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Optimal Allocation of Resources to Growth and Reproduction: Implications for Age and Size at Maturity

Jan Kozłowski

The schedule of growth and reproduction is crucial to maximization of fitness. Models of optimal allocation of limiting resources are useful tools for predicting age and size at maturity – key components of fitness – for all lifestyles. Early models considered annual plants. Recently, they have been generalized to other short-lived organisms and also to perennials in which growth and reproduction schedules following maturation can be predicted. A review of existing models shows that differences in trophic conditions and mortality are the main sources of inter- and intraspecific variation in size.

When we ask why a species in a given place is of a given size, typical answers invoke climatic conditions, metabolic properties, interspecific competition, predator–prey interactions, food particle size and so forth. Since these causes are not mutually exclusive, they cannot help us to determine the optimal size for that species, or whether it is the optimal size for that place. The theory of optimal resource allocation is a framework in which such specific problems can be solved with specific models.

There is still controversy about which resources limit plants and animals[1-3]. Here, I formally consider energy. The idea that life history evolution is constrained by the energy entering the organism was postulated by Gadgil and Bossert in a seminal paper[4]. Cohen[5] produced the first explicit model for optimizing the allocation of limited energy to growth or reproduction.

The basic model

Energetic limitation of organisms implies the importance of optimal energy allocation for size and age at maturity. Each calorie allocated to growth could, in principle, be allocated to reproduction, and *vice*

versa. Building the vegetative body means investment in better survival and/or greater future reproduction. When investments in the vegetative body are not completely paid back as future reproductive products, growth has been too great. Conversely, investment in vegetative machinery has been too small when the gain in current reproduction does not completely compensate for losses in future reproduction due to lower present vegetative allocation. Thus, the goal of the theoretician is to find the optimal division of energy during an organism's lifespan.

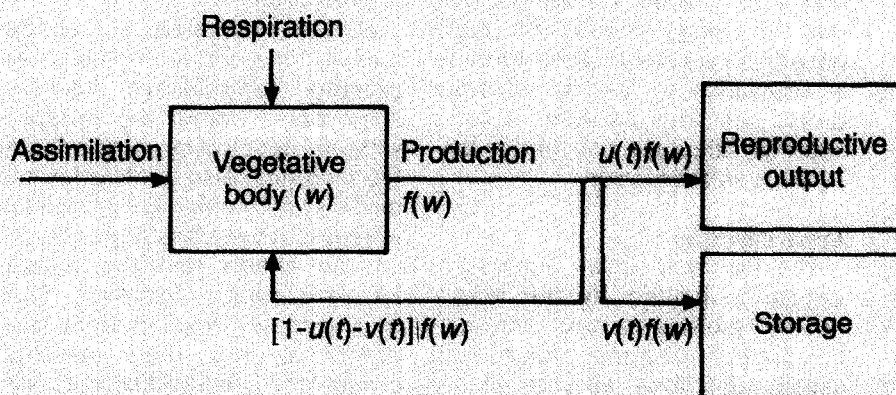Box 1 presents the problem of optimal energy allocation. To treat the problem mathematically (i.e. convert it to a system of equations) requires many additional assumptions. Two modelling strategies are possible: building a universal (and complicated) model or building specific (and relatively simple) models, each tailored for a restricted group of organisms. The papers reviewed here use the second strategy, which not only leads to simplicity but also reveals sources of diversity in life histories.

For optimal resource allocation, the first problem is what measure of fitness to use. In other words, what is to be maximized? The intrinsic rate of increase, *r*, is the most widely used fitness measure

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Box 1. Schematic representation of energy allocation

An organism assimilates and dissipates energy at size-dependent rates, and at each moment t allocates the fraction $u(t)$ of surplus energy to reproduction, the fraction $v(t)$ to storage and the remaining part to increase its size w, at a production rate $f(w)$. Control variables $u(t)$ and $v(t)$ are optimized in order to maximize lifetime reproductive output. An additional assumption is that maintenance costs are not optimized, and that they always have priority.

Box 2. Optimal growth trajectories for annual organisms
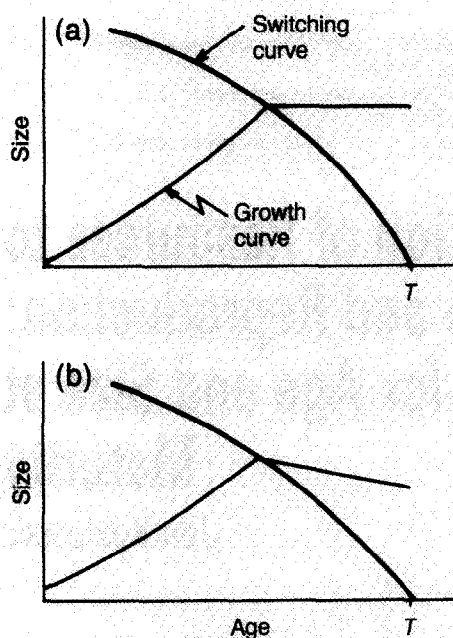
The switching curve represents optimal combinations of age and size at the time of switching from vegetative to reproductive growth (i.e. the age and size at maturity). Not all points on the curve are accessible. Before the switch to reproduction occurs, an organism must grow according to its growth potential, represented by the growth curve. The intersection of these two lines represents the actual age and size at maturity. An individual should grow until the switching curve is reached; then it should allocate all the surplus energy to reproduction. If lost tissues are replaced, size stays constant after the switch (a). If lost tissues are not replaced, size decreases toward the end of the season (b). The shape of the switching curve depends both on the specificity of the model and on the parameters. The length of the season is denoted by T.

in life history studies. In allocation models, expected lifetime allocation of energy to reproduction is maximized. Under the assumption that the energy content of a single offspring is constant, such a measure is equivalent to lifetime offspring production. This measure is valid and equivalent to r only under constant population size[6].

Annual organisms

The life cycle of an annual organism is limited by the length of the growing season. An optimal pattern of energy allocation is usually as follows: allocate all the surplus energy to vegetative growth, then switch suddenly and completely, allocating all the energy to reproduction. This result is very robust and is not influenced by loss or senescence of tissues or by mode of reproduction (releasing

accumulated reproductive energy continuously, in repeated clutches or in one clutch at the end of the season)[5,7–10]. Energy should be allocated to reproduction from the switch until the end of the season; several switches back and forth between vegetative and reproductive growth may be optimal, but they should always be complete, with no simultaneous growth and reproduction[9].

Field data contradict these findings, tending to show a gradual switch[11–13]. Several reasons for a gradual switch have been proposed according to optimal-allocation theory. For instance, a gradual switch from growth to reproduction is optimal in the unrealistic case when the cost of producing one offspring increases with family size[14]. The optimality of a gradual switch has also been proved for growing seasons of random length[15]. This result rests on several assumptions and should not be treated uncritically. For example, the geometric mean of r must be maximized; this only seems reasonable for annuals that do not produce seed banks. Also, fruits or diapausing eggs that are immature at the end of the season must be considered lost to make a gradual switch optimal; this assumption is hardly ever justified because organisms can transfer some of their own resources from vegetative to reproductive parts when external sources of energy are cut off. Even when these assumptions are satisfied, a gradual switch is optimal only under a narrow range of parameters[15].

Design constraints are another reason for gradual switches. For example, reproductive organs in some plants cannot be produced without developing new vegetative modules. Also, most allocation models assume that the growth rate of reproductive parts depends only on the energy that the vegetative parts supply. However, reproductive parts develop from small primordia, and their maximum growth rate is limited by their size. This may mean that either a gradual switch or storing of some materials for later reproductive allotment is optimal[16,17].

Despite these reservations, it is reasonable to accept an immediate switch as a first approximation, and

then to ask when in the season this switch should take place, as shown in Box 2.

When production rate, $f(w)$ from Box 1, is a linear function of the vegetative body size, the switching curve is a vertical line[5,7,8] (Fig. 1). This line's distance from the end of the season is independent of season length. The distance depends on the production rate (high production = late switching) and on mortality (higher mortality = earlier switch to reproductive allocation). The latter does not occur under mass reproduction at the end of the season. The location of the switching line also depends on the rate of vegetative tissue loss[7] (larger losses = earlier switching). The ability to relocate some resources from the vegetative body to reproductive parts at the end of the season delays the switch[18] (Fig. 1a).

The timing of the switch (relative to the end of the season) and the length of the season strongly affect body size (Fig. 1b). In the linear model, initial size affects size but not age at maturity.

In a more realistic case, when the production rate function $f(w)$ decreases with increasing body size, the switching curve is no longer a vertical line but a concave one, as shown in Box 2. In plants, the decrease in production rate with size results from self-shading and an increasing proportion of supporting tissues. In animals, the rate of production declines and can be approximated as an allometric function of body size with the exponent smaller than one[19,20].

The effect of production rate, mortality and resource reallocation from vegetative to reproductive parts is qualitatively the same as in the linear model. Because of technical difficulties, all existing nonlinear models neglect tissue loss, but they probably have the same qualitative effect as in the linear model. The period of reproductive allocation is longer for longer seasons; that is not the case in the linear model. The initial size of the organism affects both age and size at maturity[18].

Optimal size at maturity in an aseasonal environment

The models of optimal resource allocation for annual plants were published before the models for

aseasonal environments, which are simpler. The problem can be presented graphically in three-dimensional space (Fig. 2)[21].

The volume of the solid shown in Fig. 2a represents fitness – the amount of energy expected to be allocated to reproduction throughout life. Prolonging the growth period (without reproduction) increases the reproduction rate (the height of the solid), but this will also shorten its base (probability of survival). Optimal age at maturity (and size at maturity as a result) maximizes the volume of the solid[21].

If mortality is size independent, at least above some threshold size too small for maturation, the optimal solution is to keep allocating all the surplus energy to growth as long as $df(w)/dw \times E > 1.0$, where $df(w)/dw$ is the rate of change of production with size and E is life expectancy. (At lower values of this product, it is optimal to allocate all the surplus energy to reproduction.) Life expectancy under constant mortality m equals $1/m$, so the condition for optimal allocation of energy to growth can be rewritten as $df(w)/dw > m$, or in a more general form, which does not assume a constant population number, $df(w)/dw > m + r$. For any concave $f(w)$, high mortality and high intrinsic rate of increase promote early maturation at a small size.

This model can be modified for size-dependent mortality (when a decrease of mortality with size results in a delay in maturation) and for different units of vegetative and reproductive production, such as calories and eggs[21]. If the solid is cut at the end of the season, we get the annual life history model[21]. Other alterations are as yet unexplored: if production rate varies with age or season, the height of the solid also will vary.

The model can be modified for long-lived animals with determinate growth (growth ceasing at maturation) in a seasonal environment[21], with the basic prediction that the production rate and mortality always act together in determining age and size at maturity. This explains the pattern known for mammals: after the effect of size is removed, a positive interspecific relationship exists between the age at maturity and adult lifespan[22,23].
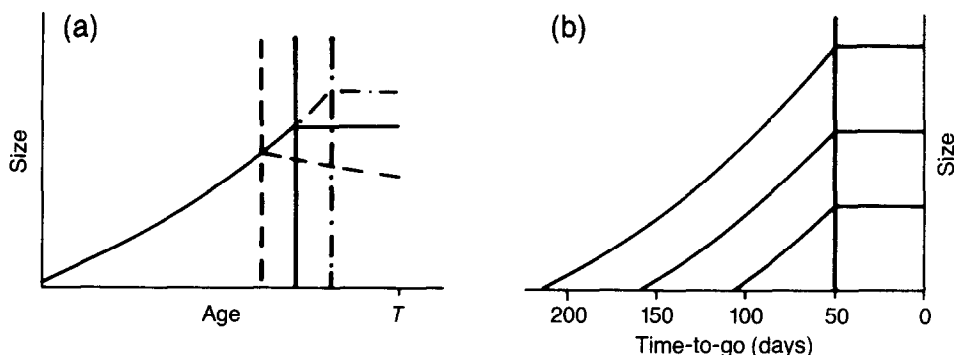

Fig. 1. Optimal trajectories for growth when the production rate depends linearly on vegetative size. The switching curves are vertical lines; their position in relation to the end of the season depends on the specific production rate and on other model characteristics. (a) Optimal switching to reproduction is delayed if some resources from the vegetative body are reallocated to reproductive output (dot-dashed lines), and speeded up if some vegetative organs are lost (dashed lines). (b) For linear production rates, optimal switching time in relation to the end of the season is independent of season length T, although size at switching strongly depends on T. Time-to-go represents the time left to the end of the season. *(b) from Ref. 18 with permission.*

Perennial iteroparous organisms

For perennial organisms, the strategy leading to maximum reproductive output in a given season is not necessarily the optimal one, for some investments in vegetative growth can be paid back in future seasons. Therefore, perennial organisms should allocate less of their surplus energy to reproduction each year than a hypothetical annual that is the same in all respects except lifespan. The additional investment in vegetative growth is more likely to be repaid under low mortality, so mortality must have a dominant role in the optimal allocation schedule.

Existing models of optimal energy allocation consider only perennials that do not reproduce vegetatively. They yield conflicting predictions. Some models predict purely vegetative growth before the onset of maturation, then only regrowth to the previous size at the beginning of each season followed by allocation of energy into reproduction and storage[17,24,25]. Other models predict many years of mixed vegetative and reproductive growth with more energy devoted to reproduction as the organism ages[26–28].

The conflict is resolved by Pugliese and Kozłowski[29]. Models predicting many years of mixed allocation assume that the whole vegetative body remains intact for the next year. Such an assumption
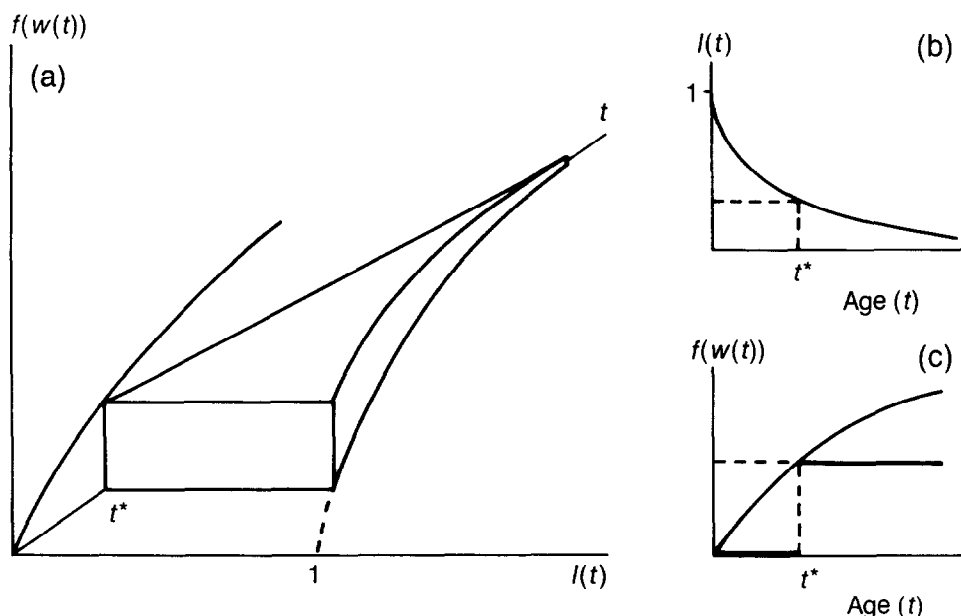

Fig. 2. Fitness measured as lifetime energy allocation to reproduction. (a) The solid whose volume represents fitness in three-dimensional space, with age, t, probability of surviving to a given age, $l(t)$, and potential rate of energy allocation to reproduction, $f(w(t))$, as dimensions. (b) The projection of the solid on the $(t, l(t))$ plane. (c) The projection of the solid on the $(t, f(w(t)))$ plane. The thin line represents the potential production rate for a growing organism; the thick line is the current rate of allocation to reproduction – zero before switching to reproduction and at some level thereafter that is dependent on size at switching. Age of maturation is denoted by t^*. *Adapted from Ref. 21 with permission.*
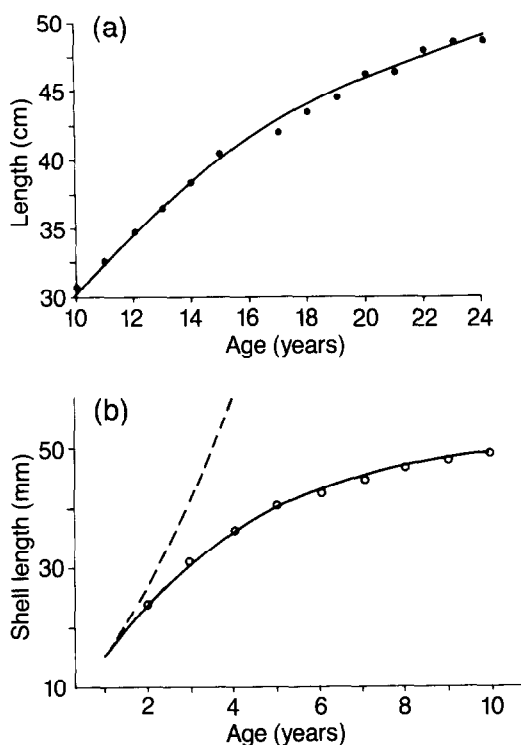
Fig. 3. (a) Predicted (line) and observed (circles) growth curves for St Mary's Bay American plaice (*Hippoglossoides platessoides*). Adapted from Ref. 26 with permission. (b) Predicted (solid line) and observed (circles) growth curves for the gastropod *Conus pennaceus* from Hawaii. Broken line shows the potential growth curve should reproduction not occur. From Ref. 28 with permission.

is reasonable for animals. Indeed, these models are supported by field data on fish[26,28] and molluscs[28]. In models that predict at most one year of mixed reproduction, it is assumed that nothing is left for the next season except some storage to promote spring regrowth. Such an assumption is reasonable for some herbs. (Iwasa and Cohen[17] extended their results to deciduous trees, but that seems unjustified. Trunks and branches should not be neglected because they drain energy that otherwise would be in leaves or reproductive organs.)

There is a critical proportion of the vegetative body that must remain for the next season for mixed vegetative and reproductive allocation to occur[29]. This critical level strongly depends on winter mortality: when the probability of surviving to the next season is low, even a low proportion of persistent organs makes mixed allocation optimal. Tissues may be persistent in a literal sense, as trunks or branches of trees, but reallocation of resources from the vegetative body to storage at the end of the season may work as well if the process is intense enough.

Although structural carbon cannot be moved, a large proportion of nitrogen and other nutrients is often moved underground before winter[30].

Above and below the threshold proportion of persistent tissues, the optimal solution differs qualitatively: an organism either increases in size after maturation or not. Actually, the difference is not very dramatic. When the proportion only slightly exceeds the threshold, the increase of size after the first reproduction is small, and the amount of growth after maturation increases with the proportion of persistent tissues[29].

It is not surprising that productivity affects both size at maturity and the final size that can be attained, and to a lesser extent age at first reproduction[28]. More interestingly, at the same level of production, mortality very strongly affects age and size at maturity and the ratio of the size at first reproduction and the final size[28]. When mortality is very heavy, it is even optimal to start reproduction in the first year, when the organism is small. Delaying maturity, which is optimal under low mortality, leads to a large or very large size, especially when the proportion of persistent tissues is high. More growth takes place after maturation if mortality is high[28].

Growth curves of organisms are typically S-shaped. The reasons why this should be so for animals with determinate growth are not clear. Organisms with indeterminate growth should be able to grow according to convex curves; their S-shaped growth curves may result from the optimality of allocating more and more energy to reproduction with age, which produces growth curves closely resembling those in Fig. 3. This hypothesis is supported by the fact that in fish and reptiles exhibiting sexual size dimorphism, growth curves start to differ when the smaller sex matures[31,32].

Conclusions

Models of optimal allocation of resources are conceptually very simple and well defined. The mathematics can be complex, especially if optimal-control theory is used, but it provides a field for fruitful co-operation between biologists and mathematicians.

The optimization approach is used in all the models presented here. When size-dependent interactions between individuals are very important, game theory may be more appropriate[33].

The allocation models reviewed here do not exhaust the richness of lifestyles found in nature, and for quantitative studies I strongly recommend building specific models. The existing models, although they draw our attention to some important relationships and illustrate what can be done, do not constitute a comprehensive theory.

Several aspects of optimal-allocation theory are poorly explored. When trophic conditions are heterogenous in space, both the individual growth curves and the switching curves are affected. Reaction norms for age and size at maturity can be keyed to trophic conditions[34,35]. Although more attention has been paid in the last five years to perennial organisms, there are still no allocation models for plants reproducing both generatively and vegetatively. It is not clear at present how to attack this problem, which is crucial for understanding the life history evolution of most plants.

Both intra- and interspecific competition affect the size-specific production rate or survivability or both. With the aid of allocation models, the effect of crowding and competition on age at maturity and size of organisms can be studied. They can also help us understand why one sibling species can outcompete another in a given place[36].

A function describing the dependence of production rate on body size can be estimated on the basis of optimal-foraging theory and bioenergetics, as shown recently by Kenneth and Roughgarden[37] for tropical lizards. A simple allocation model may provide the nucleus of a much richer model incorporating many biological details.

The main point of this review is that the size of living organisms must always be considered in terms of the entire lifespan[38]. Small organisms are usually small not because smallness improves fecundity or lowers mortality but because it

takes time to grow large, and with heavy mortality the investment in growth would never be paid back as increased fecundity. So optimal size depends strongly on mortality, but mortality is often size dependent. This reciprocal relationship is surely one source of the great variability of life histories found in nature.

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Moose and Birch: How to Live on Low-quality Diets

Erkki Haukioja and Kari Lehtilä

Ten years ago, the question of forage use by moose largely focused on whether nutritive factors or secondary compounds determined their use of individual tree species. Today, it is clear that both are important. Research during the last few years has tried to explain the hierarchical decisions in the foraging patterns of moose.

Moose (*Alces alces*) are one of the largest terrestrial mammals of the hemiboreal region. Birches (*Betula pendula* and *B. pubescens* in Eurasia and *B. papyrifera* in America) are of only medium or poor nutritional quality compared with other moose browse species[1–3], but because they are so common they often represent the bulk of the winter forage.

In the early 1980s, two different hypotheses were presented to explain forage choice by moose. Belovsky[4] stated that moose maximize the net intake of energy, and demonstrated that it was possible to predict forage use with the aid of a simple index of nutrient value. At the same time, Bryant and Kuropat[5] reviewed plant–browser interactions and emphasized the importance of plant secondary compounds, which reputedly affect food choice and are important for plants because they help reduce herbivory.

Here, we concentrate on two aspects of winter foraging. First, what kind of factors, chemical and physical, make a particular plant or part of plant preferable for moose browsing, and how does the availability of forage modify forage use? Second, how does birch respond to moose browsing?

Food selection in winter

Food selection by moose occurs on a hierarchy of scales. In the autumn, moose may migrate hundreds of kilometers. During winter, the animals normally move several kilometers in a week[6]. When actually feeding, moose can select among adjacent trees, select twigs within trees and decide the size of bite taken from a twig. The search for favourable wintering grounds, the choice of plant species[1,6–8], regulation of bite size[6,7,9] and the amount of biomass removed per tree[6–8] are different aspects of forage selection.

Moose browse more selectively when forage quantity and quality are high[6,10]. In experimental birch stands, moose moved more from birch to birch and ate smaller bites and fewer twigs from individual trees in stands of high density[10]. (A smaller bite diameter means higher digestibility[2,10].)

Similar results were obtained in other habitats. In a habitat of low quality – where birch was the main available winter browse – moose ate birch almost exclusively,

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