Mathematical Biology

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Dynamic energy budget models with size-dependent hazard rates

Abstract. We formulate and analyze two dynamic energy budget models, a net assimilation model with constant allocation strategy and a net production model with a 2-stage allocation strategy, with the objective of determining strategies that maximize the expected lifetime reproductive energy. The per capita death rate depends on the organism's size, as for example when the main cause of death is predation by a small predator. In the analysis of the net production model, the size at maturity is calculated along with the probability of reaching that size. We show that a small probability of survival to maturity is incompatible with the simple assumption of an exponential survival probability. We demonstrate that when the hazard rate is significantly greater for small individuals than large ones, it is possible for the optimum strategy to be for an individual to grow to a large size in spite of an arbitrarily small probabililty of survival to maturity. Numerical simulations indicate how the optimal allocation strategies depend on the parameter values.

1. Introduction

Dynamic energy budget (DEB) models describe the time history of various state variables of an individual organism, such as size and resource storage, by describing the rates at which some limiting resource is assimilated and utilized for growth, maintenance, and reproduction. The limiting resource is generally called "energy," although it may as well be a specific nutrient such as carbon or nitrogen. DEB models are of two different types, depending on the rule used for allocation of energy. In a net assimilation model [4,9], a certain fraction κ of assimilated energy is allocated to the combined processes of maintenance and growth, with the remainder allocated to reproduction. In a net production model [7], maintenance is deducted from the assimilated energy first, after which a certain fraction α of the surplus energy is allocated to growth and the remainder to reproduction. Both models are often modified to allow for energy storage as well. DEB models have been used to fit experimental data [10,14] and also to consider theoretical issues [7].

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Dynamic energy budget models provide a context to study how an organism might develop a strategy to optimize its overall fitness, measured, for example, by its net reproductive output. The idea of maximizing energy allocated to reproduction was originally developed in [1, 8, 17]. These problems can often be formulated as optimal control problems, where the allocation function α, or κ, is the control, the net reproductive output is the objective function, and the DEB models provide the dynamics, or state equations. Life history problems for both plants and animals have been studied in this way ([3, 5, 6, 12, 13, 15, 16, 18]), and researchers have shown that both bang-bang strategies and non-bang-bang strategies are possible, depending upon the dynamics, the fitness measure, the initial conditions, or the time over which the system is observed. It is also common in the literature to assume that the allocation functions are constant, or piecewise constant if an organism's life history involves distinct stages in which the values of the allocation parameters are constant in each stage. (In fact, it is not actually reasonable for the allocation parameter α to be constant in a net production model, as will be shown in the analysis below).

DEB models must incorporate assumptions about the probability of survival for an individual organism. The survival probability is sometimes modeled simply as an exponential decay function [7]. In other cases, the survival probability is based on a physiological hazard rate [4, 9]. The exponential model is simple and therefore good for investigations in which the mechanisms of mortality are not of interest, but such studies cannot yield information regarding the effect of ecological niche on life history. The physiological hazard rate is appropriate when mortality is caused primarily by physiological factors; however, this assumption is reasonable only for a limited number of species. For many species, the principle cause of mortality is predation. Therefore, our aim in this work is to develop and study DEB models having mortality relationships with an ecological basis. It will be shown that certain key results are profoundly influenced by the assumptions made regarding the mechanism of mortality.

In this investigation, we formulate a life history problem for a general case where the allocation parameters are allowed to vary with development; however, we analyze only the relatively simple cases of constant κ, corresponding to an organism with only one life stage, and piecewise constant α, corresponding to an organism with distinct juvenile and adult stages. Under these assumptions, the life history strategy reduces to at most a set of two constant allocation parameter values and a prescribed condition for the transition between the two stages. In this simple setting, we can make theoretical predictions concerning the relative biological merit of certain life history strategies. Our model is composed of three parts: a dynamical equation for growth (given here as length) coming from the DEB model, a dynamical model for survival probability, and an objective function giving the expected lifetime reproductive energy use in terms of the length history and survival probability. The survival probability component incorporates two effects: a constant per capita loss due to random misfortunes, corresponding to the standard exponential survival probability, and a density-dependent loss due to predation, with Holling Type II functional form. The predation rate includes a factor that decreases as the organism grows too large for some of the potential predators. Given these equations

and input data regarding the food quality, we determine a life-history strategy that maximizes expected reproductive energy. In the analysis of the 2-stage net production model with a bang-bang (growth-reproduction) strategy, we calculate the optimum size at maturity and the probability that the organism reaches that size. We show that classical DEB models with constant per capita hazard rate have the limitation that they always predict a high probability of reaching maturity (at least 13%) even when the hazard rate is arbitrarily large. This leads us to examine the model with size-dependent predation in the hope of determining conditions that predict the possibility of an optimal strategy resulting in a large size at maturity with a small probability of reaching that size.

2. Mathematical Models

We seek to develop a model to predict the growth and reproduction patterns of a species based on the characteristics of individual organisms, particularly the strategy used to allocate resources. In anticipation of nondimensionalization, we use the superscript $*$ to refer to any dimensional quantity. Let g^* and r^* represent the cumulative energy spent by an individual on growth and reproduction. The rates at which these quantities increase depend on a^* and m^*, the rates (energy/time) at which energy is assimilated and used for maintenance, and on the allocation rule used in the model. Let x^*, S^*, and V^* be the length, surface area, and volume of the organism, and let p be the probability of survival to time t^*.

The energy available to an organism is allocated in some manner to growth, maintenance, and reproduction. This allocation is described by one of two basic rules. In a **net assimilation model**, the organism allocates a fraction κ of its energy to somatic uses, namely growth and maintenance, and the remainder to reproduction:

$$\frac{dg^*}{dt^*} = \kappa a^* - m^*, \quad \frac{dr^*}{dt^*} = (1 - \kappa)a^*. \tag{1}$$

In a **net production model**, the organism allocates a fraction α of its surplus energy (assimilation minus maintenance) to growth and the remainder to other uses; hence,

$$\frac{dg^*}{dt^*} = \alpha(a^* - m^*), \quad \frac{dr^*}{dt^*} = (1 - \alpha)(a^* - m^*). \tag{2}$$

The allocation parameters κ and α could possibly be constant, but they could also be dependent in a stepwise or continuous manner on the life stage.

Assimilation and Maintenance   The size of an individual is given by the length, surface area, and volume, and the maintenance and assimilation rates are assumed to be related to these measures of size. We make the following assumptions about the relationships of these quantities:

1. The assimilation rate is proportional to surface area.
2. The rate at which energy is spent on maintenance is proportional to the organism's volume.
3. The animals maintain a constant body shape as they grow.

These assumptions yield the relationships

$$a^* = AfS^*, \quad m^* = CV^*, \quad S^* = \beta x^{*2}, \quad V^* = \gamma x^{*3}, \tag{3}$$

where A, C, β, and γ are proportionality constants and f is a dimensionless function that represents the effect of variable food quality. The parameter A measures the ideal ratio of assimilation to surface area; thus, $0 < f \leq 1$. The function f is assumed to be a smooth function of time, possibly constant but not necessarily so. The specific connection between environmental variables and the function f need not be specified for our purposes.

Gurney and Nisbet [2] note that assimilation rates have been measured to be proportional to x^n, where x is length and n a real number from 1 to 4. These authors argue that $n = 2$ and $n = 3$ are the most plausible; we choose $n = 2$ because assimilation proportional to volume implies that energetics imposes no restriction on maximum size.

Note that there is nothing in the model to make adjustments for insufficient or intermittent feeding. The model is not designed to apply to cases where an organism must store energy for future maintenance. We also omit special consideration of the embryonic stage of an animal's life cycle. The current model assumes that the organisms come into being as juveniles of infinitesimal size. This is not a serious oversimplification in an investigation of phenomena that are accumulated over the life of an animal.

The structural assumptions (3) combine to yield formulas for assimilation and maintenance rates in terms of length:

$$a^* = \beta Afx^{*2} \leq \beta Ax^{*2}, \quad m^* = \gamma Cx^{*3}.$$

If an organism puts all of its assimilated energy into maintenance and growth, and its environment is ideal ($f = 1$), then it will grow asymptotically toward its physiological maximum size L, determined by setting the ideal environment assimilation equal to the maintenance. We define the scaled length x to be the length relative to this physiological maximum. Thus,

$$x = \frac{x^*}{L}, \quad \text{where} \quad L = \frac{\beta A}{\gamma C}. \tag{4}$$

We may therefore rewrite the expressions for assimilation and maintenance as

$$a^* = a_M fx^2, \quad m^* = a_M x^3, \quad \text{where} \quad a_M = \beta AL^2 = \gamma CL^3. \tag{5}$$

Note that a_M represents the maximum possible assimilation rate.

The Growth Equation   We assume that an individual's volume at any given time is proportional to the cumulative amount of energy used for growth:

$$V^* = cg^*.$$

The growth energy is then given in terms of the length; specifically,

$$g^* = g_M x^3, \quad \text{where} \quad g_M = \frac{\gamma L^3}{c}. \tag{6}$$

Note that g_M is the amount of energy that would be invested in growth for an organism that achieves the physiological maximum. Differentiating with respect to time, we have

$$\frac{dg^*}{dt^*} = 3g_M x^2 \frac{dx}{dt^*}.$$

It is convenient at this point to scale the time by defining a dimensionless time

$$t = \frac{a_M}{3g_M} t^* = \frac{cC}{3} t^*. \tag{7}$$

The basic growth energy equations (1) and (2) reduce to scaled differential equations for the length x:

$$\begin{cases} \frac{dx}{dt} = \kappa(x) f(t) - x & \text{(net assimilation)} \\[2ex] \frac{dx}{dt} = \alpha(x)[f(t) - x] & \text{(net production)} \end{cases}. \tag{8}$$

Note that the allocation parameter κ or α is allowed to depend on the size of the individual. A particular function for one of these allocation parameters represents a life history strategy. We defer for now the question of what set of possible life history functions to consider.

Expected Cumulative Energy Allocation We define the scaled reproduction energy by

$$r = \frac{r^*}{g_M} = \frac{cr^*}{\gamma L^3} \tag{9}$$

The reproduction energy equations (1) and (2) become

$$\begin{cases} \frac{dr}{dt} = 3[1 - \kappa(x)] f(t) x^2 & \text{(net assimilation)} \\[2ex] \frac{dr}{dt} = 3[1 - \alpha(x)][f(t) x^2 - x^3] & \text{(net production)} \end{cases}.$$

Individuals accumulate reproductive energy at the rate dr/dt, but only as long as they remain alive. The expected cumulative reproduction energy must take into account the probability of survival. Thus, the expected reproductive energy, relative to g_M, up to time t is given by

$$\begin{cases} R(t) = 3 \int_0^t [1 - \kappa(x(\eta))] f(\eta) x^2(\eta) p(\eta) d\eta & \text{(net assimilation)} \\[2ex] R(t) = 3 \int_0^t [1 - \alpha(x(\eta))][f(\eta) x^2(\eta) - x^3(\eta)] p(\eta) d\eta & \text{(net production)} \end{cases}. \tag{10}$$

For comparison, we will want to consider also the expected growth energy to time t, relative to g_M, as given by

$$\begin{cases} G(t) = 3 \int_0^t [\kappa(x(\eta)) f(\eta) x^2(\eta) - x^3(\eta)] p(\eta) d\eta & \text{(net assimilation)} \\[2ex] G(t) = 3 \int_0^t \alpha(x(\eta)) [f(\eta) x^2(\eta) - x^3(\eta)] p(\eta) d\eta & \text{(net production)} \end{cases}. \tag{11}$$

Survival Probability   Typically, the survival probability in a dynamic energy budget model is taken to be a decaying exponential function. This corresponds to the assumption that the hazard rate is independent of the state of the individual. However, the principal hazard for most creatures is predation, and the risk of predation is dependent on the size of the organism. In order to use a basic predator-prey model for the survival probability p, we identify p with the population density P, relative to its maximum. To make this identification we must assume that only one generation of the species is present at any given time, and that the entire generation is of uniform size and age. While unrealistic for many species, this assumption serves the present investigation by yielding a tractable mathematical model with a rich structure.

To formulate a dynamical equation for the survival probability p, we assume that the per capita death rate has two contributions, a constant loss b due to random misfortunes, and a density-dependent loss due to predation, with a Holling Type II functional form. Thus we assume

$$\frac{dp}{dt} = -bp - \phi(x(t))\frac{vp}{v+p}, \quad p(0) = 1, \tag{12}$$

where $\phi(x)$ measures the sensitivity of the predation rate to prey size, and the constant v measures the deviation of the functional response from linear.

To determine a relation for $\phi(x)$ we note that typical organisms live in a complex environment where they are subject to predation from a variety of predators, and each predator species has a particular range of preferred prey sizes. Generally, we expect the risk of predation to be a decreasing function of size. One simple model of size-dependent predation is the function

$$\phi(x) = \frac{\rho H}{H+x}. \tag{13}$$

Here, ρ is the predation rate for newborn organisms and H is the prey size for which the predation rate is half-maximum, much the same as in the density-dependent Holling Type II response. The survival function p can only be determined in conjunction with the growth curve, but we can at least state that its graph will be concave up (a Type 3 survivorship curve [11,13]).

We note that there could perhaps be other mechanisms whereby the hazard rate would be size-dependent; here we consider only mechanisms by which the hazard rate decreases as the organism grows.

The Life History Problems   The model given by (8) and (10–13) determines the time-dependent size, survival probability, and expected energy allocations for a given allocation rule κ or α. Our interest is in comparing the results of different allocations, each of which can be thought of as a strategy by which an organism's life history is determined. We assume that natural selection favors organisms whose life history function is tuned to some average or typical set of circumstances. The most general life history problem, formulated in terms of the net assimilation or net production model above, is to determine an allocation function, or strategy, either $\kappa = \kappa(x)$ or $\alpha = \alpha(x)$, that maximizes the fitness of the organism. It is assumed

that the dynamics governing length and survival probability are given, with specific forms for the size-dependent predation rate and the food quality $f(t)$.

We take the total lifetime reproductive energy allocation as a measure of reproductive output. The manner in which the reproductive energy is spent is assumed to be unimportant. We therefore count stored energy as energy ultimately spent on reproduction, and we make no distinction between energy used to develop and maintain reproductive maturity, energy used to attract mates, energy used directly for reproduction, and energy used to care for the young. A more accurate measure of reproductive output might be the expected number of eggs, but the details of egg production from reproductive energy are an unnecessary complication. Since the number of eggs increases with the amount of reproductive energy, a strategy that yields an optimal amount of reproductive energy also yields the optimal number of eggs. Stated differently, our model does not determine the absolute fitness of a strategy, but it does serve to determine the relative fitness of a set of competing strategies.

In specific mathematical terms, the life history problems are formulated as follows:

Problem 1 (Net Assimilation). Given parameters b and ν, functions $f(t)$ and $\phi(x)$, and a set of possible life history functions Ω_κ, find $\kappa(x) \in \Omega_\kappa$ to maximize $F = R(\infty)$ as given by (10), with x given by (9) and p by (12).

Problem 2 (Net Production). Given parameters b and ν, functions $f(t)$ and $\phi(x)$, and a set of possible life history functions Ω_α, find $\alpha(x) \in \Omega_\alpha$ to maximize $F = R(\infty)$ as given by (10), with x given by (9) and p by (12).

Both problems, interpreted in their general sense, can be formulated as optimal control problems for the allocation functions.

Sufficient Conditions for Food Quality The model is not designed to deal with the problem of insufficient nutrition. It is therefore necessary to state some condition on the food quality function f to guarantee that assimilation always be sufficient to meet maintenance needs. For the case of the net assimilation model, the requirement is $\kappa(x(t))f(t) > x(t) \,\forall\, t \geq 0$. This is equivalent to the requirement $w(t) > 0$ $\forall\, t \geq 0$, where w is defined by

$$w(t) = e^t \kappa(x(t)) f(t) - e^t x(t).$$

By rearranging (8) as $[e^t x(t)]' = e^t \kappa(x(t)) f(t)$, we have

$$w'(t) = e^t [\kappa(x(t) f(t)]'.$$

Now suppose there is some time $T > 0$ such that $\kappa(x(t)) \equiv \kappa_\infty$ and $f(t) \equiv f_\infty$ for $t > T$. Then $w' = 0$ for $t > T$. We expect κ to be nonincreasing, indicating that an organism does not decrease its allocation to reproduction as it matures and reproduces, and we assume that the food quality is also nonincreasing, as this case is the one where the risk of insufficient nutrition is greatest. Under these assumptions, w is also nonincreasing; hence the minimum value of w occurs at time T

when the minimum value of food quality is reached. Thus, a sufficient condition for food quality is

$$\int_0^T \kappa(x(\tau)) \, e^{(T-\tau)} \, f(\tau) \, d\tau < \kappa_\infty f_\infty.$$

For the common case where κ is taken to be constant, the condition reduces to

$$\int_0^T e^{(T-\tau)} \, f(\tau) \, d\tau < f_\infty. \tag{14}$$

In both cases, the integral on the left is an increasing function of T, so the sufficiency condition can be thought of as a requirement that the food quality be constant beyond a sufficiently early time T. The similar sufficiency condition for food quality can be obtained for the net production model.

3. Analysis of the Net Assimilation Model

The general life history problem for the net assimilation model, as stated in Problem 1, is a difficult problem. As a first attempt to explore the effects of size-dependent predation on the solution of an optimal life history problem, we consider only the case in which the allocation parameter κ must be constant. Restricting κ to a constant simplifies the growth equation (8) to a point where it can be solved explicitly. We obtain the following problem.

Problem 3. Given parameters b and ν and functions $f(t)$ and $\phi(x)$, find $\kappa \in (0, 1)$ to maximize the fitness integral

$$F(\kappa) = 3(1 - \kappa) \int_0^\infty f(t) \, x^2(t) \, p(t) \, dt, \tag{15}$$

where

$$x(t) = \kappa e^{-t} \int_0^t e^\eta \, f(\eta) \, d\eta, \tag{16}$$

and p is given by (12).

Problem 3 can be solved numerically for any input data, given that the food quality condition (14) is met. For simplicity, we consider only the case where ϕ is given by (13), prey densities are small ($\nu + p \approx \nu$), and the environment is constant ($f = f_\infty \in (0, 1]$). The last of these assumptions reduces the length equation to the von Bertalanffy equation

$$x = f_\infty \kappa (1 - e^{-t}). \tag{17}$$

The survival probability can be found in terms of size from

$$\frac{dp}{dx} = -\left(b + \frac{\rho H}{H + x} \right) \frac{p}{f_\infty \kappa - x}, \quad p(0) = 1;$$

thus

$$p(x) = \left(1 - \frac{x}{f_\infty \kappa}\right)^{b + \frac{\rho H}{H + f_\infty \kappa}} \left(1 + \frac{x}{H}\right)^{\frac{-\rho H}{H + f_\infty \kappa}}. \tag{18}$$

The integrals for G and R are conveniently rewritten using the substitution $y = x(\eta)/f_\infty \kappa$:

$$G(t) = 3 f_\infty^3 \kappa^3 \int_0^{1 - e^{-t}} y^2 (1 - y)^{b + \frac{\rho}{1 + q\kappa}} (1 + q\kappa y)^{-\frac{\rho}{1 + q\kappa}} \, dy \tag{19}$$

and

$$R(t) = 3 f_\infty^3 \kappa^2 (1 - \kappa) \int_0^{1 - e^{-t}} y^2 (1 - y)^{b + \frac{\rho}{1 + q\kappa} - 1} (1 + q\kappa y)^{-\frac{\rho}{1 + q\kappa}} \, dy, \tag{20}$$

where we have introduced the symbol $q = f_\infty/H$ for convenience. The optimal value of κ is that which maximizes

$$F(\kappa) = 3 f_\infty^3 \kappa^2 (1 - \kappa) \int_0^1 y^2 (1 - y)^{b + \frac{\rho}{1 + q\kappa} - 1} (1 + q\kappa y)^{-\frac{\rho}{1 + q\kappa}} \, dy,$$

$$q = \frac{f_\infty}{H}. \tag{21}$$

For the special case in which the survival probability is taken to be exponential ($\rho = 0$), the problem reduces to a calculus problem, with the solution $\kappa = 2/3$. This result has been previously reported by Gurney and Nisbet [2]. Other cases must be solved numerically. Note first that F evaluates to 0 at the points $\kappa = 0$ and $\kappa = 1$ and is positive for $0 < \kappa < 1$; hence, there is a value $0 < \kappa < 1$ that maximizes F. Since the derivative of $F(\kappa)$ is complicated, it is most convenient to maximize F using a numerical line search method, such as the golden section search. Some care must be taken to evaluate the integral because of the singularity in the integrand at $y = 1$.

4. Analysis of the Net Production Model

In the net assimilation model, the allocation parameter κ can be taken as a constant for the entire life of an organism. The same can not be said of the allocation parameter α of the net production model [2]. Inherent in the net production model is the requirement that there be a maximum size X for which $\alpha = 0$. Thus, the simplest reasonable version of the net production model is that in which α is taken to be constant up to a size X and zero thereafter. In particular, we assume the well-known "bang-bang" strategy, in which the organism has a juvenile phase in which all net production is allocated to growth ($\alpha = 1$) followed by an adult phase in which all net production is allocated to reproduction.

Specifically, we assume that there is a fixed mature size $x = X$ at which the organism will make the transition from juvenile to adult. Then

$$\alpha(x) = \begin{cases} 1, & x < X \\ 0, & x \geq X \end{cases}.$$ (22)

The life history problem is now the problem of finding that value of X, given the other parameter values, that optimizes the fitness function.

Note that the bang-bang model is the simplest net production model, but could also be obtained by appropriate assumptions in the net assimilation case. One would assume that there is a juvenile stage in which $\kappa = 1$ followed by an adult stage in which κ is taken to be just enough to meet maintenance needs. The bang-bang assumption makes the model significantly more tractable by establishing a fixed size for adult organisms. In the analysis that follows, two new quantities play a particularly important part: $\tau(X)$, the time at which the transition from juvenile to adult is made, and $M(X)$, the probability of survival to the transition point.

The juvenile stage is marked by growth with no reproduction. The absence of reproduction means that nothing in the juvenile stage is relevant to the life history problem except the quantities $\tau(X)$ and $M(X)$. With α constant, the growth equation is linear and can therefore be solved, yielding the solution

$$x = e^{-t} \int_0^t e^\eta f(\eta)\, d\eta;$$ (23)

thus, the transition time τ is given implicitly as a function of X by

$$X = e^{-\tau} \int_0^\tau e^\eta f(\eta)\, d\eta.$$ (24)

In general, the survival equation (12) is nonlinear and must be solved numerically to determine $M(X)$.

For the special case of a bang-bang life history, the fitness function is given by

$$F(X) = 3 \int_{\tau(X)}^\infty [f(t)X^2 - X^3] p(t)\, dt.$$

The problem is simplified somewhat by a change of variables. Let $u = t - \tau$ be the time following the transition and let $s(u) = p(\tau + u)$ be the probability of survival for time u after transition. This yields the bang-bang version of Problem 2:

Problem 4. Given parameters b and ν and functions $f(t)$ and $\phi(x)$, find the optimal size $X^\star \in (0, 1)$ that maximizes the fitness integral

$$F(X) = 3 \int_0^\infty [f(\tau + u)X^2 - X^3]\, s(u)\, du,$$ (25)

where τ is given by (24) and s by

$$\frac{1}{s}\frac{ds}{du} = -b - \frac{\nu\phi(X)}{\nu + s}, \quad s(0) = M(X),$$ (26)

where $M(X) = p(\tau(X))$ is determined by (12).

Observe that s depends implicitly on X, but we do not represent this in our notation.

We concentrate in the sequel on a special case of Problem 4, characterized by three additional assumptions: (a) the function $\phi(x)$ is given by (13), (b) the population of adults is small, and thus $\nu + M \approx \nu$, and (c) full-grown individuals live in a constant environment, and thus $f(t) = f_\infty$ for $t > \tau$. The last two assumptions are less restrictive than the corresponding assumptions in Problem 3 for the net assimilation model because they are applied only after growth is complete.

Under these assumptions, the survival equation is easily integrated, with the result

$$s(u) = M(X)e^{-\lambda(X)u}, \quad \text{where} \quad \lambda(X) = b + \frac{\rho H}{H + X}. \qquad (27)$$

The fitness integral can also be computed explicitly, resulting in the following problem:

Problem 5. Given $\rho, b, H, \nu, f_\infty$, find the optimal size $X^\star \in (0, 1)$ that maximizes the fitness function

$$F(X) = 3(f_\infty X^2 - X^3)\lambda^{-1}(X)\, M(X), \qquad (28)$$

where

$$\lambda^{-1}(X) = \frac{H + X}{(\rho + b)H + bX}, \quad M(X) = p(\tau(X)).$$

Application of elementary calculus techniques to Problem 5 reduces the determination of the optimal size $X^\star$ to an algebra problem. (See the Appendix for details.) We have the following result.

Proposition 1. *Problem 5 has a unique solution $X^\star$ in the interval $(0, f_\infty)$; the solution is the root of the polynomial*

$$Q(X) = b(b + 3)X^3 + (2b\sigma + 4\sigma + 2bH - 2f_\infty b)X^2$$
$$+ (\sigma^2 + 3H\sigma - 3f_\infty\sigma - f_\infty bH)X - 2f_\infty H\sigma, \qquad (29)$$

where $\sigma = (\rho + b)H$.

At this point, we consider the special case in which the food availability is constant and the hazard rate is size-independent ($\rho = 0$). In this case, the growth curve (23) simplifies to

$$x = f(1 - e^{-t})$$

and the survival probability is

$$M = (1 - X/f)^b.$$

The optimum value of X is determined directly from

$$F(X) = \frac{3}{bf^b}X^2(f - X)^{1+b}$$

to be

$$X = \frac{2f}{3+b};$$

thus, the probability of reaching mature size is

$$M = \left(\frac{1+b}{3+b}\right)^b.$$

Application of L'Hôpital's Rule yields the following result.

Proposition 2. *If food availability is constant and the hazard rate is size-independent, then the probability of survival to the end of the juvenile stage is in the interval $e^{-2} < M \leq 1$. In particular, increasing the hazard rate can only reduce the survival probability to e^{-2}.*

Proposition 2 poses an interesting question, that of whether the more general model of Problem 5 always places a positive lower bound on the probability of survival to full growth. Since an arbitrarily small survivorship probability does not appear to occur when the optimal size is arbitrarily small, we focus our attention on trying to find the possibility of an arbitrarily small survivorship probability with an optimal size that is not arbitrarily small.

The relationship between the survival probability and mature size for Problem 5 is given in the following proposition, which is proved in the Appendix. The key result is that the survival probability for the general case must be of the same order of magnitude as the survival probability for the case $b = 0$, $\nu + p \approx \nu$.

Proposition 3. *Let M_0 be defined by*

$$M_0(X) = \exp\left(-\int_0^{\tau(X)} \frac{\rho H \, dt}{H + x(t)}\right). \tag{30}$$

Then

$$e^{-b\tau(X)} M_0(X) < M(X) < e^{1/\nu} M_0(X).$$

We now attempt to find conditions under which $M_0 \to 0$ without $X \to 0$. We have M_0 arbitrarily small in the limit $\rho \to \infty$. However, in this limit (29) becomes

$$Q(X) \sim b(b+3)X^3 + (2b+4)\rho H X^2 + \rho^2 H^2 X - 2f_\infty \rho H^2;$$

thus, $X \sim 2f_\infty/\rho$ as $\rho \to \infty$, with all other parameters fixed. Instead suppose ρH is fixed as $\rho \to \infty$. This corresponds to the case where the density of predators is large only for small prey.

The following result is proved in the Appendix.

Proposition 4. *Suppose $\rho H < 3f_\infty$ is fixed. Then the optimal mature size $X^\star$ of Problem 5 is bounded away from zero as $\rho \to \infty$, while the probability $M(X^\star)$ of an individual reaching maturity is not.*

5. Results and Discussion

In the single-stage net assimilation model, the optimal value for the allocation parameter κ is generally in the range $0.66 < \kappa < 0.8$, with little sensitivity to most of the parameters in the model. Thus, the model predicts that a little over two thirds of the organism's energy output goes to growth, regardless of variations in physiological parameters and environmental conditions. Figure 1 shows the expected growth and reproduction energy history for physiologically similar organisms adapted to two different environments. Each environment features adequate high-quality food ($f = 1$) and no high-density saturation ($v + p \approx v$). The plot on the left is for an organism that has adapted to an environment in which hazard rates are independent of size, with $\rho = 4$. The plot on the right is for an organism that has adapted to an environment in which hazard rates are highly dependent on size, with $\rho = 20$ and $H = 0.05$. This means that very small individuals in the size-dependent environment are five times as vulnerable to predation as individuals in the size-independent environment, but large individuals are approximately one quarter as vulnerable. The values of ρ were chosen so that the total expected energy output of an individual is about the same for both cases (0.016).

The organism that has adapted to the size-dependent environment has an allocation parameter of $\kappa = 0.83$, as compared to the value of 2/3 for the size-independent environment. Averaged over an expected lifespan, individuals in the size-dependent environment are able to allocate about 36% of their energy to reproduction, while those in the size-independent environment are able to allocate about 47% of their energy to reproduction. These results are in qualitative agreement with the expectations of intuition. Suppose a species adapted to a size-independent environment is established in a size-dependent environment. Natural selection will begin to act to favor individuals that allocate a larger share of energy to growth, because these individuals spend less of their lives in the stage where they are the most vulnerable. The cost of this change is that more of an organism's lifetime energy accumulation must be spent on growth, with the fraction spent on reproduction correspondingly less. The two environments of Figure 1 are equally hospitable in the sense that the
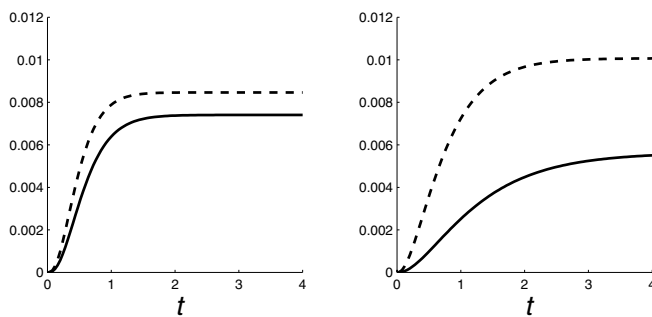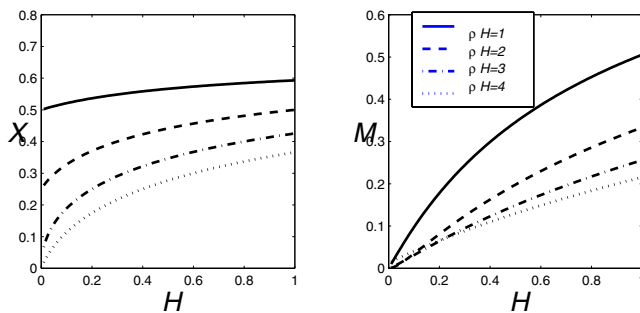

Fig. 1. Expected growth (dashed) and reproduction (solid) energy for the net assimilation model, with $f = 1$, $v + p \approx v$. The plot on the left has $b = 4$ and $\rho = 0$, while the plot on the right has $b = 0$, $\rho = 20$, and $H = 0.05$.

expected lifetime energy use is the same for individuals adapted to each environment. However, the size-dependent environment is more hostile in the sense that the organisms adapted to it must spend a larger fraction of their energy accumulation on uses not directly related to reproduction.

In the two-stage net production model, the optimal mature size depends significantly on environmental factors such as food availability and predator density. Note that this does not necessarily imply that organisms are capable of adjusting their mature length to current environmental conditions. The model indicates only the parameter values an organism will have if natural selection acts to tune the organism to some typical or average environment. The organisms may perform in a way that is considerably suboptimal when the environment differs significantly from that to which the organism is tuned. If the new environmental conditions are maintained for sufficiently many generations, we should expect natural selection to retune the organism to the new environment.

Of particular interest is the sensitivity of the optimal mature length and probability of reaching maturity to size-dependence in hazard rates, as described in Proposition 4. The results are illustrated in Figure 2. The curves illustrate the effect of predator bias toward smaller prey, given constant values of ρH. The parameter ρH is approximately a measure of the density of predators capable of preying on larger individuals. This correspondence depends mathematically on the approximation $H + X \approx X$, so it becomes more accurate when the predator bias is high. The reason for keeping ρH rather than ρ constant in these plots is to demonstrate the possibility of vanishingly-small survival probability coupled with modest mature size, a combination that is typical in wild populations. Note that when the level of predator activity is sufficiently low ($\rho H = 1$), the effect of predator bias toward smaller prey on the mature size of the prey is minimal, but the effect on the probability of survival to maturity is substantial. When the level of predator activity is above the threshold $\rho H = 3$, the optimal size decreases toward zero with increasing predator bias, and the probability of reaching maturity also decreases, although not as rapidly as when the predator level is below the threshold.

Fig. 2. Optimal mature length X and probability M of reaching optimal size for the net production model, with $f_\infty = 1$, $b = 0$, and $\nu + p \approx \nu$
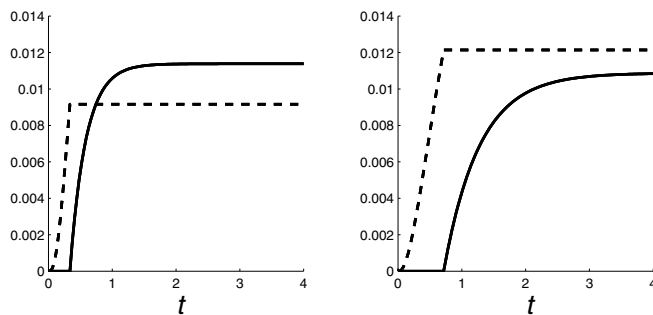
Fig. 3. Expected growth (dashed) and reproduction (solid) energy for the net production model, with $f = 1$, $\nu + p \approx \nu$. The plot on the left has $b = 4$ and $\rho = 0$, while the plot on the right has $b = 0$, $\rho = 20$, and $H = 0.05$.

The expected growth and reproduction curves for the net production model, using the same two environments as in Figure 1, appears in Figure 3. As in the 1-stage net assimilation case, the 2-stage net production model indicates significant differences in the organisms' response to environmental conditions. Compared to the environment with size-independent predation, the environment with size-dependent predation leads to a longer growth period, a larger mature size, and a smaller overall allocation of energy to reproduction. The trade-offs are the same as in the net assimilation model. Given a predator size bias, it makes sense to change from growth to reproduction at a later time, giving up a small amount of reproduction in the short term in exchange for the promise of a longer reproductive life for those individuals that do reach maturity.

6. Conclusion

The standard assumption of a size-independent hazard rate leads in the case of a 2-stage bang-bang allocation strategy to the result that the probability of reaching maturity is greater than 13%, a value that is far too high for most ectotherms in wild populations. One might expect that raising the death rate uniformly for individuals of all sizes would lead to both a lower mature size and a lower probability of survival to maturity, but this is not the case; the model predicts instead that the response to a higher death rate is limited to lower mature size. The organisms die quickly in the more dangerous environment, but they achieve full growth even more quickly because they grow very little before devoting themselves to reproduction. For many investigations using dynamic energy budget models, this error is likely to be unimportant. For those investigations in which information about the size distribution of the population is important, a size-dependent hazard rate provides one mechanism for obtaining the more realistic outcome of low probability of survival to maturity. The model must include the assumption that the hazard rate is a strongly decreasing function of size, corresponding to an environment in which the primary cause of mortality is predation and in which the danger from predators decreases as an organism becomes more capable of defending itself.

The effect of predator bias toward small prey depends considerably on the overall level ρ of predator activity, as illustrated for a specific case in Figure 2 and demonstrated in the general case by Proposition 3. At lower levels of predator activity, the optimal mature length is not very sensitive to H. The sensitivity of X to H increases as the approximate predator activity level on adults (ρH) increases, with the optimal length vanishing as $H \to 0$ if $\rho H \geq 3 f_\infty$.

7. Appendix

Proposition 1

Note that $F(X) = 0$ for both $X = 0$ and $X = f_\infty$, while $F > 0$ for $0 < X < f_\infty$ and $F < 0$ for $X > f_\infty$; hence, the global maximizer of $F(X)$ must be a critical point in the interval $0 < X < f_\infty$. The differential equation for p can be written in terms of x as

$$\frac{1}{p}\frac{dp}{dx} = -\frac{1}{f_\infty - X}\left[b + \frac{\nu\phi(X)}{\nu + p}\right], \quad p(0) = 1, \quad p(X) = M.$$

Thus, $dM/dX = dp/dx(X)$. With $\nu + M \approx \nu$, we obtain

$$\frac{1}{M}\frac{dM}{dX} = -\frac{b + \phi(X)}{f_\infty - X} = -\frac{\lambda}{f_\infty - X}.$$

By logarithmic differentiation of (27), we obtain the result

$$\frac{\partial F}{\partial X} = \frac{-Q(X)F(X)}{X(f_\infty - X)(H + X)(\sigma + bX)},$$

where Q is given by (28). Thus, the global maximizer of F must be a root of Q in the interval $(0, f_\infty)$.

Now suppose Q has more than one root in $(0, f_\infty)$. Then there must be two points in the interval at which $Q' = 0$ and one point at which $Q'' = 0$. Now $Q'(f_\infty) > 0$ and $Q''(f_\infty) > 0$, so it must be that $Q''(0) < 0$ and $Q'(0) > 0$. However, $Q''(0) < 0$ forces $\sigma + H < f_\infty$; whence $Q'(0) < 0$. This proves Proposition 1.

Proposition 3

We define three problems related to the problem of finding M:

$$\frac{dp_0}{dt} = -\frac{\rho H p_0}{H + x(t)}, \quad p_0(0) = 1, \quad M_0 = p_0(\tau).$$

$$\frac{dp_L}{dt} = -b p_L - \frac{\rho H p_L}{H + x(t)}, \quad p_L(0) = 1, \quad M_L = p_L(\tau).$$

$$\frac{dp_U}{dt} = -\frac{\rho H p_U}{H + x(t)}\frac{\nu}{\nu + p_U}, \quad p_U(0) = 1, \quad M_U = p_U(\tau).$$

Note that the latter two problems are related to the actual problem by $p_L < p < p_U$.

The three comparison problems can all be solved to yield either explicit or implicit results for the corresponding values of M.

$$M_0(X) = \exp\left(-\int_0^{\tau(X)} \frac{\rho H \, dt}{H + x(t)}\right),$$

$$M_L(X) = e^{-b\tau(X)} M_0(X),$$

and

$$M_U(X) = e^{-M_U/\nu} e^{1/\nu} M_0(X) < e^{1/\nu} M_0(X).$$

Hence,

$$e^{-b\tau(X)} M_0(X) \leq M(X) < e^{1/\nu} M_0(X).$$

Proposition 4

Suppose $\rho H = \mu < 3f_\infty$. Then $\sigma \to \mu$ and $H \to 0$ as $\rho \to \infty$. In this limit, the equation for X reduces to

$$X Q_0(X) = 0, \quad \text{where}$$
$$Q_0(X) = b(b+3)X^2 + (4\mu + 2b\mu - 2f_\infty b)X + \mu(\mu - 3f_\infty).$$

Now $Q_0(f_\infty) > 0$ and $Q_0(0) < 0$. Thus, Q_0 must have a root $X^\star$ such that $0 < X^\star < f_\infty$. This root is also a root of Q as $\rho \to \infty$, so it must be the unique solution for the optimal size. Hence, the hypotheses are sufficient to guarantee that $X^\star$ does not vanish as $\rho \to \infty$.

Now we consider M_0 as defined in Proposition 3. Using $dx = (f - x)\, dt$ and $\mu = \rho H$, M_0 is given by

$$\begin{aligned} \ln M_0 &= -\int_0^X \frac{\rho\mu \, dx}{[f(t(x)) - x](\mu + \rho x)} \\ &< -\int_0^X \frac{\rho\mu \, dx}{(1 - x)(\mu + \rho x)} = -\frac{\rho\mu}{\rho + \mu} \ln \frac{\mu + \rho X}{\mu(1 - X)}. \end{aligned}$$

Thus, $\ln M_0$ is unbounded below as $\rho \to \infty$, provided X is bounded away from 0. The result follows immediately.

References

1. Cohen, D.: Maximizing final yield when growth is limited by time or by limiting resources. J. Theor. Biol. **33**, 299–307 (1971)
2. Gurney, W.S.C., Nisbet, R.M.: Ecological Dynamics. Oxford University Press, 1998
3. King, D., Roughgarden, J.: Graded allocation of energy to growth and reproduction. Theor. Pop. Biol. **22**, 1–16 (1982)
4. Kooijman, S.A.L.M.: Dynamic Energy Mass Budgets in Biological Systems. Cambridge University Press, 2000

5. Kozlowski, J., Wiegert, R.J.: Optimal allocation of energy to growth and reproduction. Theor. Pop. Biol. **29**, 16–37 (1986)

6. Leon, J.A.: Life histories as adaptive strategies. J. Theor. Biol. **60**, 301–335 (1976)

7. Lika, K., Nisbet, R.M.: A dynamic energy budget model based on partitioning of net production. J. Math. Biol. **41**, 361–386 (2000)

8. Mirmirani, M., Oster, G.: Competition, kin selection, and evolutionary stable strategies. Theor. Pop. Biol. **13**, 304–339 (1987)

9. Nisbet, R.M., Muller, E.B., Lika, K., Kooijman, S.A.L.M.: From molecules to ecosystems through dynamic energy budget models. J. Animal Ecology **69**, 913–926 (2000)

10. Noonburg, E.G., Nisbet, R.M., McCauley, E., Gurney, W.S.C., Murdoch, W.W., de Roos, W.W.: Experimental testing of dynamic energy budget models. Funct. Ecol. **12**, 211–222 (1998)

11. Pearl, R., Miner, J.: Experimental studies on the duration of life. Q. Rev. Biol. **10**, 60–79 (1935)

12. Perrin, N.: Optimal resource allocation and the marginal value of organs. Am. Nat. **139**(6), 1344–1369 (1992)

13. Roff, D.A.: The Evolution of Life Histories: Theory and Analysis. Chapman & Hall, 1992

14. Ross, A.H., Nisbet, R.M.: Dynamic models of growth and reproduction of the mussel *Mytilus edulis* l. Funct. Ecol. **4**, 777–787 (1990)

15. Sibly, R.M., Calow, P.: Growth and resource allocation. In: Evolutionary Physiological Ecology, P. Calow, (ed.), Cambridge: Cambridge Unversity Press, 1986

16. Stearns, S.C.: The Evolution of Life Histories. Oxford University Press, 1992

17. Vincent, T.L., Pulliam, H.R.: Evolution of life histories for an asexual annual plant model. Theor. Pop. Biol. **17**, 215–231 (1980)

18. Ziolko, M., Kozlowski, J.: Evolution of body size: an optimization model. Math. Biosci. **64**, 27–143 (1983)