

Appendix B from S. R. Hall et al., “Resource Ecology of Virulence in a Planktonic Host-Parasite System: An Explanation Using Dynamic Energy Budgets”

(Am. Nat., vol. 174, no. 2, p. 149)

Step-by-Step Development and Examination of the Dynamic Energy Budget–Parasite Model

Here we provide a step-by-step development of the Kooijman (1993) dynamic energy budget (DEB) model incorporating within-host parasitism. Its development largely follows previous expositions (Kooijman 1993; Nisbet et al. 1996, 2000), complete with description of energetic stress (following Muller and Nisbet 2000; Fujiwara et al. 2004; readers should note that other representations of energetic stress might also be derived). However, we have simplified the typical presentation here (i.e., no compound parameters as in Kooijman 1993).

The Kooijman DEB Model

In this model, the rate at which energy is utilized (catabolized, C) by the host for growth, reproduction, and maintenance equals the difference between assimilation rate of energy from food (A) and the rate of change in energy reserves (dE/dt). Assimilation rate A depends on a proportionality constant a , surface area of the host L^2 (where L is length of the host as determined by a weight-length regression, $W = \alpha L^3$, which assumes that structural mass and structural volume are proportional), and the classic Type II functional response:

$$A = aL^2 \left(\frac{F/c}{h + F/c} \right), \quad (\text{B1})$$

where F is the mass of food, c is the volume of experimental container (yielding food density, F/c), and h is the half-saturation constant. Reserve energy (E), in turn, is the product of energy density (e) and structural mass (W ; i.e., $E = eW$), and it represents a storage pool of energy that is in pseudoequilibrium with energy circulating in hemolymph (blood). The rate of change of these energy reserves,

$$\frac{dE}{dt} = \frac{d(eW)}{dt} = W \frac{de}{dt} + e \frac{dW}{dt}, \quad (\text{B2})$$

involves two components: animals store more reserves by storing more reserves per unit of structural mass (involving the de/dt term) and/or by growing more structure (involving the dW/dt term). Following Kooijman (1993), we assume homeostasis of reserves; specifically, the animal regulates the reserve density at a level related to its feeding rate. With further assumptions detailed by Kooijman (1993), reserve density dynamics follow the differential equation

$$\frac{de}{dt} = \frac{aL^2}{W} \left(\frac{F/c}{h + F/c} - \frac{e}{e_M} \right), \quad (\text{B3})$$

where e_M is the maximum density of energy and animals use energy density according to first-order kinetics. If we now combine equations (B1)–(B3), utilization rate (C) becomes

$$C = A - \frac{dE}{dt} = e \left(\frac{aL^2}{e_M} - \frac{dW}{dt} \right) = E \left(\frac{aW^{2/3}}{e_M W} - \frac{dW}{W dt} \right). \quad (\text{B4})$$

When food is relatively abundant, the host allocates these “utilized” internal energy reserves toward growth versus reproduction/maturity, following the kappa (κ) rule (fig. 2). The animal allocates a fixed proportion (κ) of utilized energy to growth, and the remaining proportion ($1 - \kappa$) is allocated to development and maturation (if body size is less than structural mass at adulthood, $W < W_p$) or reproduction (if $W \geq W_p$). The κ rule, then, assumes a trade-off between growth and reproduction. Stated more formally, the host devotes utilized energy to growth and maintenance at rate

$$\kappa C = g \left(\frac{dW}{dt} \right) + mW, \quad (\text{B5})$$

where the first term on the right-hand side denotes growth of structural mass (dW/dt) and the associated cost of growing (g) and the second term represents costs to maintain current mass (at rate m). Equations (B4) and (B5) both contain the dW/dt term, so they can both be used to yield an equation for growth rate

$$\frac{dW}{dt} = W \left[\frac{\kappa a L^2 E / (e_M W) - mW}{\kappa E + gW} \right]. \quad (\text{B6})$$

Notice how this growth equation depends indirectly on food supply (F) through reserve energy E stored in the animal.

Remaining reserves are utilized for development, reproduction, and associated costs. Rate of reproduction (dR/dt) then follows

$$\frac{dR}{dt} = \left(\frac{q}{E_0} \right) \left[(1 - \kappa)C - \frac{1 - \kappa}{\kappa} mW_p \right], \quad (\text{B7})$$

where q is the cost of converting the energy reserve of the mother into the energy reserve of the offspring ($0 < q < 1$), E_0 is the energy required to produce an offspring, and $1 - \kappa$ denotes the fractional allocation of utilized energy C to development and reproduction. This equation for reproduction also includes a second term (in brackets) for “maturity maintenance” (see Kooijman 1993 for development and justification of this physiological cost). If the animal is a juvenile ($W < W_p$), it allocates energy for development at a rate equivalent to the entire term in brackets, after W_p is replaced with W . Given these assumptions, the DEB model for the growing and reproducing/developing host consists of equations (B3), (B6), and (B7).

Energetic Stress and Food Dynamics in the Kooijman Model

Before introducing parasites into this model, we must first consider the energy dynamics of starving hosts, because we assume that parasites somehow kill hosts by draining energy reserves to very low levels. We recognize that *Daphnia* individuals do not shrink in length when starved. When reserve energy becomes sufficiently low (because of low external supply of food or internal consumption by parasites) that the default allocation to growth plus maintenance (eq. [B5]) is insufficient to meet maintenance costs, we assume that the host stops growing (i.e., when $dW/dt = 0$). This no-growth point occurs when (from eq. [B6])

$$\frac{aL^2}{e_M W} E = \frac{mW}{\kappa}. \quad (\text{B8})$$

This transition to a state of moderate energetic stress (fig. 2B) arises when the rate of use of energy reserves (right-hand side) equals the rate of maintenance of existing body mass (left-hand side). Under moderate energetic

stress, the host animal still follows normal dynamics of energy-reserve homeostasis (eq. [B3]) and, as always, it must pay maintenance costs for current mass, mW , and maturity, $m(1 - \kappa) \min(W, W_p)/\kappa$. Thus, in addition to zero structural growth, a different and diminished reproductive rate (dR/dt) emerges for moderately starved animals:

$$\frac{dR}{dt} = \left(\frac{q}{E_0}\right) \left[C - mW - m \left(\frac{1 - \kappa}{\kappa} \right) W_p \right]. \quad (\text{B9})$$

Here, utilization rate C still follows that presented above (eq. [B4]), recognizing now that the structural mass of the animal does not increase ($dW/dt = 0$).

The energetic situation can worsen yet for the host. If maintenance requirements are not met by the default utilization rate, that is, $C < mW + (1 - \kappa) \min(W_p, W)/\kappa$, then allocation shifts yet again. In this “severe” state of energetic stress (fig. 2C), the animal’s utilization of energy C is set to exactly cover maintenance costs, and the animal does not reproduce (i.e., $dR/dt = 0$). Reserve dynamics (dE/dt) become

$$\frac{dE}{dt} = aL^2 \left(\frac{F/c}{h + F/c} \right) - \left[mW + m \frac{1 - \kappa}{\kappa} \min(W_p, W) \right], \quad (\text{B10})$$

which equals the assimilated energy (first term, right-hand side) minus combined maintenance costs (second term, right-hand side). Death occurs when the reserve energy is depleted ($E = 0$).

After specifying these starvation scenarios, we now turn to food dynamics. Typically, the host-grazer depletes some amount of food each day (assuming no production of that food), but in experiments food was replenished to initial conditions (F_0) daily. Therefore, between replenishment intervals (T), food density declines at rate

$$\frac{dF}{dt} = - \frac{aL^2}{\varepsilon} \frac{F/c}{h + F/c}, \quad (\text{B11})$$

where ε is the maximum conversion efficiency of the host.

Adding the Parasite and Two Key Thresholds

We assume that this parasite N feeds on energy reserves of its host, E , according to its own saturating (Type II) functional response. Thus, reserve dynamics change (from eq. [B2]) to

$$\frac{dE}{dt} = W \frac{de}{dt} + e \frac{dW}{dt} - \frac{a_N}{\varepsilon_N} \left(\frac{E}{h_N + E} \right) N, \quad (\text{B12})$$

where consumption by parasites (last term) is governed by a half-saturation constant (h_N), the maximal assimilation rate (a_N), and the conversion efficiency (ε_N) of the parasite. This parasite then grows according to a classic equation for a resource consumer (Grover 1997):

$$\frac{dN}{dt} = a_N \left(\frac{E}{h_N + E} \right) N - m_N N, \quad (\text{B13})$$

where m_N lumps various loss rates (e.g., maintenance, death) of the parasite. Use of such a simple equation greatly simplifies the dynamics of the parasite for this preliminary version of the model. In the future, a more realistic model could include a DEB for the parasite but, perhaps more importantly, a separation of fungal dynamics into budding yeast cells (which consume energy, pay maintenance costs, die, etc.) and production of spores (which likely do not consume energy or pay maintenance costs themselves). While potentially important, such details seem to be beyond the scope of this first attempt at a DEB-parasite model.

Additional Results

By varying conditions of the host for infection and parasite parameters, we gleaned additional insights into resource ecology of virulence that parallels the results presented in the text. Hosts that contain more energy reserve (e_0) on infection or become infected at larger initial size (L_0) die more quickly (fig. B1); hosts that are initially more energy rich (reserves) or take in more food resources per unit time (larger) fuel faster growth of the parasite. However, hosts with higher e_0 and L_0 values produce more offspring, die at larger sizes, and produce more parasites when they die (fig. B1). Thus, energy-rich or large hosts provide better “habitats” for obligately killing parasites. Additionally, infection decreases relative fecundity (infected/uninfected reproduction rate) of hosts differentially. Larger hosts experience less of a reduction in fecundity than do uninfected hosts (fig. B2). Furthermore, more efficient parasites, that is, those with higher assimilation rates (a_N), lower half-saturation constants (h_N), and lower loss rates (m_N), tend to elicit similar qualitative effects in their hosts. These efficient parasites tend to kill more quickly, reduce fecundity more strongly, and kill smaller hosts that yield fewer parasites (fig. B3). Conversely, less-efficient parasites (low a_N , high h_N and m_N) let hosts become larger and therefore acquire more resources per unit time; this effect, in turn, ultimately produces more parasites. However, parasites with different resource kinetics (a_N , h_N) than the example considered in the text can have quite different effects on host survivorship. For instance, in the example considered (lower a_N but also lower h_N in fig. B4a; generally, lower h_N in fig. B4b), hosts in more resource-rich environments died less quickly than did those in poor environments. Yet hosts eating more resources still qualitatively produced more parasites from larger, more fecund hosts upon death. These results suggest that parasites could have differing effects on host survivorship along gradients of resources supplied to hosts as a result of variation in resource kinetics among parasite genotypes/species; yet the resource-parasite production signal observed in the *Daphnia* example that we have documented here (fig. 1) should be robust to these considerations.

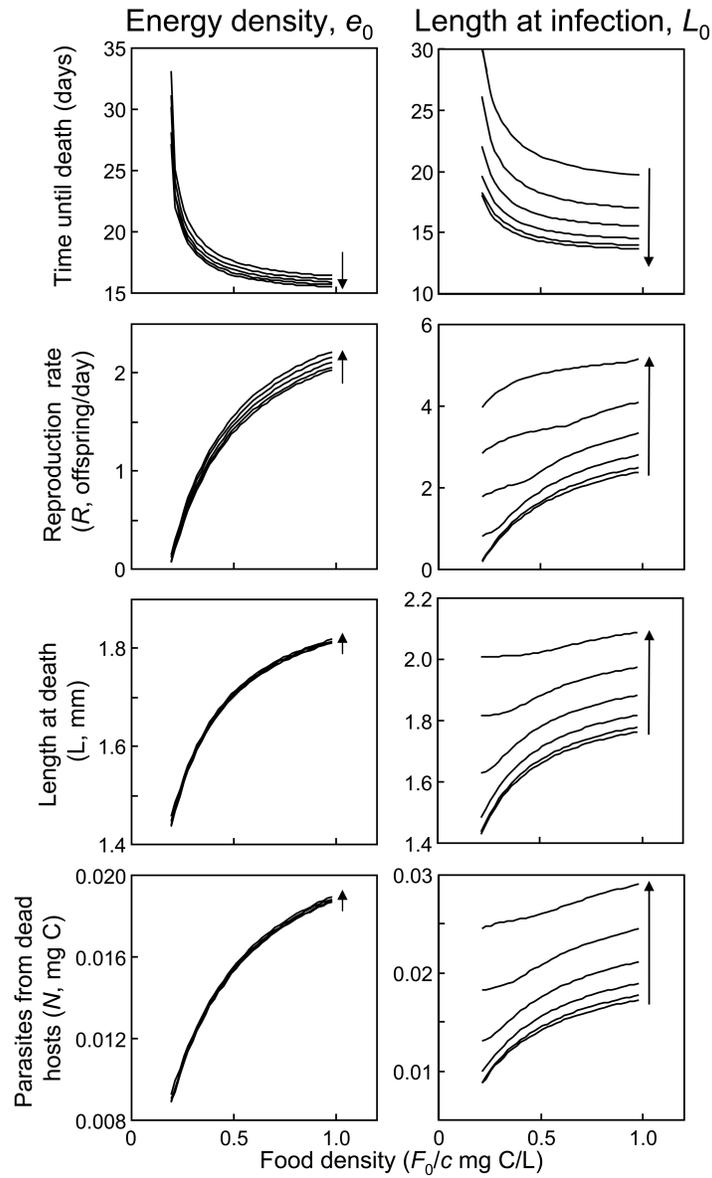


Figure B1: Variation in starting conditions of the host's initial energy density, e_0 (0.1, 0.3, 0.5, 0.7, 0.9), and length at infection, L_0 (1.0, 1.2, 1.4, 1.6, 1.8, 2.0 mm), influences key responses of hosts to infection along a gradient of resource supply (F_0/c). Arrows point in the direction of lower to higher starting conditions. Initial parasite density (N_0) is 0.002 mg C; all other parameters follow those listed in table 1.

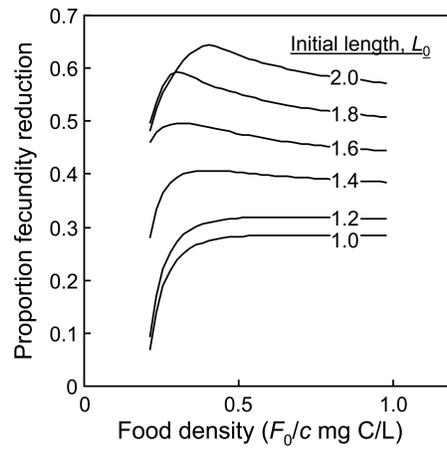


Figure B2: Initial size at infection (L_0 ; mm) influences the ratio of the fecundity of infected hosts (average number of offspring produced until time of death) to that of uninfected individuals (comparable average number of offspring but through 40 days) along a gradient of resource supply (F_0/c). Initial parasite mass (N_0) is 0.002 mg C; initial size (L_0) is 1.4 mm; energy density (e_0) is 0.9; all other parameters follow those listed in table 1.

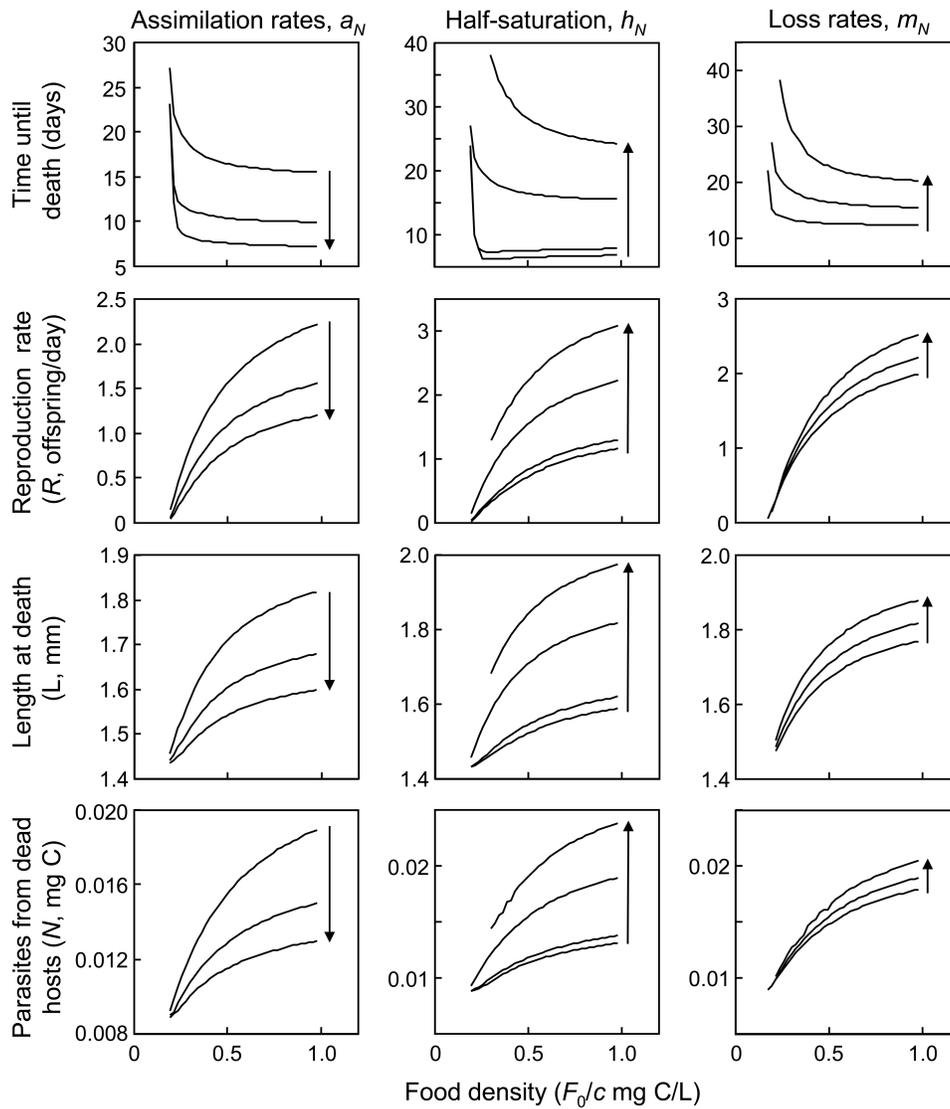


Figure B3: Variation in three key parasite parameters—assimilation rate ($a_N = 0.2, 0.4, 0.56, \text{ or } 0.72 \text{ day}^{-1}$), half-saturation constant ($h_N = 0.0005, 0.001, 0.005, \text{ or } 0.01 \text{ mg C}$), and loss rate ($m_N = 0.04, 0.08, \text{ or } 0.12 \text{ day}^{-1}$)—and response of infected hosts along gradients of resource supply (F_0/c). Arrows point in the direction of lower to higher values of these parameters. Initial parasite density (N_0) is 0.002 mg C ; initial size (L_0) is 1.4 mm ; energy density (e_0) is 0.9 ; all other parameters follow those listed in table 1.

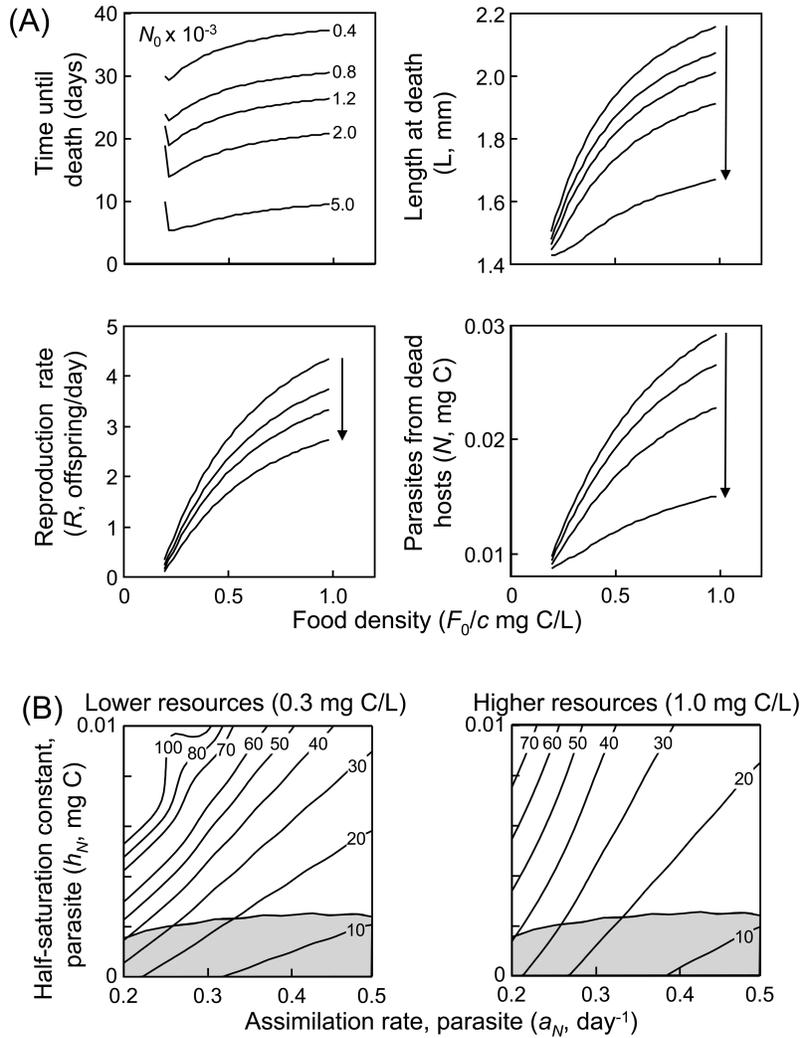


Figure B4: A, Host infected with a parasite having different resource uptake kinetics (lower assimilation rate, a_N : 0.24 day^{-1} ; lower half-saturation constant, h_N : 0.0005 mg C) exhibits markedly different survivorship than the case presented in the text (figs. 3, 4). More specifically, hosts die less quickly, not more quickly, when feeding in resource-rich environments. Contours correspond to different initial parasite loads (N_0 , mg C). Initial size: 1.4 mm; initial energy density (e_0): 0.9; all other parameters follow those listed in table 1. Arrows point from lower to higher parasite levels (N_0). B, Hosts are predicted to die more quickly at higher (1.0 mg L^{-1}) than at lower (0.3 mg L^{-1} ; *white*) resources; conversely, hosts enjoying more food die more slowly than those eating less (*gray*). Contours correspond to days until death. Initial size: 1.4 mm; initial energy density (e_0): 0.9; initial parasite mass (N_0): 0.002 mg C ; all other parameters follow those listed table 1.