

## A BIOMASS FLOW APPROACH TO POPULATION MODELS AND FOOD WEBS

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**ABSTRACT.** The dominant differential equation paradigm for modeling the population dynamics of species interacting in the framework of a food web retains at its core the basic prey-predator and competition models formulated by Alfred J. Lotka (1880–1945) and Vito Volterra (1860–1940) nearly nine decades ago. This paradigm lacks a trophic-level-independent formulation of population growth leading to ambiguities in how to treat populations that are simultaneously both prey and predator. Also, this paradigm does not fundamentally include inertial (i.e., change resisting) processes needed to account for the response of populations to fluctuating resource environments. Here I present an approach that corrects both these deficits and provides a unified framework for accounting for biomass transformation in food webs that include both live and dead components of all species in the system. This biomass transformation formulation (BTW) allows for a unified treatment of webs that include consumers of both live and dead material—both carnivores and carcassivores, herbivores and detritivores—and incorporates scavengers, parasites, and other neglected food web consumption categories in a coherent manner. I trace how BTW is an outgrowth of the metaphysiological growth modeling paradigm and I provide a general compact formulation of BTW in terms of a three-variable differential equation formulation for each species in the food web: viz., live biomass, dead biomass, and a food-intake-related measure called deficit-stress. I then illustrate the application of this new paradigm to provide insights into two-species competition in variable environments and discuss application of BTW to food webs that incorporate parasites and pathogens.

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**1. A very brief history.** Population ecology is first and foremost about how populations change over time and distribute themselves over the landscape, and then about how they interact with other species over space and time. Since the growth of organisms depends on the rates at which they consume resources—whether live or dead organisms, nutrients, photons or energy laden inorganic molecules—consumption processes are at the core of modeling population biomass dynamics.

Consumer–resource interactions come in many guises, each with its own historical modeling or quantitative narrative. Dominant narratives originating almost a century ago include Lotka-Volterra prey-predators systems and their elaborations (May [1973], Murdoch et al. [2003], Turchin [2003]) and Thompson-Nicholson-Bailey host-parasite models (Hassell [1978], Murdoch et al. [2003]). Simple plant-herbivore models have, to a large extent, inherited the Lotka-Volterra mantle, though more complex models that divide plants into various component parts, such as stems, leaves, shoots, flowers, etc., fall *inter alia* under the more complex discretized von Foester partial differential equation models (Gutierrez [1996]). Technically microparasites (viruses, bacteria, and protists) are also consumers of hosts, where the hosts themselves vary in size from bacteria to redwoods and whales. Their dynamics, however, have been modeled primarily from an epidemiological point of view going back to the SIR approach pioneered by Kermack and McKendrick in the 1920s (Anderson and May [1989], Hethcote [2000]). Over time, however, the temporal dynamic models of single populations became more elaborate with the approach of Leslie in structuring populations into age classes using an iterated matrix equation (Leslie [1945]) and of von Foerster in using a partial differential equation description (e.g., see Kot [2001]).

Over time, ecologists have come to recognize that of considerable importance to an analysis of population change is the resource intake rate of each individual (per capita consumer or per unit consumer biomass

resource intake rate), particularly how this rate depends on the density of both the resource and consumer populations. Thompson [1924] was the first to consider this in the context of host–parasite interactions when he argued that if  $z$  is the proportion of parasites per host (in this particular case parasitoid wasps) then the actual number of times a host is encountered by a parasite is given by a Poisson distribution. This is equivalent to assuming that the expected proportion of hosts escaping encounters is given by the exponential function  $e^{-az}$  (Hassell [1978]), where  $a$  is an attack intensity parameter that relates to the number of eggs each parasitoid can produce in its life time. Similar arguments were also made by Nicholson and Bailey [1935], except their encounter rate was controlled by interpreting  $z$  as density of parasites and  $a$  as a search intensity parameter. This idea became central to the development of discrete-time host-natural-enemy models in the context of arthropods attacking other arthropods, culminating in seminal texts by Varley et al. [1973] and Hassell [1978], and generalized to interpret  $z$  as function that at one limit represents “egg-limited” attack rates and another limit represents “search-limited” attack rates (e.g., see Getz and Mills [1996], Mills and Getz [1996]).

A leap forward in characterizing consumption rate processes came in the late 1950s with the experimental work of Holling [1959] that led to his conceptualization of three types of intake response-to-resource-density functions. Specifically, Holling argued that response functions must include a notion of consumer saturation from satiation or other kinds of limitation (e.g., the time it takes to handle resources before consuming them). He defined Type I, Type II, and Type III functions to be those that rise respectively linearly, hyperbolically (hence asymptotically without inflection), and logistically (hence asymptotically with inflection) to saturation.

Holling response functions rapidly came to pervade resource-consumer models, but led to intense controversy in the 1990s regarding the mechanism of saturation—was it purely dependent on the density of resources or the ratio of consumers to resources (Abrams and Ginzburg [2000]). As with all extremes, the answer lies somewhere in the middle with the relative importance of the two approaches varying with species, population densities, and other ecological factors (Getz [2011]).

The dominant paradigm today is to characterize population abundance in terms of numerical and numerical-density measures. The simplest growth models, most notably the logistic, allows abundance to be equally well interpreted in terms of biomass or biomass density. This proved particularly useful in the context of applying population models to the management of biological resources, as developed by Clark in the 1970s with his *tour de force* work on Mathematical Bioeconomics (Clark [1971, 1973, 2010]). The numerical interpretation, however, is embedded in Holling’s conceptualization of resource-consumer interactions. Specifically he defined the “numerical response” (Holling [1959]) to be “the change in the density of predators, as a result of increase in prey density.”

On the flip side of growth is the process of decline that occurs through a population itself being a resource that is extracted by individual consumers. Beyond losing biomass through extraction, a population also loses biomass through senescence (a term used here in the broad sense of representing losses from all sources of mortality other than direct extraction, including the senescence of parts of a plant but not necessarily the death of the whole plant itself). This extraction-senescence dichotomy to mortality has received little attention. In the context of population harvesting theory, a distinction is made between natural and harvesting (or fishing) mortality; but this a different dichotomy since the natural mortality includes predation and senescence, with only the exploitation of a single consumer—humans—being a separately identified source of population mortality. It may be claimed that senescence is precisely the per-capita mortality rate term in the consumer equation of the Lotka-Volterra model presented below. If the senescence rate is impacted by the process of starvation, as it surely must be, then senescence depends strongly on how well a population is able to meet its own nutritional and metabolic needs. Thus there is an important link between a population’s ability to grow through its intake rate and its rate of senescence that will increase whenever this intake rate is unable to meet basal metabolic needs. As will become apparent in the presentation below, this link is more succinctly and elegantly addressed through a biomass flow formulation than through a demographic formulation of population change.

What can be regarded as the demographic approach to modeling resource-consumers through its flowering period of 1980s and 1990s

came to full bloom at the start of new millennium with the publication of Turchin's Complex Population Dynamics [2003] and Murdoch, Briggs, and Nisbet's Consumer-Resource Dynamics [2003]. I will not attempt here to review the considerable accomplishments of the demographic approach to modeling resource-consumer interactions since there has been at least another monograph's worth of research to report beyond the 2003 publication of the two mentioned above. Rather, I will review and then synthesize my own work, much of it done in collaboration with Owen-Smith whose work on herbivore foraging theory (Owen-Smith [2002a, b]) draws strongly on a biomass flow approach that I refer to as the metaphysical approach to population modeling (Getz [1991, 1993]). The genesis of my interest in this approach goes back to the early 1980s when I published a paper on a resource per-capita approach to modeling population dynamics (Getz [1984]).

In the next section, I will provide a brief review of the metaphysiological approach. This will be followed by a presentation of recent developments using this approach. I will then review work that I have undertaken with three collaborators to better understand short comings in current approaches to modeling resource consumer interactions and conclude with a discussion of future challenges and directions.

**2. Extraction and incorporation functions.** Text book introductions to modeling the temporal interaction dynamics of a consumer population at density  $y$  feeding on a resource population at density  $x$ , when not specifically addressing arthropod prey-predator or host-parasite systems, invariably begins with a presentation of Lotka-Volterra's classic "prey-predator" model (different texts vary widely on naming variables and parameters)

$$(1) \quad \begin{aligned} \frac{dx}{dt} &= rx - axy \\ \frac{dy}{dt} &= -my + \kappa axy, \end{aligned}$$

where  $r > 0$  is the intrinsic growth rate of the resource,  $a > 0$  the extraction rate per unit resource  $\times$  consumer,  $m > 0$  is the intrinsic rate of decline of the consumer in the absence of resource, and  $\kappa \in (0, 1)$  is a biomass conversion (proportion) parameter. We note here that

the rate at which consumers extract resources in the resource equation and take in resources in the consumer equation both equal  $axy$ , with  $\kappa$  accounting for losses associated with the inefficiency of the consumer's metabolism and the fact that not all resource mass is digestible. Thus,  $\kappa axy$  is a biomass incorporation rate or, equivalently, growth rate. The principle that resource extraction and consumer incorporation (growth) rates are directly related is rarely explicitly stated and, sometimes even violated, as discussed in some detail by Ginzburg [1998]. This principle can be extended by accounting as well for diversions in the sense that not all extracted resource is ingested by consumers: some of the extracted resources are left to rot (e.g., elephants killing trees they do not consume—see Skarpe et al. [2004]) or to be consumed by scavengers (Getz [2011]).

The Lotka-Volterra model is heralded for its historical importance, but is severely limited in modern applications because of its many shortcomings. Some of these limitations are easily fixed, such as density-dependent exponential growth of the resource at a constant rate  $r$  in the absence of consumers, the lack of satiation in per-capita consumer extraction rate  $ax$  with increasing resource density  $x$ , and the fact that consumers in the absence of resources decline exponentially rather than starving rapidly to their deaths. The first two limitations are generally overcome by replacing  $r$  with a logistic growth model  $r(1 - x/K)$ , where  $K > 0$  has the interpretation of an environmental carrying capacity, and replacing  $ax$  with a saturating response function  $h(x)$ . The third shortcoming is mostly ignored, but accounted for in the metaphysiological approach (Getz [1991, 1993]) developed in the next section. Returning to response functions, currently the most widely used is Holling's *Type II response function*, which, adapting Holling's original notation, has the form

$$(2) \quad \text{Holling Type II:} \quad h(x) = \frac{ax}{b+x},$$

where  $a > 0$  is the maximum extraction rate and  $b > 0$  is the resource density at which that the value of the function is half the maximum rate. Note  $b$  is an inefficiency parameter in that as  $b \rightarrow 0$  (i.e., inefficiency is removed) the resource extraction rate is  $a$  irrespective of the density of the resource  $x > 0$ . The parameter  $b$  is also called the

half-saturation (satiation) parameter because at  $x = b$ ,  $h(x) = \frac{ab}{b+b} = \frac{a}{2}$ . A Holling Type I is the ramp version of equation (2). A ramp that passes through point  $a/2$  at  $x = b$  has the equation

$$(3) \quad \text{Holling Type I:} \quad h(x) = \begin{cases} \frac{a}{2b}x & \text{for } 0 < x \leq 2b \\ a & \text{for } x > 2b. \end{cases}$$

Population modelers, in scaling Holing's individual level functional response up to a population level, simply multiplied  $h(x)$  by the predator density  $y$ , as we see in the Lotka-Volterra model for the case  $h(x) = ax$ . Ecologists began to worry, however, that perhaps the per-capita extraction function should reflect the fact that consumers may directly interfere with one another as they went about their business of extracting resources. Thus, as often happens in science, two papers were published in the same year proposing the same remedy (Beddington [1975], DeAngelis et al. [1975]), which was to generalize  $h(x)$  to include  $y$  using a form equivalent to

$$(4) \quad \text{Beddington-DeAngelis:} \quad h(x, y) = \frac{ax}{b(1 + y/c) + x},$$

where the constant  $c > 0$ , because of the way it appears in the equation, has the natural interpretation of linearly scaling the half-maximum rate parameter  $b$  according to the units with which the consumer density  $y$  is measured. Further this form suggests the natural extension under the assumption that density should not cause  $h(x, y)$  to be hyperbolic with the maximum effect when  $y$  is close to 0 (right panel, Figure 1) (Getz [1996]), but should set in more gently, or in an inverse logistic-like fashion (left panel, Figure 1), as is the case when  $\gamma > 1$  in the more general form

$$(5) \quad h(x, y) = \frac{ax}{b(1 + (y/c)^\gamma) + x}.$$

Currently many population ecologists still prefer the functional response form  $h(x)$  expressed in equation (2) over the more general form  $h(x, y)$  expressed in equation (4), not least because equation (2) has

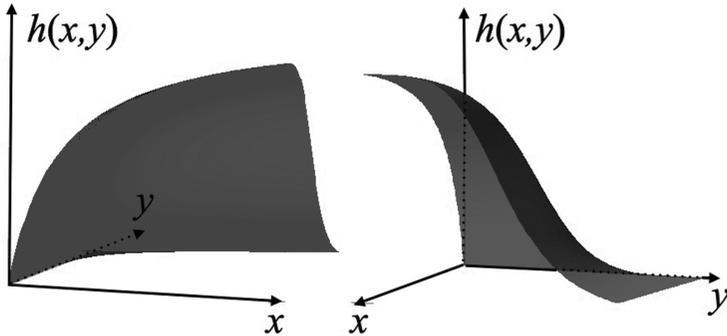


FIGURE 1. The response function in equation (5) is depicted from the perspective of the  $x$ - $h$  (left) and  $y$ - $h$  (right) planes.

fewer parameters and, hence, is more amenable to fitting the model to data and more tractable in dynamical systems analyses that involve solving equations for the equilibria of the model and determining their stability properties. In the early 1990s a fierce debate raged, as reviewed by Abrams and Ginzburg [2000], over whether the resource-dependent functional response  $h(x)$  of equation (2) or the ratio-dependent functional response (Maynard Smith and Slatkin [1973], Getz [1984])

$$(6) \quad h(x/y) = \frac{a(x/y)}{b + (x/y)} = \frac{ax}{by + x}$$

is more fundamental to characterizing resource extraction. Since both of these functional responses are special cases of the more general form  $h(x, y)$  in equation (4), which was introduced over 35 years ago, the argument appears in hindsight to be a storm in a tea cup and a question ultimately of the time scales over which the extraction rates are averaged (Getz and Schreiber [1999]).

**3. The metaphysiological formulation.** The thematic idea behind the metaphysiological model developed two decades ago (Getz [1991, 1993]) was to consider population change from a biomass flow rather than a demographic change point of view. Thus, instead of

thinking about population change in terms of birth and death rates, change was considered from the point of view of a population that has biomass flowing into and out of it. Within the population individuals accumulate biomass by extracting resources and then converting these resources into their own biomass and those of the individuals they produce. Individuals also lose biomass through extraction by other species that treat them as a resource, through their metabolic expenditures that lead to losses in the form of gases, water, and excretions, and also from losses due to generalized senescence. The latter is an umbrella for all death processes other than those relating to extraction by other species (or to cannibalism which is self-extraction).

Over the last two decades the formulation of the metaphysiological approach has been greatly improved using Owen-Smith's [2002a, b] refinements of looking separately at the processes of growth, mortality, considerations of explicitly differentiating between active and storage tissue (Getz and Owen-Smith [1999]), generalizing storage to come under the rubric of a population quality variable (Getz and Owen-Smith [2011]), and most recently splitting biomass in each species into live and dead material components (Getz [2011]). This latter presentation of the metaphysiological formulation represents a culmination of these improvements, as well as incorporation of ideas arising from efforts to identify more explicitly various inconsistencies in the current ordinary differential equation instantiation of the standard theory of temporal population dynamics.

The general formulation of a system of  $n$  interacting populations requires that for each focal population (Figure 2), denoted by  $i \in \{1, 2, \dots, n\}$ , we generate lists  $\mathcal{R}_i^x$  and  $\mathcal{R}_i^z$  of live and dead biomass of all the populations that the  $i$ th population uses for resources and lists  $\mathcal{C}_i^x$  and  $\mathcal{C}_i^z$  of all the populations that consume the live and dead biomass of the  $i$ th population. Thus, in Figure 2, the live biomass component of the focal population is simultaneously both a consumer and a resource and the dead biomass component is a resource for other populations in the food web. We use the processes indicated in Figure 2 to develop a general set of equations, under the convention that all the processes included in Figure 2 are per-capita rates. Also for purposes of symmetry and clarity, we introduce the functions (units are rates per consumer  $\times$  resource)

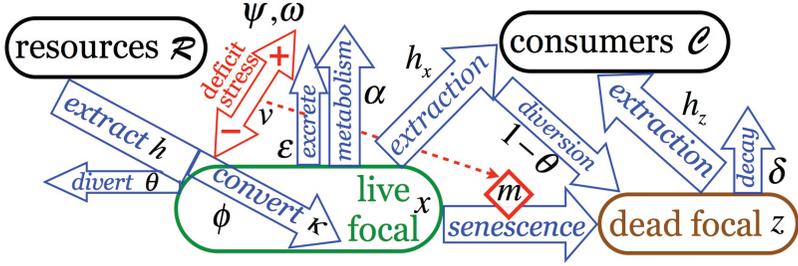


FIGURE 2. The focal individual population, represented by three variables  $x$  (live biomass, green),  $z$  (dead biomass, brown), and  $v$  (deficit-stress state, red), is both a consumer of resources  $\mathcal{R}$  (left black capsule) and resource for the consumers  $\mathcal{C}$  (right black capsule). Changes in the focal population’s temporal state  $(x(t), z(t), v(t))$  are due to the following process that form the basis for the model presented in equation (7) below (subscripts omitted in diagram): increases in live biomass depend on the converted intake or incorporation rate  $\phi > 0$  and the conversion efficiency proportion  $\kappa \in (0, 1)$ ; decreases in live biomass depend on extraction rate  $h_x > 0$ , senescence rate  $m > 0$ , basal metabolic rate  $\alpha > 0$ , and excretion rate  $\varepsilon > 0$ . Increases in dead biomass depend on the live biomass senescence rate  $m > 0$  and diversion of a proportion  $(1 - \theta) \in (0, 1)$  of the extracted biomass rate  $h_x$ , implying  $\phi = \kappa\theta h_x$ ; decreases depend on the extraction rate  $h_z > 0$  and decay rate  $\delta > 0$  (i.e., the natural breakdown by abiotic processes—a.k.a. weathering). Deficit stress is accumulated at a rate  $\psi \geq 0$  but relaxes back to 0 over time as determined by the accommodation function  $\omega$ . The senescence rate  $m$  itself is influenced (broken red arrow) by the size of the deficit stress  $v$ .

$$f = \frac{h}{x} \quad \text{and} \quad g = \frac{h}{z},$$

which are per-capita rates with respect to both the density of applicable consumers and the resources (see Getz [2011]). In formulating the general equations, the functional arguments of population  $i$ -specific processes, as well as interaction processes between populations  $i$  and  $j$ —that is the arguments of the functions  $\phi_i, f_{ij}, g_{ij}, \kappa_i^f, \kappa_i^g, \theta_{ij}, \alpha_i, m_i, \varepsilon_i, j = 1, \dots, n$  ( $f_{ii}$  and  $g_{ii}$  are permitted to account for cannibalism), where subscripts  $i$  and  $j$  index the populations involved—are omitted for simplicity. Only the arguments of the accumulation and accommodation functions  $\psi_i$  and  $\omega_i$  in the deficit-stress equation  $v_i$

are included because they are needed to properly define the integral. With this convention, though explicitly denoting the dependence of  $m_i$  on  $v_i$ , the general equations can be written as

$$(7) \quad \begin{aligned} \frac{dx_i}{dt} &= \left( \phi_i - \alpha_i - \varepsilon_i - m_i(v_i) - \sum_{j \in C_i^f} f_{ij} x_j \right) x_i \\ \frac{dz_i}{dt} &= m_i(v_i) x_i + \sum_{j \in y_i^f} (1 - \theta_{ij}) f_{ij} x_i x_j \\ &\quad - \left( \sum_{j \in C_i^g} g_{ij} x_j + \delta_i \right) z_i \\ v_i(t) &= \int_{-\infty}^t \omega_i(t-s) \psi_i(D_i(s), v_i(s)) ds, \end{aligned}$$

for  $i = 1, 2$ , where

$$\begin{aligned} D_i(s) &= \alpha_i(s) + \varepsilon_i - \phi_i(s) \quad \text{and} \\ \phi_i(t) &= \left( \sum_{j \in y_i^f} \kappa_{ij}^f \theta_{ij} f_{ij} x_j + \sum_{j \in y_i^g} \kappa_{ij}^g g_{ij} z_j \right) \Bigg|_{\text{at time } t}. \end{aligned}$$

A somewhat less general form of this system of equations was recently presented elsewhere (Getz [2011]) and referred to as a *biomass transformation web* system (BTW), as an alternative to describing the dynamics of food webs using extended Lotka-Volterra formulations (Abrams [1988], Ackland and Gallagher [2004], Cressman and Garay [2003], Moore et al. [2004], Stone and He [2007]). It is also worth noting that, in cases where it is useful to aggregate species by functional group, such as when a group of species form a tight ecological guild (Root [2001]), then the state variables in the model indexed by  $i$  might represent such a guild rather than an individual population. Of course, this level of aggregation cannot be used to address the question of

how different species in the same guild are able to coexist (Basset and Angelis [2007], Geange and Stier [2010]).

**4. Modeling issues resolved.** A number of issues associated with the application of differential equation models to population ecology have been identified, including the need for the general equations to:

- (i) be independent of trophic level considerations (Getz [1991], Getz et al. [2003])
- (ii) satisfy the principle of extraction-conversion (incorporation) fidelity (Ginzburg [1998])
- (iii) account for inertial or change resisting (e.g., storage) processes (Ginzburg [1986])
- (iv) account for heterogeneity in resources available to individual consumers (Revilla et al. [2004]).

Principles 1 and 2 are at the core of the metaphysiological approach developed two decades ago (Getz [1991, 1993]) and continue to hold in the extension of the metaphysiological approach to BTW formulation represented by equation (7). Except for the abiotic resource system that underpins the first biological trophic level in any food web, it is clear that equation (7) are independent of trophic level once the sets  $\mathcal{R}_i^x$ ,  $\mathcal{R}_i^y$ ,  $\mathcal{C}_i^x$ , and  $\mathcal{C}_i^y$  associated with the  $i$ th population have been identified. Further, the resources and consumers themselves do not need to be at trophic levels respectively below and above the  $i$ th population: this resolves the problem that omnivory in food webs distorts its trophic structure (Williams and Martinez [2004]).

Principle 3, as argued by Ginzburg and colleagues (Ginzburg [1986], Akçakaya et al. [1988], Ginzburg et al. [2004]), is essential to explain cycling in certain populations, with the primary driver of these cycles being effects that persist from one generation to another—so-called maternal effects (Inchausti and Ginzburg [1998, 2009]). Maternal effects occur over generational time scales, with the quality of the mother impacting the longevity or fecundity of her offspring. Slightly shorter term cohort effects, whereby conditions in the year of birth year of a cohort of individuals influences their subsequent survival and reproductive success also commonly occur (Lindström

and Kokko [2002]). On shorter time scales still, individuals may store fats (animals), carbohydrates (plants, see Chapin et al. [1990]), and other kinds of tissue that they then use to dampen the effects of seasonal fluctuations in the availability of the resources they need to survive and reproduce (Getz and Owen-Smith [1999], Kooi and Troost [2006]).

Inertial effects can be incorporated in one of several ways, all of which are mathematically equivalent to increasing the dimensions of the model system of equations. One approach is to add a time delay term to the model, as in the time-delayed logistic model (May [1973]). Another is to make the population equations second order either by including second order derivatives of population size with respect to time, an approach favored by Ginzburg (i.e., essentially incorporating acceleration as central to the dynamical description—see Ginzburg [1986], Ginzburg and Colyvan [2004]) or by including a second variable: the first being a measure of abundance (population size) and the second of quality (e.g., storage tissue as in Getz and Owen-Smith [1999] or other measures of average quality as in Getz and Owen-Smith [2011]).

BTW includes inertial effects in the  $i$ th population through the incorporation of the deficit-stress variable  $v_i$ . This particular inertial effect relates to the stress that organisms accumulate when they are not able to meet basic metabolic needs because the converted intake rates  $\phi_i$  are less than the sum of the basal metabolic and excretion rates  $\alpha_i + \varepsilon_i$ : i.e.,  $D_i > 0$  in equation (7). This obviously only relates to starvation time scales and, thus, not to the longer time scale cohort or maternal effects that play out throughout the complete life history of individuals affected by early experience or maternal condition. Inclusion of effects at this longer time scale requires that a suitable acceleration term be added to the abundance equation (Ginzburg and Colyvan [2004]) or age or stage structure incorporated into models (Caswell [2001]).

Consider the situation where we assume that the deficit-stress accumulation function  $\psi_i$  in equation (7) has a particularly simple ramp function form that depends only on  $D_i(t)$  and not on  $v_i(t)$  itself: viz.,  $\psi_i(t) = D_i(t)$  whenever  $D_i(t) \geq 0$  and  $\psi_i(t) = 0$  otherwise. Also assume that the relaxation function is simply exponential: that is,  $\omega_i(t) = e^{-w_i t}$  where  $w_i > 0$ . In this case, applying the fundamental theorem of

integral calculus to the third of equation (7) we obtain

$$\begin{aligned}
 \frac{dv_i}{dt} &= \frac{d}{dt} \left( e^{-w_i t} \int_{-\infty}^t e^{w_i s} \max\{0, D_i(s)\} ds \right) \\
 (8) \qquad &= -w_i v_i(t) + e^{-w_i t} \frac{d}{dt} \int_{-\infty}^t e^{w_i s} \max\{0, D_i(s)\} ds \\
 &= -w_i v_i(t) + \max\{0, D_i(t)\}.
 \end{aligned}$$

In this case, replacing the third equation in equation (7) with equation (8) yields a system of three differential equation, where the deficit-stress variable  $v_i(t)$  adds an additional dimension to the description of how the variable  $x_i$  changes over time, provided the right-hand side of the first equation in equation (7) depends on  $v_i$ . The key assumption in the BTW formulation is that the senescence function  $m_i$  depends on  $v_i$ , as indicated in Figure 2, thereby feeding in this extra dimension and, hence, inertial component into the dynamics of the live abundance variable  $x_i$ .

**5. Population growth, competition, and seasonal environments.** The model formulated above is sufficiently novel that it provides a new framework for addressing questions as simple as an exploiter-free homogenous population drawing resources from a donor-controlled flux (e.g., photons or flow-through nutrients or resource organisms). In this case, the equations for the abundance dynamics of the consumer—that is of the live biomass variable  $x(t)$ —under the assumptions used to derive equation (8) leads to the following model, where  $y(t)$  is the underlying resource,  $m(v)$  is a mortality rate that depends on the deficit-stress variable  $v$ , and the term  $\varepsilon$  is incorporated in the metabolic loss rate  $\alpha$  to obtain

$$\begin{aligned}
 (9) \qquad \frac{dx}{dt} &= (\phi(y(t), x) - \alpha - m(v))x \\
 \frac{dv}{dt} &= -wv + \max\{0, \alpha - \phi(y(t), x)\}.
 \end{aligned}$$

This model provides an alternative to the two variable ordinary differential equation growth model recently derived by Getz and Owen-Smith

[2011]. The difference is that in Getz and Owen-Smith [2011] the second variable was cast as a quality index that had no specific interpretation, and hence was more general but also more elusive in its application to real system. Here the variable  $v(t)$  has a specific meaning as a measure of the degree of starvation and, hence, suggests possible ways that it can be measured.

In the BTW formulation, equation (9) represents the fundamental growth model for any population not subject to extraction and is a replacement for the logistic growth equation that underpins resource population growth descriptions in Lotka-Volterra-type food webs. The only thing that remains is to specify the resource input function  $y(t)$ , the parameters  $\alpha$  and  $w$ , and the mortality function  $m(v)$ . If  $y(t)$  is constant then this system has an equilibrium  $(x_y, v_y)$  at:

$$(10) \quad \phi(y, x_y) - \alpha = m(v_y) \quad \text{and} \quad \phi(y, x_y) - \alpha = -wv_y.$$

Since  $m(v) > 0$  and  $-w_y < 0$  for all  $y \geq 0$ , the only possible solution is  $v_y = 0$  and  $\phi(y, x_y) = \alpha + m(0)$ . In order for a nontrivial equilibrium pair  $(x_y > 0, 0)$  to exist, we note that  $\phi(y, x)$  must depend on  $x$  otherwise  $x$  does not appear in equation (10). Thus Holling Type I (equation (3)) and II functions (equation (2)) are excluded from the model in favor of the more general Beddington-DeAngelis form (equation (4)) (cf. Getz [1991, 1993]). This does not refute Holling's [1959] formulation, which was derived in the context of individuals foraging for resources. Thus Holling's functional response is a relationship suitable for behavioral level analyses. When applying Holling's functional response relationships at a population level, scaling up from individuals to populations requires the introduction of an interference competition term (Abrams [1988], Amarasekare [2003]). This observation has important implications for the debate that raged through the 1990s regarding the relative merits of resource-dependent versus ratio-dependent functional response expressions in population growth models (for a review, see Abrams and Ginzburg [2000]): the extraction function must at least be ratio-dependent or have the more general Beddington-DeAngelis form which includes both pure ratio-dependence and pure resource-dependence as special cases.

Assuming the existence of a nontrivial equilibrium pair  $(x_y > 0, 0)$ , the Jacobian stability matrix at this equilibrium is

$$J = \begin{pmatrix} x_y \frac{\partial \phi}{\partial x} \Big|_{x=x_y} + \overbrace{\phi(y, x_y) - \alpha - m(v_y)}^{=0} x_y \frac{dm}{dv} \Big|_{v_y=0} & \\ 0 & -w \end{pmatrix}.$$

Thus whenever the population exhibits negative density dependence around the equilibrium (i.e.,  $\frac{\partial \phi}{\partial x} \Big|_{x=x_y} < 0$ ) it follows that the eigenvalues of the Jacobian, which are  $-w$  and  $x_y \frac{\partial \phi}{\partial x} \Big|_{x=x_y}$ , are both real and negative and hence the equilibrium is a stable node. Thus any oscillatory behavior that arises from this growth equation would be due to the resource input  $y(t)$  itself being oscillatory, the population  $x$  linked in a negative feedback relationship to  $y$  (e.g., as in a prey-predator interaction) or a consequence of trophic interactions with other species in the system.

A possible form for  $m(v)$  (Getz [2011]) that has the phenomenological property that mortality rates increase with stress (i.e.,  $\frac{dm}{dv} > 0$ ) is

$$(11) \quad m(v) = \frac{m_0}{1 - \frac{v}{v_s}},$$

where  $m_0$  is the background loss rate when the population is unstressed and  $v_s$  is the stress level at which the mortality rate becomes infinite: i.e., individuals immediately die at this level of deficit stress because of an extended period of severe starvation.

The growth model equation (9) provides no new insight into the growth of populations in a constant environment: as with other growth models the population will only grow if its intrinsic growth rate  $\lambda = \phi(y, 0) - \alpha - m(v) > 0$ . The strength of the model lies in the way it treats populations in fluctuating environments because of its ability to address questions relating to the interplay of mortality and deficit-stress levels as the resource environment fluctuates between levels that support growth and levels that induce starvation. As a way of illustrating the application of the model to such questions, we consider two populations  $x_1$  and  $x_2$  in a fluctuating resource environment

$y(t)$  that compete across an implicitly structured resource spectrum (e.g., the structure might relate to food particle size or spatial distribution) in a way that permits incomplete competition. If the parameters  $c_1, c_2 \in [0, 1]$  represent the degree to which intraspecific competition per unit consumer scales for consumers one and two respectively relative to interspecific competition, then the competition model takes the form (cf. how competition is dealt with in Lotka-Volterra type models in Loeuille [2010])

$$\begin{aligned}
 (12) \quad \frac{dx_1}{dt} &= (\phi_1(y(t), x_1 + c_1 x_2) - \alpha_1 - m_1(v_1))x_1 \\
 \frac{dv_1}{dt} &= -w_1 v_1 + \max\{0, \alpha_1 - \phi_1(y(t), x_1 + c_1 x_2)\} \\
 \frac{dx_2}{dt} &= (\phi_2(y(t), x_2 + c_2 x_1) - \alpha_2 - m_2(v_2))x_2 \\
 \frac{dv_2}{dt} &= -w_2 v_2 + \max\{0, \alpha_2 - \phi_2(y(t), x_2 + c_2 x_1)\}.
 \end{aligned}$$

In Figure 3 solutions to this equation are illustrated for the case where extraction has the Beddington-DeAngelis form given in equation (4) (with parameters indexed by  $i$  in the function  $h$  for the case of  $\phi_i = \kappa_i h_i(y(t), x_i + c_i x_j)$ ,  $i, j = 1, 2$  with  $j \neq i$ ) mortality is given by equation (11). Simulations of these equations demonstrate that under complete competition (i.e.,  $c_1 = c_2 = 1$ ) almost identical populations, apart from the fact that population one has at greater background mortality rate (i.e.,  $m_{01} > m_{02}$ ) but a faster deficit-stress accommodation rate (i.e.,  $w_1 > w_2$ ) can still outcompete population two provided the amplitude of the seasonal resource oscillations are sufficiently large (cf. panels A and B in Figure 3). This and other types of adaptive and life history trade-offs can be explored using equation (12) in an adaptive dynamics setting in the same way the Lotka-Volterra type models have been used in the past to explore such evolutionary questions (McGill and Brown [2007]).

**6. Gatherers, miners, movement, and space.** As already mentioned, equation (7) may explicitly identify the resources that consumers exploit to fuel their growth, but they average out spatial

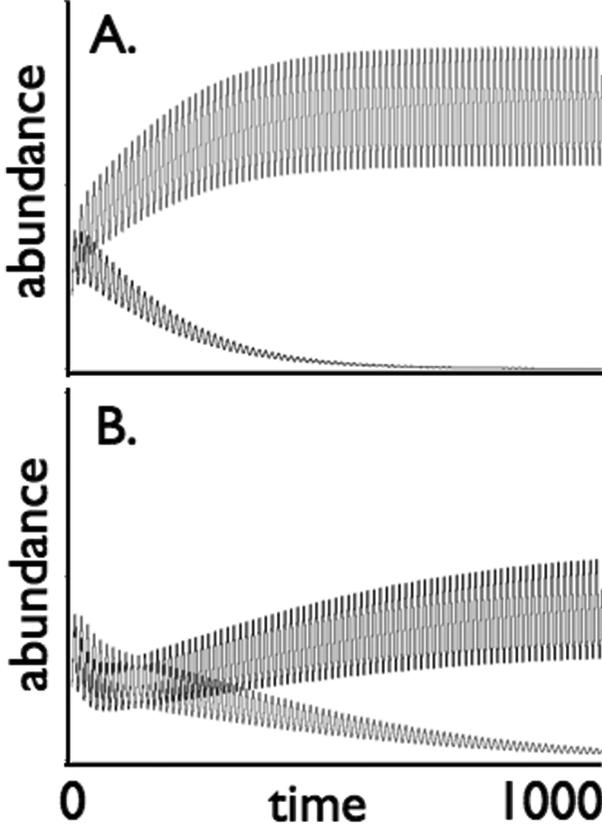


FIGURE 3. Numerical solutions  $x_1(t)$  (black) and  $x_2(t)$  (red) to equation (12) for the case  $m_i(v) = \frac{m_0 v_i}{1 - \frac{v_i}{v_{s_i}}}$  and  $\phi_i = \frac{a_i y(t)}{b_i(1 + (x_i + c_i x_j)/K) + y(t)}$ ,  $i, j = 1, 2$ ,  $j \neq i$  are plotted over the time interval  $t \in [0, 1000]$  (units are months) for parameter values  $\kappa_1 = \kappa_2 = 0.2$ ,  $a_1 = a_2 = 3$ ,  $a_1 = a_2 = 0.1$ ,  $b_1 = b_2 = 300$ ,  $c_1 = c_2 = 1$ ,  $K = 10000$ ,  $v_{s_1} = v_{s_2} = 1$ ,  $\mu_{0_1} = 0.11$ ,  $\mu_{0_1} = 0.10$ ,  $w_1 = 0.1$ ,  $w_2 = 0.06$  and resource input function  $y(t) = 1000(0.5 + \delta * \sin(2\pi t/12))$ , where **A.**  $\delta = 0.4$  and **B.**  $\delta = 0.5$ .

structures relating to the patchiness of resources. Hence equation (7) cannot explicitly address issues relating to the movement of individuals among patches and how patchiness and movement impact population growth (Revilla and Wiegand [2008]). The simplest way to extend

differential equation models, such as equation (7), is to assume a metapopulation structure (Hanski [1991], Gyllenberg and Hanski [1992]) with subpopulations occupying relatively large patches and individuals moving among subpopulations as they perceive local resources to be better in neighboring patches than their own patch. At a finer spatial scale an individual-based patch occupancy modeling approach can be taken (Moilanen [1999], Ovaskainen and Hanski [2004]).

In the presence of fluctuating resources, however, we would expect that species evolve to tolerate different deficit-stress levels before dying from starvation, as well as being able to accommodate nonlethal stress at different rates. In classifying consumer types (Figure 4), an obvious dichotomy arises between consumers that gather resources versus those that mine resources. Gatherers need to be mobile, moving across the landscape as they gather packets of resource to feed upon immediately (e.g., carnivores killing prey, herbivores eating leaves) or sequester these packets (squirrels or jays caching nuts) for future use. Miners may have a dispersal phase but are otherwise sessile while they feed by tapping into a resource pool that they have sequestered: e.g., aphids tapping into the phloem tissue of plants, ticks tapping into the blood supply of hosts, both fly larvae feeding parasitically on the flesh of live hosts, carrion fly larvae feeding on the dead flesh of a carcass.

Organisms that are miners usually have distinct life stages devoted to dispersal versus growth. Holometabolous insects—those that have complete metamorphosis from an egg through a voracious larval stage (with 100 or even 1000-fold increases in biomass) to a nonfeeding pupal transformation stage and onto an adult stage where most of the growth in biomass growth is directed to reproduction—often have larvae that are miners and adults that are dispersers. On the other hand, many hemimetabolous insects (those that do not have a complete metamorphic cycle), such as grasshoppers, crickets, cockroaches, and termites forage throughout their life cycle; though others such as aphids and scale insects have both mining and dispersal morphs. Also most vertebrates are gatherers, with some parasitic fish such as the hematophagous toothpick (candiru) fish being notable exceptions.

Once the dispersal stage of a mining species has located a food source, the feeding stage does not have to worry about starvation unless the source itself is overpopulated with individual miners and

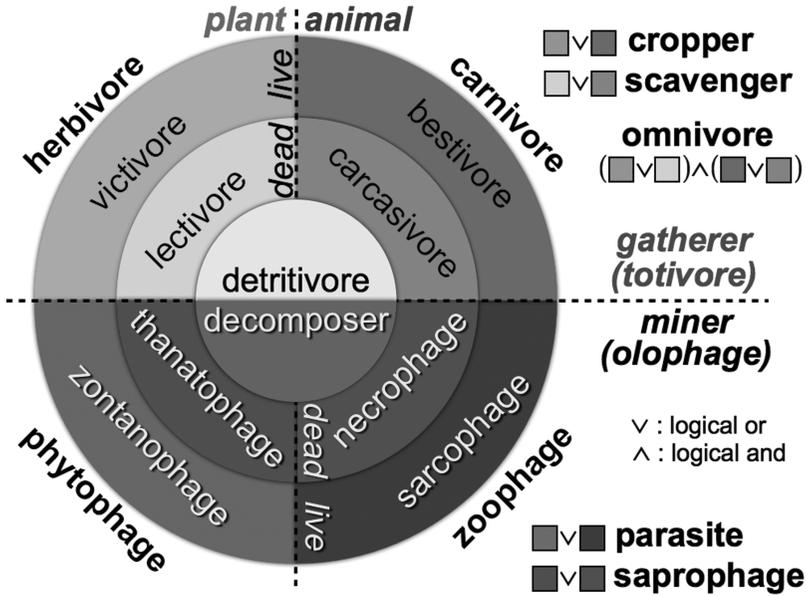


FIGURE 4. Consumer can be categorized based on material eaten (plant: green shades are live, brown shades are dead; animal: red shades are live, purple shades are dead; or particulate: gray shades) and feeding strategy (gatherer: lighter shade of each color; miner: darker shade of each color). Since, as discussed in the text, miners (olophages) and gatherers (totivores) are expected to experience very different types of fluctuations with regard to resource availability, we should expect that they evolve very different trade-offs between the way they tolerate, accumulate, and mitigate deficit stress. This translates into trade-offs for population  $i$  in values of the parameters  $w$ ,  $v_s$ , and  $b_i$  (the latter in the functions  $\phi_i$ ) in equation (12), which can be explored using the methods of adaptive dynamics (McGill and Brown [2007]) in resource settings  $y(t)$  that have different temporal properties.

is used up before most of the miners complete their feeding stage. Thus we expect miners to be selective in defending their resources rather than be adapted to staving off starvation, as is the case in polyembryonic parasitoids that have evolved a distinct defensive larval morph to fend off individuals that are not members of their clonal population (Cruz [1981]). On the other hand, we expect gatherers to adapt in some way to survive lean periods. If we consider the

deficit stress equation  $\frac{dv}{dt} = -wv + \max\{0, \alpha - \phi(y(t), x)\}$  it follows that individuals can reduce the senescence mortality rate  $m(v) = m_0/(v_s - v)$  by: (i) storing energy rich biomass when external resources are depauperate, which corresponds to a relatively large value for  $v_s$ ; (ii) rapidly mobilizing stored energy, which corresponds to relatively large  $w$ ; (iii) lowering their basal metabolism through hibernation or aestivation, which corresponds to reducing the value of  $\alpha$ ; (iv) ensuring that  $\phi(y, x) = \frac{ay}{b(1+x/c)+y}$  remains close to  $a$  by being efficient at finding resources (e.g., birds that can traverse large distances in search of food), which corresponds to a relatively small value for  $b$ . Of course, an energy cost is associated with movement so that an analysis of the trade-off between investing in processes that facilitate movement (Nathan et al. [2008]) and the gains from being able to move rapidly and efficiently are needed.

**7. Parasites and pathogens.** Parasites are different from predators in that parasites are miners of host biomass, whether plant or animal, while predators are generally carnivores or some specialist category therein (e.g., insectivores, piscivores, etc.). However, the more precise analogue of parasites in the context of a miner-gatherer dichotomy are croppers (Figure 4) and this is reinforced by the fact that prey-predator and plant-herbivore interactions are often modeled by the same Lotka-Volterra type equations (Turchin [2003]).

Since miners exploit a resource pool, parasites are generally much smaller than their hosts, as is the case of single-celled protozoans (e.g., coccidia or amoeba that cause dysentery) and multi-celled worms (e.g., various helminths and nematodes) that invade the gastrointestinal systems of vertebrates. Smaller yet are the bacterial parasites that grow in the lungs, throat, bowels of vertebrates, arthropods, and other animals, many of which are pathogenic causing sore throats (streptococci), pneumonia (pneumococci), tuberculosis (bacilli), and other debilitating and sometimes fatal diseases in their hosts. All of these parasites can be incorporated in the BTW paradigm (see Getz [2011] for a BTW model of anthrax in zebra and elephants), particularly those that colonize their hosts with populations that grow to share a significant component of the host's total biomass. For example, trematode parasites (flukes) in snails have been shown to account for up to 39% of their

host's body mass (Hechinger et al. [2009]), while in the case of tuberculosis colonies of the mycobacteria that cause the disease can grow *inter alia* in the lungs, joints, and stomachs of their victims.

In the case of pathogenic parasites, the direct impact of biomass extraction on the host population can be completely overshadowed by the direct effects of the parasite on host mortality rate. In this case, we might assume that the proportion  $p(t)$  of hosts infected with the pathogen in a mean-field model can be made a function of the biomass ratio of the parasite to the host populations at time  $t$ . In this case, the mortality rate  $m$  of the host can be made an increasing function of  $p(t)$  as well. For example, equation (11) can be replaced with  $m(v, p) = (m_0 + p(t)m_1)/(1 - \frac{v(t)}{v_s})$ , where  $m_0$  is the background mortality rate for an unstressed uninfected host and  $m_0 + m_1$  is the background mortality rate for a unstressed infected host. The effects of stress are still taken care of by the term in the denominator, although it is quite possible that the starvation point  $v_s$  may also be reduced in infected hosts.

In the case of viral infections, since the impact of pathogenic virus on their hosts is overwhelmingly through the impact of the viral population on host mortality rates, with extraction in this case playing a negligible role (Hethcote [2000]), BTW does not on its own lend itself to modeling viral-host dynamics. In this case disease classes—such as susceptible, exposed, infected, immune, etc.—need to be explicitly incorporated following methods developed in the context of the Kermack and McKendrick disease modeling paradigm (May and Anderson [1989], Hethcote [2000]).

At the parasite–predator interface are a class of organisms referred to as parasitoids that are miners in their larval stage, gatherers in their egg laying stage, and they are obligate killers of their hosts. Parasitoids are species of insect generally belonging to one of several wasp families, but also to some families of flies. Their hosts are other insects, and non-insect arthropods, such as spiders. The dominant differential equation paradigm for modeling host–parasitoid interactions has been to structure the parasitoid population into at least two stages, juvenile (i.e., larval) and adult (Nisbet and Gurney [1983], Murdoch et al. [2003]). This paradigm has proven successful in exploring a number of different host–parasitoid interaction issues, such as the effects of an invulnerable

stage class (Murdoch et al. [1987]), and issues relating to sex ratio allocation in the context of variable host size (Murdoch et al. [1992]). Clearly such questions are best answered using a demographic modeling approach. On the other hand, BTW has been designed to answer a different set of questions, such as the role parasitoids and parasite may play in structuring food webs—a problem of some interest to food web ecologist (Lafferty et al. [2008]), and the impact parasites might have in increasing the vulnerability of host species to consumption by predators (Hudson et al. [1992]).

**8. Conclusion.** Although equations (7) have been formulated to model a population of individuals, the same set of equations can be applied to a subset of individuals or, even when applicable, to the change in biomass of single individuals. In the context of a population model, equations (7) imply homogeneity among individuals with respect to various traits or states of individuals such as size or age. In general, however, individuals vary with regard to a particular trait or state. Numerous genres of population models have been developed that include age either as a continuous variable, resulting in a partial differential equation description of the population process of change (e.g., see Kot [2001]) or that divide the population up into a number of discrete age or stage classes, as in Leslie's [1945] age-structured matrix models and nonlinear versions of such models (e.g., Cross and Getz [2006], Wilmers and Getz [2004]). However, assuming that each individual in the population is exposed to a different set of environmental conditions by virtue of its location on a heterogeneous landscape possess a whole new set of problems in terms of implementing systems of differential equations as mean field descriptions of the outcome of such variation (Ovaskainen and Cornell [2006]). Yet such differences in exposure are a critical aspect of population ecology (Palmer et al. [1997], Floater [2001], Revilla et al. [2004], Revilla and Wiegand [2008]).

Effective incorporation of spatial heterogeneity in ordinary differential equation models remains a challenging problem, but possible provided heterogeneity does not vary too rapidly over space (Ovaskainen and Cornell [2006]). The easiest approach is to apply individual or agent-based models in simulation frameworks, but this limits the application of analytical approaches to obtain insights into the behaviour of the system as a whole. The development of a coherent theory when

access to resources varies among individuals remains an open problem. With increasing computing power, however, the trend in applying numerical methods to study both specific and general dynamic food webs is shifting from population-level formulations to individual-based formulations. The value, however, of a top-down population modeling approach remains in the context of mean-field analyses (Ovaskainen and Cornell [2006]), particularly if models are designed to be elaborated at subgroup and individual levels: in this case, a mean-field analysis provides a road map without which interpreting more complicated individual-based simulation analyses becomes impossible. BTW has these properties. The formulation, as we see in equations (7), has been developed in terms of per-unit-biomass or per-capita process functions with the mean-field description implemented in the abundance equation by simply multiplying these per capita rates by the abundance itself. Further, the deficit-stress equation is based on formulating the extent to which each individual (i.e., individuals on average in the mean-field interpretation) fails to meet its basal metabolic needs. Of course, at the individual level, although we can interpret the per-capita intake rate  $\phi$  either as an average rate or we calculate this rate from a series of discrete feeding events that are then averaged over a suitable time interval  $\tau$  for which the average value of  $v$  is  $\bar{v}$ , at the individual level the mortality process would have to be reinterpreted as a probability of death  $p_m(\tau) = 1 - e^{-m(\bar{v})\tau}$  rather than an average rate. An individual level approach also allows us to account in finer detail for heterogeneities arising from variable infection rates in webs that include parasites.

As has been argued by Owen-Smith [2005, 2008, 2011], the metaphysiological approach is particularly amenable to a mean-field treatment because population dynamics are smoother from a biomass than from a demographic point of view (e.g., births correspond to changes in number but much less dramatically to changes in biomass). Changes in biomass can follow changes in resource abundance without having to invoke greater changes in numbers of individuals than actually occurs, because individuals themselves can lose or gain weight: they get leaner when resources are scarce and fatten when resources are abundant. The development of the metaphysiological framework into the more elaborate BTW formulation presented here provides additional power to the mean-field approach in dealing with the inertial processes associated

with starvation and storage. It does not, however, deal with the realities of heterogeneous resource exposure and how this leads to variation in the stress-deficit state among individuals in the population. How best to deal with this issue remains a challenge. But this challenge can be met through individual-based models that follow metaphysiological principles implemented at the individual level.

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