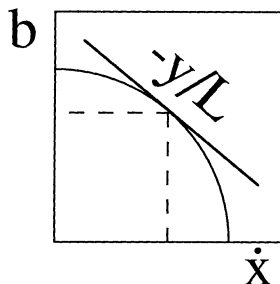


Figure 4 A convex trade-off between fecundity  $b$  and growth  $\dot{x}$ . In this case the solution is interior, with the optimal allocation given by setting  $\partial b/\partial \dot{x} = -y/L$ .

(namely, the size of the dorsal brood chamber) is responsible for the intermediate strategies of some cladoceran species. However, intermediate strategies may also result from other assumptions (see below), so convexity cannot simply be inferred from observed strategy.

Let us now consider the case of several subsystems constrained by a linear allocation trade-off, such as roots vs shoots in plants or distinct organs in animals (Figure 2b; 32, 33, 34, 52, 73, 81, 82, 84). From Equation 2:

$$H = Lb + \sum_{i=1}^n y_i \dot{x}_i - mLv, \quad 8.$$

and so the Hamiltonian is linear in the  $u_i$  if  $\dot{x} \propto u$ . In this case, a simultaneous allocation to several organs is the optimal solution if the  $y_i$  equalize over a nonzero period of time (the state-space strategy is then a singular arc). The trajectory along the singular arc is calculated by setting  $y_i = y_j$  and  $\dot{y}_i = \dot{y}_j$ . It turns out that the marginal value of organs (in increasing the function  $P/m$ , defined above) plays a crucial role, in that only the organ(s) with the highest marginal value receive allocation, so that balanced growth occurs only as long as organs have identical marginal values:

$$\frac{\partial \frac{P}{m}}{\partial x_i} = \frac{\partial \frac{P}{m}}{\partial x_j}. \quad 9.$$

This means that at each point in its development the organism so allocates its resources that it increases  $P/m$  as fast as possible. This has the result that its developmental trajectory climbs the  $P/m$  landscape where its contours have slope  $-1$  (Figure 5a), following a singular arc. One consequence is that organisms must have, at every age, the body composition that maximizes

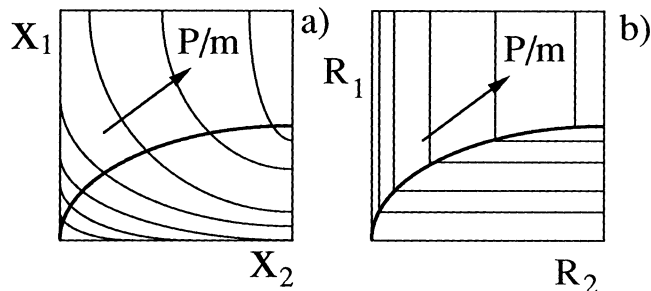


Figure 5  $P/m$  isoclines, (a) in state space, and (b) in resource-uptake space. In the cases represented, the optimal growth trajectories (bold curves) are singular arcs, found by joining all the points where  $P/m$  is equally limited by organs  $x_1$  and  $x_2$  (or resources  $R_1$  and  $R_2$ ).

$P/m$ , given their body mass (52). Reproduction occurs as soon as these marginal values no longer exceed unity (Equation 6). Iwasa & Roughgarden (32) argue that the patterns of ontogeny and plasticity of root/shoot ratios in plants are largely consistent with their optimization model. These results also have interesting implications concerning life-history strategies. An example concerns the productivity-survival trade-off: Early in life, the function  $P/m$  is more sensitive to a change in productivity than to a change in mortality (52). As the individual ages,  $P/m$  becomes more and more sensitive to changes in survival; this has the consequence that an organism should invest first into organs enhancing production, and then, later in life, in organs enhancing survival. This result may explain the two very general patterns, (i) that specific growth rate decreases with age (76), resulting in sigmoids patterns of growth (e.g. 85), and (ii) that mortality also decreases with age, reaching a minimum at onset of maturity (30).

If organs are specialized for the acquisition of particular resources, such as water, light, or nutrients for plants, how does this affect production/mortality? If resource  $i$  is acquired at rate  $R_i$  when organ  $i$  is in state  $x_i$ , then Equation 9 becomes:

$$\frac{\partial \frac{P}{m}}{\partial R_i} \frac{\partial R_i}{\partial x_i} = \frac{\partial \frac{P}{m}}{\partial R_j} \frac{\partial R_j}{\partial x_j}. \quad 10.$$

So the developmental trajectory climbs the  $P/m$  landscape in resource-uptake space, where its contours have slope  $-\frac{\partial R_i/\partial x_i}{\partial R_j/\partial x_j}$ . Along a singular arc, all resources limit fitness, though not necessarily to the same extent: adding one unit of  $R_i$  or  $R_j$  will have the same effect on  $P/m$  only if  $dR_i/dx_i = dR_j/dx_j$ . In the special case of essential resources (Figure 5b), then Equation 10 is only satisfied at the corner, where both  $\partial(P/m)/\partial R_i$  and  $\partial(P/m)/\partial R_j = 0$ , leading to matching of body components (symmorphosis; 71). This approach has been developed by Tilman and collaborators (e.g. 24, 83), who further simplify the problem by taking no account of reproduction or survival (they assume that production rate is maximized).

**CONTROL-DEPENDENT RATES** It might be that production and mortality depend on control variables as well as state variables (Figure 2c). The case of growth-dependent mortality (76) exemplifies this possibility. Considering a single somatic state variable and a single control variable, we have, as in equation 4:

$$H = L(1 - u) \frac{P}{x_0} + yuP - m(u)Lv. \quad 11.$$

This differs from Equation 4 in that  $m(u)$  is now a function of  $u$ . If  $m(u)$  is concave, then  $H(u)$  is convex, with a possible interior maximum ( $0 < u^* < 1$ ), implying indeterminate growth. Such a concavity in  $m(u)$  could arise if, for instance, mortality increases more and more rapidly as the proportion of available energy invested toward reproduction increases (this might be the case in planktonic cladocerans, for example, due to selective visual predation by fish on egg-bearing females) (54).

**EXTENSION TO INCLUDE MAINTENANCE** So far only the allocation to soma and reproduction has been considered but the basic model can be extended to include other allocations. To illustrate this point we briefly suggest how optimal allocation to maintenance might be investigated. Let  $A$  be the net energy available for production and maintenance (Figure 2d). Two control variables are necessary to specify the system's behaviour: let  $u_1$  be the proportion of  $A$  allocated to growth, and  $u_2$  that to maintenance. The Hamiltonian takes the form:

$$H = L(1 - u_1 - u_2) \frac{A}{x_0} + y u_1 A - m(u_2) L v \quad 12.$$

The optimal maintenance allocation is found by setting  $dH/du_2$  to zero; i.e.  $\partial m/\partial u_2 = -A/vx_0$ . Since  $m = r^* + \mu$ , and  $r^*$  is here considered a constant,  $\frac{\partial m}{\partial u_2} = \frac{\partial \mu}{\partial u_2}$ . Assuming that mortality is a concave decreasing function of  $u_2$ , this result implies that maintenance should increase with reproductive value  $v$ —more should be spent to preserve a more valuable soma (see also 26, 75).

This approach could be further developed to include metabolic rate, e.g. assuming that  $u_2$  affects energy acquisition as well as mortality. This would allow to derive optimal metabolism to body mass allometries.

### *Annual Environment*

The previous section demonstrated that the optimal allocation policy depends on the way state and control variables affect production and mortality rates when their effects are time-invariant. In seasonal environments, such effects vary with time. In this section we introduce such temporal constraints. We first deal with annual organisms, whose lifespan is limited by season's end (e.g. some plants and invertebrates). In such organisms, the start of a season constrains the onset of juvenile development, which may therefore be independent of the timing of reproduction. In this situation expected fecundity  $(\int_0^T l(t)b(t)dt)$  is a suitable index for fitness if mortality of seeds or eggs does not depend on date of release.

There are two possible formulations for the mathematical problem. The



time-specific fecundity (weighted by survival) may be taken as the intermediate function (e.g. 67). Alternatively, the total seed yield at the end of the season may be considered the final function, and the intermediate function may be dropped (e.g. 14, 36, Appendix).

**LIMITED LIFESPAN** In this subsection, the only temporal constraint considered is a limited lifespan. We assume that the organism in effect knows the time horizon and that control variables affect production and/or mortality only through their effects on state variables.

In the first model considered here, we further assume that the somatic state affects production rate only, not mortality (16, 39, 40, 45, 46, 48, 84, 89). The Hamiltonian is written as in Equation 4, but, due to the new terminal condition  $y(T) = 0$ ,  $y$  turns out to be equal to the factor weighting reproduction ( $1/x_0$ ) when

$$\frac{\partial P}{\partial x} \frac{1 - e^{-\mu(T-t)}}{\mu} = 1. \quad 13.$$

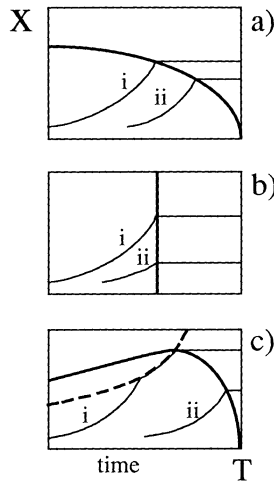
(equation 31 in Ziolkowski and Kozłowski—89). The first term in the left-hand side of equation (13) is the marginal value of soma, and the second term represents the life expectancy of an individual aged  $t$ . Thus, reproduction should occur when the marginal value of the soma is the inverse of life expectancy. As compared to Equation 6, introducing a time horizon induces an earlier onset of reproduction, because life expectancy decreases. Equation 13 can be interpreted as follows: noting that during the period of pure reproduction, the reproductive value equals the product of fecundity and life expectancy:

$$v = b \frac{1 - e^{-\mu(T-t)}}{\mu} = \frac{P}{x_0} \frac{1 - e^{-\mu(T-t)}}{\mu}; \quad 14.$$

it follows from equation 13 that reproduction should occur when  $\partial v / \partial x = 1/x_0$ , which is the coefficient for transforming reproductive allocation into offspring (see above our similar interpretation to Equation 6 and Figure 3a). Thus, maturity should again occur when the pay-off from increased size (increased reproductive value) is balanced by its cost (no immediate reproduction).

A bang-bang strategy as predicted here, implying a sharp switch from vegetative growth to reproduction, has been documented in many annuals such as crop plants (16, 48), and there is some comparative and experimental evidence supporting the predictions about the timing of the switch (e.g. 37, 48). In the case of crop plants the time horizon is fixed by harvest and presumably is highly predictable.

Equation 13, known (for obvious reasons) as the switching curve, can also



**Figure 6** Size ( $x$ ) as a function of time. Thin curves represent growth curves, and the optimal switch from growth to reproduction occurs on the bold curve. Growth curves start at size  $x_0$  at various times but all end at “season end” which is here used as a reference point. Thus growth curve (i) corresponds to a long season and curve (ii) to a short season. Maturity occurs on reaching the bold curve, so in (a) animals should mature later, at a larger size, if the season is longer. In this way the bold curve represents a reaction norm for size and age at maturity in relation to season length. In (b) the reaction norm is a vertical line. If the bold curve has a maximum (c), the optimal strategy may include a period of intermediate growth along a singular arc (dashed line).

be interpreted as a norm of reaction, describing optimal maturation age and size as a function of environmental conditions (productivity and mortality) and time constraints ( $T$ ). This is illustrated in Figure 6a, for constant environment but variable season length. Here the norm of reaction is a monotonically decreasing function of age. In Cohen (16), production is proportional to vegetative biomass ( $P = \beta x$ ), and there is no mortality ( $\mu = 0$ ) so that Equation 13 reduces to  $\beta(T - t) = 1$ , which means that maturity should occur at a fixed date before the season’s end, independent of size. Indeed, Cohen (16) notes that late-flowering plants in cold temperate climates tend to flower at a fixed date. This corresponds to a vertical norm of reaction (Figure 6b). Similarly, in the case where no time constraints occur, Equation 6 can be interpreted as a horizontal norm of reaction: Maturity depends only on somatic state, and is not affected by age, because life-expectancy does not vary after the onset of maturity.

If both production and mortality rates depend on soma, then Equation 13 becomes:

$$\frac{\partial \left[ \frac{P(1 - e^{-\mu(T-t)})}{\mu} \right]}{\partial x} = 1 \quad 15.$$

(55). It follows from Equation 14 that reproduction again should occur when  $\partial v/\partial x = 1/x_0$ . This function also represents a norm of reaction for size/age at maturity but is somewhat particular in that it may have a maximum (Figure 6c). As discussed in (55), growth trajectories cannot reach this curve to the left of its maximum, and this implies the existence of a singular arc that reaches the curve at its maximum (Figure 6c). The optimal strategy is to begin with a period of pure growth (as long as the growth trajectory remains below the singular arc), followed by a period of simultaneous allocation to growth and reproduction (indeterminate growth), during which the growth trajectory is on the singular arc. Finally, all allocation is to reproduction after Equation 15 is met at its maximum. Such a singular arc may arise if mortality and production either both increase or both decrease with size. This has the intuitive meaning that the costs and the benefits of further growth equalize over a nonzero period of time. It is worth noting that Taylor & Gabriel (22, 78) reach the same conclusion, using a numerical approach. An analytical derivation of the singular arc is given by Perrin et al (55), who further discuss this situation and its biological interpretation.

**UNPREDICTABLE LIFESPAN** Another interesting situation, involving a singular solution and simultaneous allocation to growth and reproduction, arises if lifespan is not only limited but also unpredictable (in the sense that there are no environmental cues to season's end available to the organism). This situation was first formalized by Cohen (16; see also 2) in a discrete-time model. King & Roughgarden (36) give the following continuous-time formulation in terms of PMP for an annual plant model with no mortality. Let  $x_1$  be the vegetative part and  $x_2$  the seed yield of that plant (Figure 2b). The total seed yield over a season depends on season length, say  $\tau$ . If  $\tau$  varies over years, then the geometric mean of  $x_2$  (or the arithmetic mean of its logarithm) is a suitable measure of fitness since there is no seed mortality. A distribution of  $\tau$  over years has to be assumed; if, for instance, all  $\tau$  between 0 and  $T$  are equally probable, then the objective becomes:

$$\text{Max} \int_0^T \log x_2(\tau) d\tau, \quad 16.$$

and the Hamiltonian:

$$H = \log x_2 + y_1 \dot{x}_1 + y_2 \dot{x}_2, \quad 17.$$

i.e.:

$$H = \log x_2 + P[y_2 + u(y_1 - y_2)]. \quad 18.$$

This Hamiltonian is linear in  $u$ . It turns out that the logarithmic term in Equation 18 means that a singular arc is possible (i.e.  $y_1 = y_2$  over a nonzero period of time). The biological interpretation of the intermediate strategy in this case is that of bet-hedging in the face of environmental uncertainty (2). According to Cohen (16), this may explain the intermediate strategies of many annual plants in deserts, where the length of the growing period is extremely variable and unpredictable. King & Roughgarden (36) also propose that the unpredictability of water supply on the upper slopes of the Cascade Mountains is responsible for the intermediate strategy of a local *Polygonum* species. It is worth noting that unpredictability may also arise from spatial heterogeneity in environmental conditions if seeds from a single parent spread randomly among environments.

**STORAGE AND ENERGY TRANSFER AMONG STATE VARIABLES** A temporally variable environment may make storage useful, storage being broadly defined as any allocated energy that can be reallocated to meet special needs as necessary. In our framework, this kind of reallocation can be formalized as an energy transfer among compartments (Figure 2g). Energy transfer from  $x_2$  to  $x_1$  becomes useful as soon as the marginal value of the latter exceeds that of the former (i.e.  $y_2 < y_1$ ). It is as if the objectives were to reach the singular arc (when the  $y$ 's are equal) as fast as possible, and this can be done more readily if direct energy transfers between compartments are possible.

**REALLOCATION OF VEGETATIVE MASS** In the simplest case, let us consider a single state variable (vegetative soma) that affects production only (not mortality). Whereas before we did not allow the possibility of reallocating soma (decreasing body size), now we allow it. The problem is thus growth vs reproduction with a time horizon, as before, and the optimal policy is still bang-bang, maturity occurring when  $y$  and  $l/x_0$  equalize. In the absence of a time horizon these two functions remain equal over the reproductive period (i.e. both somatic and reproductive allocations have the same marginal value). But a time horizon makes them cross, so that  $l/x_0$  exceeds  $y$  after the onset of maturity. This means reproduction is then more valuable than investment in soma, thus selecting for reallocation of vegetative biomass to reproduction. If we assume that a proportion  $\alpha$  of the vegetative body can be used for additional reproduction at the end of the season, then the condition for a switch Equation 13 becomes:

$$\frac{\hat{u}P}{\partial x} \frac{1 - e^{-\mu(T-t)}}{\mu} = 1 - \alpha e^{-\mu(T-t)} \quad 19.$$

(Equation 12 in 39). In Cohen's treatment (16),  $P = \beta x$  and  $\mu = 0$ , so that Equation 19 reduces to  $\beta(T - t) = 1 - \alpha$ . The interpretation of Equation 19, relative to Equation 13, is that, if reallocation is possible, then growth is allowed for a longer period of time, and the switch to reproduction occurs later in life, at a larger size.

**TRUE STORAGE ORGANS** Some organs may have a pure storage function. This is illustrated in Figure 2e where the only function of energy stored in  $x_2$  is to be reallocated for seed production. Under what circumstances are such organs adaptive? If the returns from reproductive allocation are constant (i.e. fecundity is proportional to reproductive allocation, with a time-constant coefficient), then storage is useless: energy is better invested directly into reproduction. But if these returns increase with time, then storing energy may become adaptive. This type of situation is analyzed by Schaffer et al (67), who also assume seasonal fluctuations in returns from somatic investments (i.e. productivity per unit leaf weight depends on season). Formally, their model has two somatic variables (vegetative mass  $x_1$  and storage  $x_2$ ) and three control variables (Figure 2e). Production  $P$  is assumed proportional to photosynthetic mass  $x_1$ , but the coefficient varies with time:  $P = \alpha(t)x_1$ . Growth and storage are also proportional to investments, with no time variation:  $\dot{x}_1 = \beta_1 u_1 P$  and  $\dot{x}_2 = \beta_2 u_2 P - u_3 x_2$ . The  $\beta$ s are efficiency coefficients, and the two terms in the second storage equation correspond to input and output respectively (Figure 2e). Fecundity is proportional to investment, but the coefficient varies with season:  $b = \beta_3(t)[(1 - u_1 - u_2)P + u_3 x_2]$ . The two terms in brackets correspond to direct allocation and to reallocation from storage, respectively. There is no mortality, and fitness is measured by expected fecundity. The Hamiltonian

$$H = b + y_1 \dot{x}_1 + y_2 \dot{x}_2 \quad 20.$$

is linear in the controls, and there is no singular arc. Thus the optimal strategy is a sequence of boundary values, separated by switches. Whether storage is optimal depends on the value of efficiency coefficients and on the way returns vary with time. For storage to be useful,

$$y_2(t)\beta_2 > y_1(t)\beta_1 \text{ and } y_2(t)\beta_2 > \beta_3(t). \quad 21.$$

With time-invariant parameters  $\beta_1$  and  $\beta_2$ , this can happen if both  $y_1(t)$  (i.e. the value of vegetative investment) and  $\beta_3(t)$  (i.e. the value of immediate reproduction) are low, and  $y_2(t)$  is high (i.e. good prospects for returns from delayed reproductive allocation). Thus, when prospects are bad for produc-

tivity and momentarily bad for reproduction, energy is better stored for future reproduction. Schaffer et al (67) provide an example in which the optimal sequence includes first pure growth ( $u_1 = 1$ ), then pure storage ( $u_2 = 1$ ), then pure reproduction ( $u_1 = u_2 = 0$ ), first from photosynthate only ( $u_3 = 0$ ), then from both photosynthate and storage ( $u_3 = 1$ ). The contrasting allocation strategies of two annuals, *Camissonia boothii* and *Plantago insularis*, apparently support their model: *C. boothii*, which relies more on insects for pollination (and thus on a specific time of the year), stores larger amounts of nonstructural carbohydrates (67).

Chiariello & Roughgarden (14) studied a similar situation, in which the coefficient for transforming reproductive allocation into seeds ( $\beta_3$ ) is time-constant, but there is some seed mortality and vegetative losses due to grazing (Fig 2f). Because of seed loss, these authors chose to model seed mass as a third state variable ( $x_3(t)$ ), the final value of which represents fitness. There are therefore three state variables and no intermediate function, so that the Hamiltonian becomes:

$$\text{Max } H = y_1 \dot{x}_1 + y_2 \dot{x}_2 + y_3 \dot{x}_3 \quad 22.$$

For storage allocation to be useful,

$$y_2(t)\beta_2 > y_1(t)\beta_1 \text{ and } y_2(t)\beta_2 > y_3(t)\beta_3 \quad 23.$$

This condition is similar to Equation 21 above, except that the changes with time now affect  $y_3$  rather than  $\beta_3$ . It is still true that other coefficients being equal, storage is adaptive when  $y_3(t)$  is low and  $y_2(t)$  is high, which means that storage early in the season is adaptive if  $y_3$  increases with time. In this case the benefits from storage are due to seed mortality, because early produced seeds contribute less to the total seed yield (at the end of the season) than late-produced seeds. Indeed, introducing seed mortality is simply another way to make the returns from reproductive allocations increase with time. The contrasting strategies of two seasonal ecotypes of the grassland annual *Hemizonia luzulifolia* fit this model: The autumnal ecotype has a higher seed-loss rate and a higher storage level than the vernal ecotype (14).

It is also worth noting that a temporary constraint on the maximal allocation to reproduction may also select for a temporary storage of energy, as suggested by Kozlowski & Ziolk (41).

**MULTIPLE SWITCHES** King & Roughgarden (35) analyzed a model originally proposed by Denholm (19), which comprises two state variables: vegetative mass ( $x_1$ ) and reproductive mass ( $x_2$ ), with no transfer among them. Fitness is measured by reproductive mass at the end of the season,  $x_2(T)$ . Production is proportional to vegetative mass, and some losses from  $x_1$  and  $x_2$  are assumed ( $\mu_1$  and  $\mu_2$ , respectively). The time-derivatives of the state variables are  $\dot{x}_1$

$= (u\beta_1 - \mu_1)x_1$  and  $\dot{x}_2 = (1 - u)\beta_2x_1 - \mu_2x_2$ . If the  $\beta$  and  $\mu$  parameters are time-invariant, then a single switch is optimal, as in classical models (16, 84). However, if  $\beta$  and  $\mu$  vary with time, then multiple switches between growth and reproduction may occur. Such a situation may occur in particular if there exists a time interval during the season where  $\beta_1(t) < \mu_1(t) - \mu_2(t)$ . Thus, an early bout of reproduction may be promoted by a momentary decrease in the efficiency of transforming resources into vegetative biomass, large midseason vegetative losses ( $\mu_1$ ), and/or low seed losses ( $\mu_2$ ). It is worth noting that  $\mu_2$  might even be negative, if reproduction biomass contributes to photosynthesis (e.g. 4). This model, which further exemplifies the effect of time-dependent returns on optimal allocation strategies, may explain double reproductive periods in the two annuals *Plantago aristata* and *Teesdalia nudicaulis*, due to mid-summer bursts of vegetative losses (35).

This model serves to introduce the case of perennial organisms, where annual cycles of mortality promote multiple switches from growth to reproduction, implying several reproductive periods.

### *Fluctuating Environments*

Here we stay with seasonal environments, but allow model organisms to survive the winter season (e.g. 31, 38, 40, 46, 58, 59, 60, 65). The model may also apply to other kinds of fluctuations, for example, nycthemeral photoperiods in unicellular algae (17), or variable food supplies in microorganisms (50). The optimal policy may be investigated by means of PMP, as shown with an explicit example by (65). The optimal life-long strategy is split into a series of annual objectives ( $J$ ) that comprise both an intermediate ( $I$ ) and a final ( $F$ ) function (Appendix). The intermediate function corresponds to the current-year reproduction, and the final function to the reproductive value at the end of the year. The life-long optimal strategy may then be calculated backward from the last year, using the recurrence relationship identifying the objective ( $J$ ) for a given year (i.e. reproductive value at the start of year  $j$ ) with the final function ( $F$ ) of the preceding one (i.e. residual reproductive value at the end of year  $j - 1$ ). This is analogous to William's comment mentioned in the Introduction.

If the Hamiltonian is linear in the controls, then the strategy within years is bang-bang, which reduces the problem to locating the switching times (e.g. 38).

**MODEL WITHOUT STORAGE** The simplest model, developed by Mirmirani & Oster (46) and Kozłowski & Uchmanski (38), considers a single physiological state variable (body mass), which may grow during the vegetative period but remains stable in between (winter). This model may apply to perennial animals or to evergreen plants. Production ( $P$ ) depends on body mass  $x$ , but mortality



(which occurs only during winter) does not. The time horizon is fixed, and the population is assumed stable ( $r^* = 0$ ). Thus the discounting factor  $e^{-r^*t}$  can be dropped from Euler-Lotka, so that expected fecundity is a suitable fitness measure.

This model is a generalization of that for annuals studied by Kozłowski & Wiegert (39) which, under the same assumptions, yields a bang-bang strategy. Here the strategy is also bang-bang within years, and the condition for switching from growth to reproduction during the year  $j$  is a generalization of Equation 13, viz:

$$\sum_{i=j}^n \frac{\partial P}{\partial x_i} P_i(T-t) S_{ji} = P_j, \quad 24.$$

where the subscript  $i$  designates the value taken by the variable at the onset of reproduction during year  $i$ ,  $T - t$  is the time left before the season ends, and  $S_{ji}$  is survival from year  $j$  to year  $i$ . It is easy to verify that Equation 24 and Equation 13 coincide for  $n = 1$  and  $\mu = 0$  (annual organisms without mortality during the vegetative season).

Although the strategy is bang-bang within years, Equation 24 nevertheless describes a kind of indeterminate strategy, in that some growth can occur after maturity. Indeterminate growth stems here from multiple switches, not from intermediate allocation since growth and reproduction do not occur simultaneously. Multiple switches occur because winter mortality is here a discrete event, occurring between vegetative periods, and it may be adaptive to reproduce just before winter. Further, the larger the mortality, the more growth occurs after first reproduction. As the time spent on seed production increases each season (46), the overall growth curve is sigmoid. This pattern (sigmoid growth and yearly reproduction) is indeed widespread among woody plants, e.g. trees. The allocation patterns of two marine molluscs (*Conus pennaceus* and *Chlamys islandicus*) and a fish (*Salvellinus alpinus*) also fit the model well (38).

**MODELS WITH STORAGE** The simplest situation involving storage assumes deterministic fluctuations in the production rate (17, 50). A specific example is photoperiod in unicellular algae (17). The daily photosynthate may be allocated to vegetative structures, reproduction, or storage. Stored energy is used for metabolism and/or reproduction. The analysis shows that the optimal strategy is first to grow, then to store during each productive period (day). During the nonproductive period (night), the stored energy is used for metabolism and reproduction. Because storage is costly, only the exact amount needed is stored, and this amount increases with the probability of starvation. These results oppose a classical interpretation of storage (references in 17) in



which the energy stored is simply that surplus to the demands of growth, which is assumed to occur at the maximum possible rate. Storage allocation in *Chlamydomonas reinhardtii* fits this model, increasing as mean productivity decreases and as variance in productivity increases (17). Perrin et al (53) also show an increase in the storage level of *Daphnia magna* when food supply varies.

Storage may also benefit perennial organisms. Unlike evergreens, deciduous perennial plants drop part of their vegetative mass at the end of each season and have to reconstruct it at the start of the following one. This situation can be modeled by considering the soma as composed of two compartments, corresponding to persisting and nonpersisting parts (e.g. 31, 58, 65). Some of the energy from the nonpersisting compartment can be relocated to the persisting part (which may be broadly referred to as a storage compartment) at the end of the vegetative season, and it can be used to rebuild the vegetative mass at the onset of the following season if the plants survive the winter. The amount of storage may, or may not, affect mortality, which, in the models developed so far, occurs only during winter.

In the model studied by Schaffer (65; Figure 2g), storage does affect winter survival, and a time horizon is imposed. The Hamiltonian is:

$$H = P[u_1 y_1 \beta_1 + u_2 y_2 \beta_2 + (1 - u_1 - u_2) \beta_3] \quad 25.$$

where the first term in the brackets corresponds to vegetative growth ( $\dot{x}_1$ ), the second term to storage ( $\dot{x}_2$ ), and the third term to reproduction. It turns out that the factors weighting reproduction ( $\beta_3$ ) and storage ( $y_2 \beta_2$ ) are time-invariant within seasons (due to the absence of mortality, and because  $H$  is not an explicit function of the amount of storage), while the factor weighting growth ( $y_1 \beta_1$ ) decreases during each season. Growth is always optimal at the season's start, and this is followed by storage (without reproduction) if  $y_2 \beta_2$  exceeds  $\beta_3$ , but by reproduction (without storage) if the reverse is true (Figure 7). Since the absence of storage means certain death, Schaffer (65) concluded

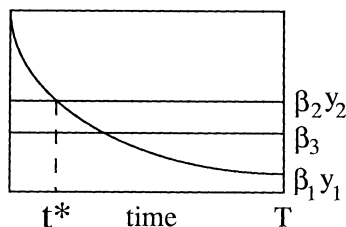


Figure 7 How the priorities of growth, storage and reproduction might change with time. The factor weighting growth ( $y_1 \beta_1$ ) decreases with time, while those weighting storage ( $y_2 \beta_2$ ) and reproduction ( $\beta_3$ ) do not. Thus, the optimal strategy comprises a period of growth (from 0 to  $t^*$ ), followed by a period of storage (from  $t^*$  to  $T$ ). No reproduction occurs, because  $y_2 \beta_2 > \beta_3$ .

that the optimal strategy under these assumptions is necessarily monocarpic (i.e. semelparous), but his analysis ignores the possibility of a singular arc: The optimal strategy might include a period where allocation is such that the returns from storage and reproduction equalize over several years ( $y_2\beta_2 = \beta_3$ ). This possibility would correspond to an iteroparous strategy, similar to that discussed in the previous section.

Indeed, Pugliese (58) investigated a similar model and found an iteroparous strategy to be optimal (storage and reproduction within the same year). There is no time horizon in his model, so that an equilibrium state exists, which is reached after a few years without reproduction. For some production and mortality functions, the optimal strategy involves multiple switches and indeterminate growth. However, Pugliese's model predicts a single switch and determinate growth under the assumptions of size-independent winter mortality, and production a monotonically increasing and convex function of vegetative mass, apparently *contradicting* (38).

The same apparent paradox arises from Iwasa & Cohen's (31) model, which uses a slightly different approach: The energy stored during a season (which does not affect winter mortality) can be relocated either to regrowth at the start of the following year or to reproduction at the end of the current one. Thus, the within-year objective is simply to maximize storage. Accordingly, the within-season condition for the optimal switch from growth to storage reduces to that for annuals without mortality:  $(T - t)\partial P/\partial x_1 = 1$  (their Equation 7d). The optimal life-long strategy turns out to be either an annual (all first-year storage devoted to reproduction), or an iteroparous perennial (storage partially allocated to regrowth). Not surprisingly, the latter option is favored by low winter mortality and high storage efficiency. But more interestingly, the iteroparous strategy is again determinate (no further growth after maturity). This last point corroborates the results of Pugliese (58) but again seems to oppose those of Kozłowski & Uchmanski (38).

This apparent paradox has been resolved by Pugliese & Kozłowski (60), who showed that there exists a critical proportion of persistent organs,  $q_c$  say, above which the optimal strategy is indeterminate. The value of  $q_c$  depends directly on winter survival. High survival produces a high  $q_c$  value, which means that most of the vegetative parts must persist over winter for further growth to be favored. In the Kozłowski & Uchmanski (38) model, all vegetative parts are persistent, so there is always further growth. By contrast, only the storage compartment survives in the Pugliese (58) and Iwasa & Cohen (31) models, so that no growth occurs after maturity.

The prediction is therefore that, among perennials, indeterminate growth should be more common among evergreens, while plants surviving winter via underground structures (bulbs) should adopt a determinate growth strategy.

## DISCUSSION

The dynamic optimization approach to resource allocation provides a way of comparing the selection pressures on particular investments at different ages, taking into account how these investments affect the organism's state and thereby its prospective reproduction. The costate variables of Pontryagin's maximum principle, which measure these pressures directly ( $\partial(\text{fitness})/\partial x_j(t)$ ), can also be thought of as representing the marginal values of investments. The optimal policy is obviously to allocate resources where selection pressures are highest, and simultaneous allocation to several subsystems can be optimal if these pressures are equal. This optimality principle should be borne in mind as we now outline our main results concerning balanced growth, the optimal timing of the switch to reproduction, indeterminate growth, and storage allocation, and as we consider how and to what extent model predictions can be tested.

### *Balanced Growth*

A first application of the optimality principle concerns balanced growth and patterns of ontogeny. The question of allometric growth has long been envisaged solely from a descriptive point of view (28, 85). By tackling this question in an evolutionary adaptive framework, optimal allocation models have moved a few steps toward providing a functional basis for a theory of ontogeny, even for rather complex life cycles (52, 86). According to our optimality principle, allocation to several organs or subsystems should be simultaneous if the selection pressures on them are equal, and this leads to expressions involving the ratio of production to extended mortality (Equations 9 and 10), which are explicit functions of the state variables  $x_i$ . Thus the optimality principle leads to precise predictions about ontogeny that depend specifically on state-space geography (Figure 5a). Observed patterns of growth and survival during ontogeny as well as plasticity in resource allocation are generally in good agreement with predictions (32, 52, 73). However, a precise knowledge of state-space geography (i.e.  $P/m$  as a function of state variables—Figure 5a) would be required to test the models further. As far as modeling is concerned, further theoretical consideration of multiple-resources acquisition (as in Tilman's work 83a) would be welcome.

### *Growth vs Reproduction*

The question of growth versus reproduction is a special case of balanced growth: Allocation should be simultaneous when the selection pressure to increase soma ( $x$ ) equals that on reproduction ( $R$ ). In the present context, this may be expressed:

$$v(t)/\partial x(t) = \partial b/\partial R \quad 26.$$

which is easy to solve, provided reproductive value  $v(t)$  can be made an explicit function of soma.

**DETERMINATE GROWTH** When the optimal policy is determinate growth, Equation 26 gives the condition for an optimal switch: for constant fecundity, the reproductive value  $v(t)$  is simply the product of fecundity and (discounted) life expectancy (e.g. Equation 15), both of which are explicit functions of soma. Thus, the conditions for an optimal switch are readily derived from Equation 26, for both constant environments (Equation 6) and annual environments, whether soma affects production only (Equation 13) or also mortality (Equation 15).

The proximity of a time horizon ( $T$ ) selects for an earlier onset of reproduction, while the ability to relocate some of the vegetative biomass ( $\alpha$ ) into reproduction selects for a delay. Quantitative predications are more specific, including switching curves (Figure 6) as functions of  $\alpha$ ,  $T$ , and the dependencies of  $P$  and  $m$  on soma. There is some circumstantial support for these predictions: Cohen (16), for instance, notes that maturity is more age dependent in late-flowering annuals than in early-flowering, in accordance with predictions (Figure 6a). The patterns of size versus age dependence in plants are well documented (42), but further information of  $T$ ,  $\alpha$ , and dependencies of  $P$  and  $m$  on soma is necessary for a full evaluation of these models.

**INDETERMINATE GROWTH** Indeterminate growth may result either from intermediate allocation or from multiple switches. In the case of intermediate allocation, Equation 26 must be satisfied along the optimal trajectory (e.g. Equation 7). In the case of multiple switches, an optimal-switch condition applies (e.g. Equation 24). In which of these models is indeterminate growth favored, and in which cases is it due to intermediate rather than multiple-switches strategy?

In a constant environment, nonlinearities in the trade-offs between growth and reproduction or between  $u$  and  $m$  may select for an intermediate strategy, depending on the precise shapes of the trade-off curves, and presumably (though this has not been explored) nonlinearities may have the same effects in all environments. On the other hand, linear trade-offs cannot select for indeterminate growth in a constant environment.

In annual seasonal environments, unpredictable season length may select for intermediate allocation, either with or without storage, and fixed season length may, if production  $P$  and extended mortality  $m$  are both increasing (or both decreasing) functions of body size. In addition, constraints on the

maximum rate of reproductive allocation may select for allocation of excess energy to growth, and thereby for an intermediate strategy.

Multiple switches require fluctuations in the environment such as winter bursts of mortality in perennials. With storage, multiple switches may be selected if many vegetative organs persist between seasons or, with no storage, if the adult mortality rate is high.

The current position is therefore that many possibilities have been considered, but not all (e.g. nonlinear trade-offs in nonconstant environments), and several cases are known in which indeterminate growth is selected, but we are not yet in the secure position of having explored all reasonable possibilities, nor can we yet provide an exhaustive list of factors selecting for indeterminate growth. Factors so far identified include nonlinear trade-offs, variable season lengths, and  $P$  and  $m$  both increasing (or decreasing) functions of body size. Is it likely that these alone can account for the many known cases of indeterminate growth in plants, animals, and other organisms? While we cannot at this stage provide an answer, the following considerations are worth noting. The dependence of  $P$  and  $m$  on body size can be established relatively easily, and data probably already exist for some species that would allow one to assess whether  $P$  and  $m$  are both increasing or both decreasing functions of body size. If not, then the model of (55) cannot provide an explanation of indeterminate growth. Similarly, the variability of season length is relatively easy to investigate. If there is little or no variation, then the models of (2, 16, 36) cannot be the explanation of indeterminate growth. Identifying the shapes of trade-off curves if they are nonlinear is more laborious (see e.g. 49, 62, 72).

### *Storage and Reallocation*

The biological importance of storage has long been recognized (e.g. 56, plus other papers from this symposium), but its functional aspects have not always been fully acknowledged; some authors, for instance (references in 17), have proposed that organisms store energy only when it occurs in excess of maximum feasible growth. The dynamic optimization approach reviewed here identifies cases in which energy storage and reallocation are adaptive. Reallocation from one organ to another should occur if the marginal value of the latter exceeds that of the former. This happens in annuals toward the end of the season, thus selecting for reallocation from vegetative mass to reproduction. True storage organs may evolve if the returns from direct allocation are momentarily bad. This may happen in annuals if the returns from reproduction increase during the season, and in perennials if there is winter loss of vegetative parts. While some circumstantial evidence favors these predictions, more extensive comparative data would be welcome.

In all situations investigated so far, energy allocation to storage, when

adaptive, is bang-bang. However, all these situations involve deterministic environments, and unpredictability in returns from somatic or reproductive allocations may select for intermediate allocation strategy. This remains to be investigated.

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#### APPENDIX

Pontryagin's Maximum Principle (PMP) is a method of solving problems of form: choose a control vector  $\mathbf{u}(t)$  for all values of time  $t$  from initial time 0 to terminal time  $T$  so as to maximize the *objective function*  $J$ :

$$\text{Max}_{\mathbf{u}(t)} J = \int_0^T I(\mathbf{x}(t), \mathbf{u}(t), t) dt + F(\mathbf{x}(T), T),$$

where  $I$  and  $F$  are called intermediate and final functions respectively, and  $\mathbf{x}$  is the state vector. PMP states that a necessary condition for a maximum in  $J$  is that at every time  $\mathbf{u}$  maximizes the Hamiltonian  $H$ :

$$\text{Max}_{\mathbf{u}(t)} H(\mathbf{u}(t)) = I + \mathbf{y}(t)\dot{\mathbf{x}}(t)$$

The costate vector  $\mathbf{y}(t)$  is found by integrating back from the terminal condition  $\mathbf{y}(T) = \partial F / \partial \mathbf{x}(T)$  using the relationship  $d\mathbf{y}/dt = -\partial H / \partial \mathbf{x}$ .

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