

Published in final edited form as:

Ecol Lett. 2011 February ; 14(2): 113–124. doi:10.1111/j.1461-0248.2010.01566.x.

Biomass transformation webs provide a unified approach to consumer–resource modelling

Wayne M. Getz*

Department of Environmental Science, Policy and Management, University of California at Berkeley, Berkeley, CA 94720-3114, USA; Stellenbosch Institute for Advanced Study (STIAS), Wallenberg Research Centre at Stellenbosch University, Marais Street, Stellenbosch 7600, South Africa

Abstract

An approach to modelling food web biomass flows among live and dead compartments within and among species is formulated using metaphysiological principles that characterise population growth in terms of basal metabolism, feeding, senescence and exploitation. This leads to a unified approach to modelling interactions among plants, herbivores, carnivores, scavengers, parasites and their resources. Also, dichotomising sessile miners from mobile gatherers of resources, with relevance to feeding and starvation time scales, suggests a new classification scheme involving 10 primary categories of consumer types. These types, in various combinations, rigorously distinguish scavenger from parasite, herbivory from phytophagy and detritivore from decomposer. Application of the approach to particular consumer–resource interactions is demonstrated, culminating in the construction of an anthrax-centred food web model, with parameters applicable to Etosha National Park, Namibia, where deaths of elephants and zebra from the bacterial pathogen, *Bacillus anthracis*, provide significant subsidies to jackals, vultures and other scavengers.

Keywords

Anthrax; *Bacillus anthracis*; Etosha National Park; food web models; host–parasite; jackals; metaphysiological models; plant–herbivore; prey–predator; scavengers

INTRODUCTION

Current approaches to modelling food webs (Pimm 1982; Winemiller & Polis 1996) come in many guises including Lotka–Volterra community assemblages (Ackland & Gallagher 2004), modified Lotka–Volterra trophic webs (Arditi & Michalski 1995; Getz *et al.* 2003), information theoretical aspects of trophic flow (Ulanowicz 2004), trophic flow models

© 2010 Blackwell Publishing Ltd/CNRS

*Correspondence: getz@nature.berkeley.edu.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Consumer categories.

Appendix S2. Differential equation for deficit stress variable.

Appendix S3. Cropping and scavenging.

Appendix S4. Anthrax in ENP: model.

Appendix S5. Anthrax in ENP: parameters.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organised for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

(Jordán 2000), trophic mass-balance models (Moloney *et al.* 2005), energy flow models (Jordán 2000), bioenergetic models (Romanuk *et al.* 2009), ecological networks (Brose 2010; Jørgensen & Fath 2006), nutrient cycling (Allen & Gillooly 2009) and carbon flows (Sandberg *et al.* 2000; Finlay *et al.* 2002). Each approach best addresses a specific class of questions such as stability properties (Neutel *et al.* 2002), effects of web structure on productivity (Carpenter *et al.* 1985) or biodiversity (Bascompte 2009), transport properties among spatial elements (Polis *et al.* 1997; Power & Dietrich 2002) or linkage structure (Williams & Martinez 2000). None of these approaches embeds into food webs, as seamlessly as the biomass transformation web (BTW) approach developed here, all possible consumer types, particularly scavengers and parasites.

Many food web studies include one or more detrital components (Moore *et al.* 2004; Szwabiński *et al.* 2010). However, BTW takes this a step further by dividing populations into both live and dead biomass components, as well as classifying consumers of plant, animal or particulate organic material based on whether they mine or gather resources. As a result, BTW leads to a natural 10-way classification of basic consumer categories (Fig. 1). Here, miners are idealised as sessile extractors of pooled resources such as phloem-feeding aphids or blood-sucking ticks, and gatherers are idealised as mobile extractors of resource packets such as grasshoppers eating leaves or cats hunting prey. The relevance of this miner–gatherer dichotomy will become clearer in the general modelling section when we consider how resource deficits over various periods of time affect biomass dynamics and may ultimately lead to starvation of individuals.

The general formulation of BTW, presented in the next section, uses metaphysiological concepts of biomass dynamics (Getz 1991, 1993, 2009) to characterise growth in terms of consumption, conversion (digestion and anabolism) and metabolism, as well as mortality in terms of both extraction (i.e. the population in question is a resource for other populations in the food web) and senescence. In the BTW formulation, senescence is regarded as mortality due to all factors other than extraction, and thus includes deaths due to ageing, non-infectious disease (e.g. cancer, organ failure), starvation and infectious disease when the agent of the disease is itself not explicitly modelled within the food web. At the end of this article, although, a BTW model that explicitly includes the pathogenic bacterium, *Bacillus anthracis*, as a consumer in its own right, and hence affects its hosts through the processes of extraction rather than senescence, is formulated to study the dynamics of a food web centred around the occurrence of anthrax in large mammalian herbivores (primarily zebra and elephant) in Etosha National Park (ENP), Namibia. One of the interesting questions that will be explored is the effect of carcass subsidies from anthrax deaths on the population dynamics of black-backed jackal (*Canis mesomelas*) scavengers.

Before we can formulate a model that includes elephants (*Loxodonta africana*), zebra (*Equus quagga*), *B. anthracis*, jackals and various small mammal species that are predated by jackals, we need to develop a general approach to modelling such food webs. As no general paradigm currently exists that includes scavengers (jackals in our case) and parasites (*B. anthracis* in our case), our first task is to develop such a paradigm, which we call BTW because of its focus on biomass transfers among food web components. The novelty of the approach, however, requires that we both clarify the kinds of consumers occurring in BTWs – that is, the 10 categories referred to earlier – and develop details needed to capture differences among consumer types within the context of our unified approach to modelling all types of consumer–resource interactions. Of course, no general formulation can cover the complexities of all consumer–resource interactions. The range covered by the formulation presented here, however, is much broader than other existing formulations, as illustrated in the final section of this article, where a BTW model is presented of an anthrax-centred food web in ENP.

GENERAL BTW FORMULATION

Biomass transformation web is based on a set of principles that specify how the abundances of live, $x_i(t)$, and dead, $y_i(t)$, biomass of the i th ($i = 1, \dots, n$) population or functional group, referred to as compartments in a food web, change over time. Biomass can be transferred among compartments as a result of processes of extraction, diversion, conversion, metabolism, live biomass senescence or dead biomass decay back into environmental constituents (nutrients, organic molecules, etc.) (Box 1). The latter for simplicity are represented by the aggregated scalar concentration variable y_0 that can be generalised to a multivariable vector, as needed. Additionally, if individuals in the i th group take in less biomass or resources than are required to meet basal metabolic needs, then they accumulate a feeding deficit stress $v_i(t)$ over time. This deficit can be accommodated by drawing upon an implicit stored live biomass component (e.g. stored in the form of fats or sugars) allowing accommodation to take place over extended periods of time (McCue 2010). This accommodation occurs through organisms adjusting growth and reproduction schedules until resource intake is restored to needed levels or individuals ultimately die from the starvation when critical (i.e. final starvation) levels $v_i(t) = v_i^s$ reached. The appropriate forms of the functions that determine the accumulation and accommodation rates and the way senescence depends on $v_i(t)$ are likely to be influenced by the feeding ecology of species i , with gatherers more likely than miners able to tolerate extensive periods of stress from deficit feeding (i.e. starvation).

From these considerations, the state of a BTW at time $t \geq 0$ is represented by the vectors $\mathbf{x}(t) = (x_1(t), \dots, x_n(t))'$, $\mathbf{y}(t) = (y_0(t), y_1(t), \dots, y_n(t))'$ and $\mathbf{v}(t) = (v_1(t), \dots, v_n(t))$ (where ' denotes vector transpose because vectors have column rather than row representations). The equations of BTW are formulated in Box 1 with descriptions of variables, process functions and parameters listed in Table 1. These BTW equations (eqn 2) include the influence of the accumulated deficit stress on live biomass senescence into dead biomass. This senescence happens at an accelerating rate with increasing deficit stress until the rate is infinitely fast when starvation level v_i^s is reached. Throughout the formulation of the BTW equations, we consider various functions with arguments \mathbf{x} , \mathbf{y} , \mathbf{v} and t . For notational convenience, when a function, say $\phi_i(\mathbf{x}(t), \mathbf{y}(t), t)$, is considered purely in terms of time, we use the notation $\tilde{\phi}_i(t) = \phi_i(\mathbf{x}(t), \mathbf{y}(t), t)$ to avoid confusion.

In closing, the general formulation presented in Box 1 does not explicitly account for faecal waste or external inputs (Polis *et al.* 1997) other than y_0 . The BTW formulation can easily be extended to include one or more faecal waste components (e.g. in systems where different species of dung beetle exploit the dung of different species, as in Larsen *et al.* 2006) and other external drivers (e.g. emigration) as needed.

Box 1 General formulation

Biomass extraction

Extraction of live and dead biomass from j to live i is at rates $f_{ji}(\mathbf{x}, \mathbf{y}, t)x_jx_i$ and $g_{ji}(\mathbf{x}, \mathbf{y}, t)y_jx_i$, respectively (these functions are 0 if a trophic relationship is absent).

Live biomass diversion

Only a proportion $\theta_{ji}(\mathbf{x}, \mathbf{y}, t)$ of extracted live biomass j actually flows into i , the remainder flows to dead biomass j .

Live and dead biomass conversion

Biomass flowing from live and dead j into i is converted with efficiencies $k_{ji}^f(\mathbf{x}, \mathbf{y}, t)$ and $k_{ji}^g(\mathbf{x}, \mathbf{y}, t)$, respectively.

Biomass incorporation

The per capita rate at which biomass is incorporated from all sources into live i is from the above (omitting functional arguments)

$$\phi_i = \sum_{j=1}^n (k_{ji}^f \theta_{ji} f_{ji} x_j + k_{ji}^g g_{ji} y_j). \quad (1)$$

Biomass metabolisation

The per capita rate at which biomass is metabolised into water and other by-products is $\tilde{\alpha}(t) = \alpha_i(\mathbf{x}, \mathbf{y}, t)$ (dependence on \mathbf{x} and \mathbf{y} is likely to be weak).

Deficit stress accumulation and accommodation

Whenever $\tilde{\phi}_i(t) - \tilde{\alpha}_i(t) < 0$ for extended periods of time, a deficit stress variable $v_i(t)$ monitors this deficit via a deficit stress accumulation-rate function V_i that depends on both current storage deficit stress $v_i(t)$ and current net converted biomass rate $\tilde{\phi}_i(t) - \tilde{\alpha}_i(t)$. A discounting function $w_i(t-s)$ that approaches zero as time $s > 0$ recedes into the past is used to account for accommodation of this feeding deficit stress through reductions in growth and reproduction rates.

Live biomass senescence

Each unit in the population is subject to a per capita senescence rate m_i that includes all sources of mortality other than extraction, where m_i has a minimum background rate that increases with increasing $v_i(t)$ such that $m_i(\cdot, v_i) \rightarrow \infty$ as $v_i \rightarrow v_i^s$, where v_i^s is a death-by-starvation level.

Dead biomass decay

For population i dead biomass decays back into the environment at a per capita rate $\delta_i(\mathbf{x}, \mathbf{y}, t)$ (any dependence on \mathbf{x} and \mathbf{y} is likely to be weak).

Accounting for all these processes in a model that averages out spatial structure produces the dynamic model (omitting process functional arguments except in the last equation where they are needed for clarity),

$$\begin{aligned} \frac{dx_i}{dt} &= \phi_i x_i - \sum_{j=1}^n f_{ij} x_j x_i - m_i x_i - \alpha_i x_i \quad (\text{recall } m_i \text{ depends on } v_i), \\ \frac{dy_i}{dt} &= m_i x_i + \sum_{j=1}^n (1 - \theta_{ji}) f_{ij} x_j x_i - \sum_{j=1}^n g_{ij} x_j y_i - \delta_i y_i, \\ v_i(t) &= \int_{-\infty}^t w_i(t-s) V_i(\tilde{\alpha}_i(s) - \tilde{\phi}_i(s), v_i(s)) ds. \end{aligned} \quad (2)$$

The last integral equation can be transformed into a differential equation, as discussed in Appendix S2.

CONSUMER CATEGORIES AND TERMINOLOGY

One of the concepts associated with BTW that requires refinement is how to treat consumers that feed exclusively on live vs. dead material. In particular, terms exist to distinguish between consumers of live and dead flesh but not in the case of plant material. Another concept, which is an area for future research, relates to how we should characterise the

effects of deficit stress on senescence in different kinds of consumers, particularly gatherers vs. miners. In particular, we need to develop ways of characterising the deficit stress accumulation-rate functions $V_i(\alpha_i(t) - \phi_i(t), v_i(t))$ and the deficit stress accommodation functions $w_i(t)$ that are consumer-type dependent. To facilitate such refinements in modelling the effects of deficit resource intake on different kinds of consumers, the categorisation scheme presented in Fig. 1 (cf. Appendix S1 and Table S1) unambiguously defines consumer categories that distinguish among consumer types. In particular, the scheme proposes that the words decomposer and detritivore should be reserved for organisms that, respectively, mine and gather bits of organic matter independent of source.

Beyond the 10 primary categories illustrated in Fig. 1, we can also classify the consumer world into various compound categories that are useful to consider when developing the specific structure of the general equations presented in eqn 2 (Box 1). Four such categories, three of which already exist, take on the following rigorous definitions: *parasites* and *croppers* are miners and gatherers of live biomass, respectively, whereas *saprophages* and *scavengers* are miners and gatherers of dead biomass, respectively.

In the development of these categories and when considering the processes that affect growth and senescence in formulating the basic building blocks presented in the next section, we focus on what we call first-order processes and factors and differentiate between direct and indirect effects as defined by:

Order effect of processes and factors

The sensitivity of the output of a model to perturbations of model parameters, either singly or in combination, has various but precise mathematical definitions (Saltelli *et al.* 2000). Using any appropriate analytical method, if the sensitivity of some output to a process or factor represented through parameter perturbations is an order of magnitude (i.e. 1 unit on a log₁₀ scale) greater than another, then the effect of the process or factor on the measure can be said to be of order one higher than the other, with the highest being first order. In our formulations, we focus only on first-order processes and factors that dominate demographic times scales, recognising that second- and lower-order processes and factors may have importance on ecological succession and evolutionary time scales.

Direct vs. indirect extraction effects

In the context of BTW only, we define factors (parameters, process descriptions) that have direct extraction effects to be those that alter the values of the biomass extraction rates $f_{ij}(\mathbf{x}, \mathbf{y})$ and $g_{ij}(\mathbf{x}, \mathbf{y})$ for any given state (\mathbf{x}, \mathbf{y}) . All other types of factors are said to have indirect extraction effects [i.e. they ultimately affect extraction through their influence on the state (\mathbf{x}, \mathbf{y})].

SOME BASIC BUILDING BLOCKS

Before developing a model of a particular system and exploring its behaviour, it is useful to consider some specific building block functions for representing the processes of extraction, diversion and mortality transformation.

Isolated population growth

As a first step in developing our understanding of BTW dynamics, we consider the canonical example of a single population described by biomass variables $x(t)$ and $y(t)$ growing in a constant environmental resource matrix at level $z(t)$, which we use instead of y_0 to reduce the use of subscripts. Furthermore, as we are now dealing with only one population, we can drop all subscripts under the assumption that the population is isolated

from extraction by other populations. Assuming that the metabolic maintenance rate α is constant, and as discussed in Appendix S2 that the deficit stress accumulation function is simply $\bar{V}(s) = \max\{0, (\alpha - \bar{\phi}(t))\}$, it follows from eqn 2 (Box 1) that the equations for the variables $x(t)$ and $v(t)$ satisfy the closed system

$$\begin{aligned} \frac{dx}{dt} &= (\phi(z, x) - m(x, v) - \alpha)x, \\ \frac{dv}{dt} &= \max\{0, (\alpha - \bar{\phi}(t))\} - \max\{0, (\alpha - \bar{\phi}(t - t_s))\}. \end{aligned} \quad (3)$$

Once $x(t)$ and $v(t)$ have been found, then the dead compartment can be generated from the

$$\text{equation } \frac{dy}{dt} = (m(x, v) + \alpha)x - \delta y.$$

Equation 3 constitute a two-variable description of inertial population growth that represents a mechanistic alternative to the more axiomatic approach taken by Ginzburg and Colyvan (2004) and the more phenomenological quantity–quality approach taken by Getz & Owen-Smith (in preparation). In particularising these equations, we note from eqn 1 for constant conversion and diversion proportions k and the θ , respectively, that the form of biomass incorporation function $\phi(z, x) = k\theta f(z, x)z$ depends on $f(z, x)$. The form we select is that of a Holling Type II, where the half-maximum-extraction parameter b is modified as discussed in Getz (1993) to incorporate the effects of abrupt intraspecific competition (Getz 1996). Thus, our extraction and biomass incorporation functions, respectively, are

$$f(z, x) = \frac{a}{b\left(1 + \left(\frac{x}{c}\right)^\gamma\right) + z}$$

and

$$\phi(z, x) = \frac{k\theta az}{b\left(1 + \left(\frac{x}{c}\right)^\gamma\right) + z},$$

where $a > 0$ is the maximum extraction rate, $b > 0$ is a resource level that reduces the intake rate to half its maximum when interspecific competition is absent (formally as $x \rightarrow 0$) and $c \geq 0$ is a parameter that determines the intensity of interspecific competition for a given abruptness parameter $\gamma \geq 1$. The key difference between eqn 4 and a Holling Type II functional response is the dependence of the denominator on the consumer biomass abundance x . This dependence is required when extractive rates are reduced under conditions of diminishing availability of resources per unit consumer (Getz 1984; Abrams & Ginzburg 2000). In this case, competition is directly experienced through interference (Abrams 1988) rather than emerging indirectly through reductions in future levels of resource.

Moreover, for simplicity, we assume that the per capita senescence function $m(x, v)$ is separable in the variables x and v and can be expressed in the form

$$m(x, v) = \mu(x) \frac{v^s}{v^s - v}. \quad (5)$$

This form implies $m(x, v) \rightarrow \infty$ as $v \rightarrow v^s$, with the result that the population plunges to zero when the starvation deficit limit v^s is reached.

A general form for $\mu(x)$ that allows us to account for density-related effects that either reduce or increase mortality with increasing density is:

$$\mu(x) = \frac{\mu_0 + \mu_1 x}{1 + \mu_2 x},$$

where we assume that $\mu_i \geq 0$, $i = 1, 2$ or 3 and $\mu(x) > 0$ for all $x > 0$.

Consumer–resource interactions

Consumer–resource interactions were first considered in the context of prey–predator, plant–herbivore and host–parasite systems (Murdoch *et al.* 2003; Turchin 2003) and are the core motif of a food web (Bascompte 2009; Bascompte & Melián 2005). We can dynamically isolate this interaction from a surrounding food web by assuming that:

1. The resource population consumes biomass, nutrients or energy, which is at an abundance or concentration of $y_0(t)$ in the environment, through a recipient-controlled process.
2. The extractive part of consumer mortality (the other part is the senescence process) is determined by an external input to the system (e.g. a constant or donor-controlled harvesting rate).

In our treatment below, we assume y_0 to be an underlying constant or specified time-varying environmental input, x_1 to be a resource population that lives off of y_0 and x_2 to be a consumer that most generally consumes x_1 , y_1 , y_2 and influences all the rates (Fig. 2), but is itself subject only to senescence mortality. The biomass flows and transformations that generally occur can be categorised as follows, with cannibalism now emerging very naturally because of the live–dead biomass dichotomy:

Resource growth transformation—The total biomass (or nutrient if the population is at the lowest trophic level in a food chain) flow rate $f_{01}y_0x_1$ is transformed from y_0 into x_1 .

Resource death transformation—The total biomass flow rate m_1x_1 is transformed from live resource x_1 into dead resources y_1 .

Diversion transformation—A proportion θ_{12} of the total extracted biomass flow rate $f_{12}x_1x_2$ is transformed from live resource x_1 into dead resources y_1 .

Extracted live biomass transformation—A proportion $(1-\theta_{12})$ of the total biomass flow rate $f_{12}x_1x_2$ is transformed from live resource x_1 into cropper or parasitic consumer biomass x_2 .

Cannibalistic transformation—Biomass flow f_{ii} from live resource or consumer population x_i is transformed back into consumer biomass x_i .

Extracted dead biomass transformation—Biomass flow g_{12} from dead resources y_1 transformed into consumer biomass x_2 . (As mentioned above, in a more general treatment, we can separate out coprophagy by adding an explicit faecal waste variable z_1 to the resource population.)

Consumer death transformation—Total biomass flow rate m_2x_2 from live consumers x_2 is transformed into dead consumers y_2 .

Cannibalistic-scavenger transformation—Biomass flow g_{ii} from dead resource or consumer population y_i is transformed into consumer biomass x_i .

In the context of the feeding flows f_{12} and f_{22} , as formulated in our general model given by eqn 2, we need to account for, using our θ_{i2} functions ($i = 1, 2$), the dual transformation processes of live-to-live and live-to-dead flows as a result of consumer feeding activities and, of course, we also need to account for conversion inefficiencies through the conversion functions K_i . With the above focal transformation processes, and for simplicity confining cannibalism to the consumer alone, we obtain the following consumer–resource model of a closed system (if subsidies flow into the web from the outside, then these need to be included, e.g. see Polis *et al.* 1997) as a special case of the general BTW model (Fig. 2) presented in eqn 2 (Box 1):

$$\begin{aligned} \frac{dx_i}{dt} &= (\phi_i - \alpha_i - m_i - f_{i2}x_2) x_i, \\ \frac{dy_i}{dt} &= (\alpha_i + m_i) x_i + (1 + \theta_{i2}) f_{i2}x_i x_2 - (g_{i2}x_2 + \delta_i) y_i, \quad i=1, 2, \\ v_i(t) &= \int_{-\infty}^t w_i(t-s) V_i(\tilde{\alpha}_i(s) - \tilde{\phi}_i(s), v_i(s)) ds, \end{aligned} \quad (6)$$

where

$$\phi_i = k_{01}^f f_{01} y_0,$$

and

$$\phi_2 = k_{12}^f \theta_{12} f_{12} x_1 + k_{22}^f \theta_{22} f_{22} x_2 + k_{12}^g g_{12} y_1 + k_{22}^g g_{22} y_2.$$

Various special cases arise by allowing different combinations of the extraction rates f_{12} , g_{12} , f_{22} and g_{22} to be non-zero (Table 2) along with zero or non-zero diversion functions θ_{12} and θ_{22} (e.g. panels a–d in Fig. 3). Additional cases arise when considering harassment and stress-inducing first-order effects that consumers may have on resource individuals. Three of these are as follows:

Extraction harassment—The per capita rate $f_{01}y_0$ at which the resource population extracts food (or energy) from the environment is a non-increasing function of consumer

density x_2 : that is, $\frac{df_{01}}{dx_2} \leq 0$. A case in point is predator avoidance by elk in Yellowstone has led to elk feeding at higher elevations for longer periods of time in the spring. This has had the ecological knock-on effect of allowing aspen seedlings at lower elevations to survive and stands of aspen trees to recover (Ripple & Beschta 2007).

Exploitation stress effects on growth—The conversion functions k_{12}^f and k_{12}^g may vary due to the stress that herbivores induce on plants or predators induce on prey. For example, wild dogs reduce the rate at which their prey are able to reproduce (Creel *et al.* 2009), while some herbivores invoke a defensive response in plants (Karban 2008) that diverts resources that would otherwise have been allocated to growth and reproduction.

Feeding deficit stress effects on senescence—The per capita rate m_1 of the resource population is a non-increasing function of x_2 because consumers may induce a

feeding deficit stress response of some kind on individuals in the resource population that leads to increased mortality rates through senescence. The most ubiquitous examples are parasites that are pathogenic to some degree.

Croppers, diverters and harassers

Croppers, defined above to be primarily gatherers of live animal or plant biomass, may or may not divert a significant flow of resource biomass to the dead resource compartment. Herbivorous grasshoppers, for example, divert up to 40% of what they eat (Gandar 1982), while carnivorous cheetahs divert up to 15% of what they hunt (Marker *et al.* 2003). They may also harass individuals in the resource population. Yellowstone wolves, for example, fit into the cropper–diverter–harasser category and play a critical role in stabilising populations that scavenge on wolf-produced carrion by producing elk carcasses year round and reducing the strong pulse of elk carcass towards the end of winter (Wilmers *et al.* 2003; Wilmers & Getz 2005).

By definition since croppers strictly do not scavenge and if they are not cannibals then the only non-zero extraction function in eqn 6 is f_{12} , which consequently in this case does not depend to first order on the dead biomass components y_1 and y_2 (Table 2). Furthermore, in the simplest case, we assume that at least to first order, the per capita senescence rates m_i , $i = 1, 2$, of individuals in the resource and cropper populations depend only on the deficit stress variables v_i . Thus, applying eqn 5 to each population for constant background senescence

rates $\mu_i > 0$, we obtain $m_i(v_i) = \frac{\mu_i v_i^s}{v_i^s - v_i}$. In this case, the differential equations in resource and cropper abundance x_1 and x_2 , respectively, are independent of variables y_1 and y_2 . Under these assumptions, we can write down the following four-variable inertial model as a special case of eqn 6 for croppers that also may harass the resource:

$$\begin{aligned} \frac{dx_1}{dt} &= \left(\phi_1 - \alpha_1 - \frac{\mu_1 v_1^s}{v_1^s - v_1} - f_{12} x_2 \right) x_1 \\ \frac{dx_2}{dt} &= \left(\phi_2 - \alpha_2 - \frac{\mu_2 v_2^s}{v_2^s - v_2} \right) x_2 \\ v_i(t) &= \int_{-\infty}^t w_i(t-s) V_i(\tilde{\alpha}_i(s) - \tilde{\phi}_i(s), v_i(s)) ds, \quad i=1, 2, \end{aligned} \quad (7)$$

where

$$\phi_1 = k_1 \theta_1 f_{01} y_0 \quad \text{and} \quad \phi_2 = k_2 f_{12} x_1. \quad (8)$$

The effects of harassment of resource individuals can be incorporated by generalising the feeding f_{01} to be a monotonically decreasing function of x_2 . In this case, the simple extension of eqn 4 to

$$f_{01}(y_0, x_1, x_2) = \frac{a_1}{b_1 \left(1 + \left(\frac{x_1}{c_1} + \frac{x_2}{c_{12}} \right)^\gamma \right) + y_0} \quad (9)$$

suffices for some constant $c_{12} > 0$.

Parasites and pathogens

All types of organisms in food webs can be parasites and their hosts can be any kind of organism (Marcogliese & Cone 1997; Lafferty *et al.* 2008). Parasites, as defined in Fig. 1, are miners of live biomass. Thus, on the gather–miner spectrum, the opposite of parasites are

croppers, while on the live–dead spectrum, the opposite of parasites are saprophages. Parasites are not obligate killers, although some groups are such as insect parasitoids (Godfray 1994). Macro-endoparasites that consume a significant proportion of their host's biomass, with up to 39% of the soft tissue body mass being accounted for by trematodes in one host snail species (Hechinger *et al.* 2009), have a direct effect on their hosts through biomass extraction. In addition, such parasites usually have an indirect effect through increasing their host's senescence rate. Microparasites (fungi, protozoans, bacteria and viruses) are much less likely to have direct effects on the biomass of their hosts, but those that are pathogenic may have considerable indirect effects on senescence. Some microparasites have evolved to become symbiotic, example being flagellate protozoan parasites of the termite gut that help termites digest cellulose.

An important issue relating to host–parasite dynamics is the question of average parasite load at the population level vs. actual parasite load in individual hosts. This problem can and has been addressed in several ways, bearing in mind that a curvilinear, but monotonically increasing relationship between host densities and parasite abundance is likely to occur, as has been demonstrated in the context of gastrointestinal strongylid nematodes across 19 mammalian host species (Arneberg *et al.* 1998). When parasite infections are widespread among all individuals in a host population, then a simple approach to modelling parasite population abundance is to assume that all dynamics can be characterised in terms of an average infection intensity u in the host population. In this case, if the host and parasite populations have live biomass abundances x_1 and x_2 , respectively, then the proportion of

host biomass infected is $P_{\text{inf}} = \frac{x_2}{ux_1}$.

This approach of using an average intensity of parasitism across all hosts is likely to be more applicable to macroparasite infections, such as those by nematodes, cestodes and trematodes, than bacterial or viral infections where individuals are regarded as either infected or not infected. Moreover, in the latter case, dose of infection may be a factor in determining whether an individual host succumbs to an associated disease (Claridge *et al.* 2002). The use of average intensities of infection may also be applicable to microscopic parasites such as coccidia found in the gastrointestinal tracts of almost all vertebrate ruminants or even malarial plasmodia, where abundance in hosts (mosquito vectors in this case – see Dawes *et al.* 2009) is important in determining the death rate. Additional complexities arise, such as parasites increasing the vulnerability of their hosts to predators (Hudson *et al.* 1992); but we leave such complexities to future studies.

Parasite death rates themselves occur both independent of host deaths – that is, when the parasites die within the host or during the process of transmission from one host to another – and with the death of host individuals (Fig. 2). In some cases, parasites may cause disease but then jump from one host to another before the death of the host. This is particularly true of ectoparasites, such as ticks, that vector various diseases including Rocky Mountain spotted fever and Lyme disease in humans. In this case, however, three rather than two species are involved.

In our BTW model, the process of transmission itself is not explicitly considered, but assumed to occur at finer temporal and possibly spatial scales than the spatio-temporal scale of the BTW paradigm. To obtain this finer level of resolution requires that we divide the population further into susceptible and infected individuals with transmission assumed to follow either a mass-action principle, a frequency-dependent transmission principle, or, more generally, a saturating rate for which mass-action and frequency-dependent transmission are special cases (McCallum *et al.* 2001).

With these various points in mind, one approach is to assume the existence of a background host mortality rate that is enhanced by the presence of the parasites x_2 to yield the expression:

$$m_1 = \frac{(\mu_1 + \mu_{12}x_2)v_1^s}{v_1^s - v_1}, \quad (10)$$

for constants $\mu_1 > 0$ and $\mu_{12} \geq 0$. One might also assume that the parasite has a background mortality rate as the parasite is cleared from hosts by mechanisms that relate to the host immune system and parasite senescence. Additionally, in many cases, parasites might die along with hosts at a rate proportional to the parasite-induced host death rate, where this

factor of proportionality depends on the ratio $\frac{x_2}{x_1}$. Under these assumptions, it follows that

$$\begin{aligned} m_2x_2 &= \frac{\mu_2v_1^s}{v_1^s - v_1}x_2 + \mu_{21}\frac{x_2}{x_1}m_1x_1 \\ &= ((\mu_2 + \mu_{21}\mu_1) + \mu_{21}\mu_{12}x_2)\frac{v_1^sx_2}{v_1^s - v_1}, \end{aligned}$$

where we note that μ_{21} has a value that takes account of the factor $1/u$ mentioned above in calculating the proportion p_{inf} discussed above.

Viral and, in most cases, bacterial pathogens need to be treated differently than parasites whose primary effect on the host is the resources extracted from the host population. In the case of microbial pathogens that either kill their hosts or go on to be defeated by the host's immune system, the first-order effect is the increase in the mortality rate of hosts rather than a decrease in the host biomass. In this case, the pathogen's abundance x_2 may best be measured as the number of pathogens per unit biomass of host (or per unit volume of the host's blood, phloem tissue or cytoplasm). As discussed in the next section, for microparasites such as *B. anthracis*, the infectious agent are spores that enter the environment soon after the death of a host. In this case, all other factors equal, the rate of growth of the number of *B. anthracis* spores in the environment will be proportional to the

pathogen-induced mortality $\frac{\mu_{12}x_2v_1^s}{v_1^s - v_1}$. Thus, it follows that

$$\phi_2 = \frac{a_2(\mu_1 + \mu_{12}x_2)v_1^s}{v_1^s - v_1}, \quad (11)$$

where $a_2 > 0$, the rate at which a diseased carcass contributes spores to the environment, may itself depend on many other factors such as the presence of scavengers to open the carcass. Moreover, the background mortality rate m_2 of spores x_2 in the environment may decrease with increasing density x_2 of spores, if spores at infectious sites are degraded at a greater per-capita rate when present at high than at low densities. In this case, to first order, we might assume $m_2 = \mu_2 + \mu_{22}x_2$. If we now ignore the inertial component [by forcing $v(t) \equiv 0$ for all t], then the host-pathogen equations that arise are:

$$\begin{aligned} \frac{dx_1}{dt} &= \left(\frac{k_1 a_1 y_{01}}{b_1 \left(1 + \left(\frac{x_1}{c_1} \right)^{\gamma_1} \right) + y_{01}} - \alpha_1 - (\mu_1 + \mu_{12}x_2) \right) x_1, \\ \frac{dx_2}{dt} &= (a_2 \mu_{12} x_1 - \alpha_2 - \mu_2 - \mu_{22} x_2) x_2, \end{aligned} \quad (12)$$

which provides a novel alternative formulation to numerous existing approaches (e.g. Murdoch *et al.* 2003).

ANTHRAX IN ETOSHA

In the development of a model that can address questions relating to both endemic and outbreak dynamics of pathogens in food webs, with specific application to an anthrax-centred food web in ENP, Namibia, we draw upon eqn 2, as well as equations developed in Appendix S3 modelling the interaction of a consumer that is both a cropper and scavenger in a food web. *Bacillus anthracis*, the agent responsible for anthrax, is a Gram-positive bacterium that persists in a sporulated life stage in patches of suitable soil – referred to here as locally infectious zones (LIZs) – where its ability to infect herbivores decays over time (Hugh-Jones & Blackburn 2009). During the ENP wet season, individual zebra, springbok, wildebeest and oryx ingest lethal doses of *B. anthracis* spores, contract the anthrax disease and die (Lindeque & Turnbull 1994). On the other hand, individual elephants range widely and are more likely to die of anthrax during the dry season. Diseased carcasses year round are open by various carcassivores (several kinds of vultures) and carnivores (hyenas and lions), but especially black-backed jackals (*Canis mesomelas*) that are both carcassivores and opportunistic croppers of small mammals (rodents, lagomorphs, newborn springbok), birds, reptiles, invertebrates (e.g. dung beetles), and even seeds and fruit (Kaunda & Skinner 2003).

The area of ENP around Okaukuejo is semi-arid, where outbreaks of anthrax predictably occur each year (the mean annual rainfall at Okaukuejo was 384 mm from 1934–2007 – see Turner *et al.* 2010) and consequently ecologically less complex than anthrax in wetter savanna systems such as Zimbabwe, where outbreaks are less predictable and can be highly disruptive to the ecosystem (Hugh-Jones & Blackburn 2009). As the dominant anthrax-mediated transformation process of live-to-dead animal biomass each year around Okaukuejo occurs in the zebra (*Equus quagga*) and elephant populations (*Loxodonta africana*), a combined population of these two species provides the focal live resource (x_1) and dead (y_1) resource compartments in a model of anthrax in ENP (Fig. 4; Appendix S4), although anthrax does infect many other species in ENP.

Bacillus anthracis spores (abundance x_2) are distributed within LIZs across a several 1000 km² grazing plain in ENP. A simple spatially aggregated BTW model of anthrax dynamics can be developed, as detailed in Appendix S4, using eqn 12 to model the *B. anthracis* spore–host (elephant/zebra) interaction. By simply varying the growth parameter a_2 in eqn 12, this model nicely replicates both endemic and epidemic disease dynamics (Fig. 5). Further in the latter case, the outbreaks do not cause the host population to collapse to exceptionally low levels, a situation typical of dynamics predicated by Lotka–Volterra type models. More specifically, in panel (a) (Fig. 5), the population converges to an endemic phase that it similarly converges to in panel (b) when the density-dependent mortality factor μ_{22} is removed (i.e. set to zero). As the factor a_2 controlling the number of spores entering the environment per unit biomass of infected carcass is increased from $a_2 = 0.5$ (panel b) to $a_2 = 0.8$ (panel c), regular outbreaks that appear slightly dampened over time occur every 3 years, although the severity dramatically increases and frequency decreases to once every 7–8 years when the spore production rate increases by 50% to $a_2 = 1.2$. Thus, the relatively simple two-dimensional model represented by eqn 12 is easily able to capture the range of observed endemicity of anthrax in ENP to the subdecadal and decadal outbreaks in places such as Kruger National Park in South Africa and wildland areas in Zimbabwe (Hugh-Jones & Blackburn 2009).

An additional compartment in the model is live jackal biomass at abundance x_3 , as jackals scavenge both diseased carcasses and those arising from lion and hyena kills. Jackals also scavenge other carcass species and crop a variety of small animals that we structurally represent through live (x_4) and dead (y_4) resource biomass compartments in the model (Fig. 4; Appendix S4). To keep the model simple, lions (*Panthera leo*) and spotted hyena (*Crocuta crocuta*) that prey upon the various ungulates are included in the environment as donor-controlled cropper–scavenger extraction processes (Appendix S4).

If we now include inertial variables v_1 , v_3 and v_4 (i.e. for all the live biomass compartments except anthrax x_2), then the resulting BTW models contains nine dynamic equations, as detailed in Appendix S4. This model, in lumping together trophic functional groups such as ‘elephants and zebra’ and ‘other small mammals’, and in ignoring spatial and seasonal structure, is obviously crude. Constructing a model that splits apart these functional groups, and includes migratory seasonal movements and other spatio-temporal structures, is a task worthy of several PhD studies. Thus, the analysis here is only meant to illustrate how a model based on BTW principles can be assembled rather than reflect the current state of biological knowledge of the system under consideration. To this end, the parameters derived in Appendix S5 are crude ballpark estimates that allow the model to be used as a tool for suggesting research priorities and directions rather than answering well-posed research questions. This is appropriate given that current abundance estimates are rather crude and, in particular, jackal abundances are not known within a factor of two of real levels, while the distribution of anthrax spores across the landscape is unknown.

For the set of parameter values given in Table S2 (Appendix S5), the model presented in Appendix S4 predicts the equilibrium values (which can be interpreted as long-term averages) $(\hat{x}_1, \hat{y}_1, \hat{x}_2, \hat{x}_3, \hat{y}_3, \hat{x}_4)' = (7437, 70.0, 31.2, 2351, 3.49, 57.6)$ (units are metric tons except for x_2 , which needs further studies to ground the arbitrary units used here). An important approach to exploring models with uncertain parameter values is to carry out some kind of sensitivity analysis (Saltelli *et al* 2000) as a way to use the model to inform ecologists what parameters in the model are most critical to characterising variables of interest. For example, we see from panel (a) in Fig. 6 that halving the jackal maximum extraction rate parameter a_4 results in the reduction of the predicted equilibrium by 1/3. Also if we ask the question what will happen if jackal were to only scavenge carcasses (i.e. setting $wf=0$), then the jackal population falls by three quarters when $a_4 = 0.16$ or collapses completely when $a_4 = 0.08$.

The jackal population in panel (a) (Fig. 6) is modelled under endemic anthrax conditions. If the system is perturbed into outbreak mode by setting $\mu_{22} = 0$, then under conditions where the jackal population only scavenge, during an outbreak the population may nearly double and then rapidly decline at the end of an outbreak (panel b in Fig. 6). The reason why the decline is rapid is apparent from the graph of v_4 in panel (b) (Fig. 6): at the end of an outbreak, once the excess carcasses have all been consumed, the elevated jackal population begins to starve, as evidenced by the rapid rise in the value of v_4 , and the effects of accelerated senescence due to the associated deficit stress now set in.

CONCLUSION

Consumer–resource models can be traced back to the work of Lotka and Volterra in the mid 1920s, with much of the current work on this topic (Murdoch *et al.* 2003; Turchin 2003) rooted in Lotka and Volterra's original two-dimensional formulation. The Lotka–Volterra model with its extensions to include various types of nonlinear predator–response-to-prey–density functions has been applied to quite different kinds of consumer–resource processes, including plant–herbivore, prey–predator and host–parasite interactions; but also with a notable lack of focus on scavenger–carrion interactions (Nuria & Fotuna 2006). The BTW

presented here deals with all these various consumer–resource interactions, but its approach to growth as a function of biomass extraction leads more naturally than Lotka–Volterra-like approaches to distinguishing among different kinds of consumer through incorporation of biomass diversion, scavenging, parasitism and consumer-harassment processes. The price we pay for this refinement is that the general consumer–resource formulation is now four to six rather than two dynamically linked equations, although, as we have seen, the dimension can be reduced to two when focusing on special cases. The gain though is considerable in that our view of the kinds of resource–consumer interactions that can occur (Fig. 1; Appendix S1) is now considerably enlarged. Along with this enlargement comes a whole new set of ecological and evolutionary questions that can be addressed in a quantitatively rigorous framework using methodologies, such as evolutionarily stable strategy theory, that have proved their worth when used in conjunction with Lotka–Volterra type formulations of population interactions (Cressman & Garay 2003). Among these questions are how might we expect the dynamics of the feeding deficit stress variables v_i to reflect the life history dichotomy of miners vs. gatherers. This is an issue that relates to time constants associated with rates of feeding deficit stress accumulation and accommodation, as well as time-to-death under complete starvation and how life histories evolve to deal with variable interresource encounter periods for gatherers. Moreover, for many species, metabolic rates may adaptively decrease when food intake rates do not meet normal metabolic needs [i.e.

periods where v_i increases because $\varphi_i - \alpha_i$, so that $\frac{d\alpha_i}{dv} < 0$ is an adaptive strategy], as is the case of animals that go into hibernation during seasonal resource dearths.

Although the formulation, through the inclusion of the feeding deficit stress variables v_i , deals with the problem that population processes need to include inertial effects, including the well-studied maternal effect (Inchausti & Ginzburg 1998), the approach ultimately needs to be generalised to take into account two forms of heterogeneity that apply to all paradigms and not just BTW. The first form is spatial heterogeneity and requires elaboration of how particular population processes vary over space and how animals move to mitigate gradients in these processes that naturally arise, such as moving to places where feeding rates can be higher or where they are less likely to succumb to being extracted by predators. The second form is individual variation due to both genetic and random processes, in which two individuals in the same place are subject to different rates of food acquisitions, different rates of parasitism and different risks of being consumed by other species. This results in a phenomenon known as buffering (Revilla & Wiegand 2008).

One of the strengths of BTW is that it provides a unified framework in which the approach to modelling populations to first order is independent of the trophic level. Another strength of BTW is that it deals with scavengers just as easily as it does with croppers or parasites. Thus, it has application to a much wider array of food web systems than current methods generally have including systems of importance to disease management or conservation biology. A case in point is evaluating how many dead trees are needed to sustain the white-backed woodpecker that relies on insect larvae that use dead trees as a food source during winter (Gjerde *et al.* 2005).

The BTW presented here is an outgrowth of the metaphysiological approach to modelling trophic interactions (Getz 1991, 1993). This approach, by taking a biomass flow rather than a birth-death-migration viewpoint of growth, formulates growth in terms of extraction and senescent processes, rather than directly in terms of the state variables themselves. This allows the formulation of equations to be unified across trophic levels, as evidenced by the general model (Box 1). In addition, the structure of the equations is rather transparent and, hence, easily implemented for particular systems, as illustrated in our derivation of the nine-variable anthrax BTW model in Appendix S4.

In terms of food web theory itself, by extending populations to account separately for both live and dead biomass, new topological relationships emerge and the strength of these relationships, as mediated by scavengers, parasites, disease and senescence processes, can now be included. This topological refinement will affect such characterising measures as L , the number of feeding relationships in webs, which has been used in a number of food web studies (e.g. Williams & Martinez 2000; Romanuk *et al.* 2009). As Lazzaro *et al.* (2009) recently pointed out: ‘The structure and dynamics of prey populations are shaped by the foraging behaviours of their predators. Yet, there is still little documentation on how distinct predator foraging types control biodiversity, food web architecture and ecosystem functioning’. This statement was made in the context of foraging strategies *per se* (e.g. visual vs. filter feeders) rather than in the context of biomass type (*viz.* live vs. dead). The statement applies equally well to the BTW formulation, which places live and dead material on an explicit co-footing. Similar considerations arise in the context of adaptive foraging in food webs with flexible topology (Křivan & Schmitz 2003), particularly in the context of adaptive scavenging. The BTW formulation provides a paradigm for exploring these various questions more thoroughly and systematically than before. Furthermore, once we move beyond homogeneous to spatially structured webs, the need for a miner–gatherer dichotomy takes on additional force when the ecological aspects of movement (Nathan *et al.* 2008) are introduced.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

I thank Steve Bellan, Paul Cross, Lev Ginzburg, Matt Plucinski, Mary Power, Norman Owen-Smith and Wendy Turner for comments, and especially Peter Baxter for extensive comments and various references. This research was supported by NIH Grant GM083863 and the Stellenbosch Institute for Advanced Study in South Africa.

REFERENCES

- Abrams PA. Resource productivity–consumer species diversity: simple models of competition in spatially heterogeneous environments. *Ecology*. 1988; 69:1418–1433.
- Abrams PA, Ginzburg LR. The nature of predation: prey dependent, ratio dependent or neither. *Trends Ecol. Evol.* 2000; 15:337–341. [PubMed: 10884706]
- Ackland GJ, Gallagher ID. Stabilization of large generalized Lotka–Volterra foodwebs by evolutionary feedback. *Phys. Rev. Lett.* 2004; 93:158701. [PubMed: 15524949]
- Allen AP, Gillooly JF. Towards an integration of ecological stoichiometry and the metabolic theory of ecology to better understand nutrient cycling. *Ecol. Lett.* 2009; 12:369–384. [PubMed: 19379132]
- Arneberg P, Skorpington A, Grenfell B, Read AF. Host densities as determinants of abundance in parasite communities. *Proc. R. Soc. Lond. B.* 1998; 265:1283–1289.
- Arditi R, Michalski J. Food web structure at equilibrium and far from it: is it the same? *Proc. R. Soc. Biol. Sci.* 1995; 259:217–222.
- Bascompte J. Disentangling the web of life. *Science*. 2009; 325:416–419. [PubMed: 19628856]
- Bascompte J, Melián CJ. Simple trophic modules for complex food webs. *Ecology*. 2005; 86:2868–2873.
- Brose U. Improving nature conservancy strategies by ecological network theory. *Basic Appl. Ecol.* 2010; 11:1–5.
- Carpenter SR, Kitchell JF, Hodgson JR. Cascading trophic interactions and lake productivity. *BioScience*. 1985; 35:634–639.
- Claridge JA, Sawyer RG, Schulman AM, McLemore EC, Young JS. Blood transfusions correlate with infections in trauma patients in a dose-dependent manner. *Am. Surg.* 2002; 68:566–572. [PubMed: 12132734]

- Creel S, Creel NM. Communal hunting and pack size in African wild dogs, *Lycaon pictus*. *Anim. Behav.* 1995; 50:1325–1339.
- Creel S, Winnie JA, Christianson D. Glucocorticoid stress hormones and the effect of predation risk on elk reproduction. *Proc. Nat. Acad. Sci.* 2009; 106:12388–12393. [PubMed: 19617549]
- Cressman R, Garay J. Evolutionary stability in Lotka–Volterra systems. *J. Theor. Biol.* 2003; 222:233–245. [PubMed: 12727458]
- Dawes E, Churcher T, Zhuang S, Sinden R, Basañez M-G. Anopheles mortality is both age- and Plasmodium-density dependent: implications for malaria transmission. *Malar. J.* 2009; 8:228. [PubMed: 19822012]
- Finlay JC, Khandwala S, Power ME. Spatial scales of carbon flow in a river food web. *Ecology.* 2002; 83:1845–1859.
- Gandar MV. The dynamics and trophic ecology of grasshoppers (acridoidea) in a south-african savanna – trophic ecology of grasshoppers in south-african savanna. *Oecologia.* 1982; 54:370–378.
- Getz WM. Population dynamics: a resource per capita approach. *J. Theor. Biol.* 1984; 108:623–644.
- Getz WM. A unified approach to multispecies modeling. *Nat. Resour. Model.* 1991; 5:393–421.
- Getz WM. Metaphysiological and evolutionary dynamics of populations exploiting constant and interactive resources: r-K selection revisited. *Evol. Ecol.* 1993; 7:287–305.
- Getz WM. A hypothesis regarding the abruptness of density dependence and the growth rate of populations. *Ecology.* 1996; 77:2014–2026.
- Getz WM. Disease and the dynamics of foodwebs. *PLoS Biol.* 2009; 7(9):e1000209. [PubMed: 19787027]
- Getz WM, Westerhoff HV, Hofmeyr JHS, Snoep JL. Control analysis of trophic chains. *Ecol. Model.* 2003; 168:153–171.
- Ginzburg, L.; Colyvan, M. *Ecological Orbits: How Planets Move and Populations Grow.* Oxford University Press; New York: 2004. p. 166
- Ginzburg LR. Assuming reproduction to be a function of consumption raises doubts about some population predator-prey models. *J. Anim. Ecol.* 1998; 67:325–327.
- Gjerde I, Saetersdal M, Nilsen T. Abundance of two threatened woodpecker species in relation to the proportion of spruce plantations in native pine forests of western Norway. *Biodivers. Conserv.* 2005; 14:377–393.
- Godfray, HCJ. *Parasitoids: Behavioural and Evolutionary Ecology.* Princeton University Press; Princeton, NJ: 1994.
- Hechinger RF, Lafferty KD, Mancini FT III, Warner RR, Kuris AM. How large is the hand in the puppet? Ecological and evolutionary factors affecting on body mass of 15 trematode parasitic castrators in their snail host. *Evol. Ecol.* 2009; 23:651–667.
- Hopcraft JGC, Sinclair ARE, Packer C. Planning for success: Serengeti lions seek prey accessibility rather than abundance. *J. Anim. Ecol.* 2006; 74:559–566.
- Hudson PJ, Newborn D, Dobson AP. Regulation and stability of a free-living host-parasite system: trichostrongylus tenuis in red grouse. I. Monitoring and parasite reduction experiments. *J. Anim. Ecol.* 1992; 61:477–486.
- Hugh-Jones M, Blackburn J. The ecology of *Bacillus anthracis*. *Mol. Aspects. Med.* 2009; 30:356–367. [PubMed: 19720074]
- Inchausti P, Ginzburg LR. Small mammal cycles in northern Europe: pattern and evidence for a maternal effect hypothesis. *J. Anim. Ecol.* 1998; 67:180–194.
- Jordán F. Is the role of trophic control larger in a stressed ecosystem? *Community Ecol.* 2000; 1:139–146.
- Jørgensen SE, Fath B. Examination of ecological networks. *Ecol. Model.* 2006; 196:283–288.
- Karban R. Plant behavior and communication. *Ecol. Lett.* 2008; 11:727–739. [PubMed: 18400016]
- Křiván V, Schmitz OJ. Adaptive foraging and flexible food web topology. *Evol. Ecol. Res.* 2003; 5:623–652.
- Kaunda SKK, Skinner JD. Black-backed jackal diet at Mokolodi Nature Reserve, Botswana. *Afr. J. Ecol.* 2003; 41:39–46.

- Lafferty KD, Allesina S, Arim M, Briggs CJ, De Leo G, Dobson AP, et al. Parasites in food webs: the ultimate missing links. *Ecol. Lett.* 2008; 11:533–546. [PubMed: 18462196]
- Larsen TH, Lopera A, Forsyth A. Extreme trophic and habitat specialization by Peruvian dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). *Coleopt. Bull.* 2006; 60:315–324.
- Lazzaro X, Lacroix G, Gauzens B, Gignoux J, Legendre S. Predator foraging behaviour drives food-web topological structure. *J. Anim. Ecol.* 2009; 78:1307–1317. [PubMed: 19619219]
- Lindeque PM, Turnbull PCB. Ecology and epidemiology of anthrax in the Etosha National Park, Namibia. *Onderstepoort. J. Vet. Res.* 1994; 61:71–83. [PubMed: 7898901]
- Marcogliese DJ, Cone DK. Food webs: a plea for parasites. *Trends Ecol. Evol.* 1997; 12:320–325. [PubMed: 21238094]
- Margalida A, Bertran J, Boudet J, Heredia R. Hatching asynchrony, sibling aggression and cannibalism in the Bearded Vulture *Gypaetus barbatus*. *Ibis.* 2004; 146:386–393.
- Marker LL, Muntifering JR, Dickman AJ, Mills MGL, Macdonald DW. Quantifying prey preferences of free-ranging Namibian cheetahs. *S. Afr. J. Wildl. Res.* 2003; 33:43–53.
- McCallum H, Barlow N, Hone J. How should pathogen transmission be modelled? *Trends Ecol. Evol.* 2001; 16:295–300. [PubMed: 11369107]
- McCue MD. Starvation physiology: reviewing the different strategies animals use to survive a common challenge. *Comp. Biochem. Physiol. A.* 2010; 156:1–18.
- Mckillup SC, Mckillup RV. The feeding behaviour of *Thalamita crenata* (Portunidae, Decapoda), a cannibalistic marine scavenger. *Mar. Freshw. Behav. Physiol.* 1996; 28:255–267.
- Moloney CL, Jarre A, Arancibia H, Bozec Y-M, Neira S, Roux J-P, et al. Comparing the Benguela and Humboldt marine upwelling ecosystems with indicators derived from inter-calibrated models. *ICES J. Mar. Sci.* 2005; 62:493–502.
- Moore JC, Coleman EL, de Ruiter DC, Dong PC, Hastings QA, Johnson NC, et al. Detritus, trophic dynamics and biodiversity. *Ecol. Lett.* 2004; 7:584–600.
- Murdoch, WW.; Briggs, CJ.; Nisbet, RM. *Consumer–Resource Dynamics*. Princeton University Press; Princeton, NJ: 2003.
- Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, et al. A movement ecology paradigm for unifying organismal movement research. *Proc. Natl Acad. Sci. USA.* 2008; 105:19052–19059. [PubMed: 19060196]
- Neutel A-M, Heesterbeek JAP, de Ruiter PC. Stability in real food webs: weak links in long loops. *Science.* 2002; 296:1120–1123. [PubMed: 12004131]
- Nuria S, Fotuna MA. The nested structure of a scavenger community. *Proc. R. Soc. B.* 2006; 274:1101–1108.
- Pimm, S. *Food Webs*. Chapman and Hall; London: 1982.
- Polis GA, Anderson WB, Holt RD. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annu. Rev. Ecol. Syst.* 1997; 28:289–316.
- Power ME, Dietrich WE. Food webs in river networks. *Ecol. Res.* 2002; 17:451–471.
- Revilla E, Wiegand T. Individual movement behavior, matrix heterogeneity, and the dynamics of spatially structured populations. *PNAS.* 2008; 105:19120–19125. [PubMed: 19060193]
- Ripple WJ, Beschta RL. Restoring Yellowstones aspen with wolves. *Biol. Conserv.* 2007; 138:514–519.
- Robbins RL, McCreery EK. Dominant female cannibalism in the African wild dog. *Afr. J. Ecol.* 2001; 38:91–92.
- Romanuk TN, Zhou Y, Borse U, Berlow E, Williams RJ, Martinez ND. Predicting invasion success in complex ecological networks. *Proc. R. Soc. B.* 2009; 364:1743–1754.
- Saltelli, A.; Chan, K.; Scott, EM. *Sensitivity Analysis*. John Wiley; West Sussex, UK: 2000.
- Sandberg J, Elmgren R, Wulff F. Carbon flows in Baltic Sea food webs — a re-evaluation using a mass balance approach. *J. Mar. Syst.* 2000; 25:249–260.
- Schoombie SW, Getz WM. Evolutionary stable density-dependent strategies in a generalized Beverton and Holt model. *Theor. Popul. Biol.* 1998; 53:216–235. [PubMed: 9682025]
- Selva N, Fortuna MA. The nested structure of a scavenger community. *Proc. R. Soc. B.* 2007; 274:1101–1108.

- Skarpe C, Aarrestad PA, Andreassen HP, Dhillion SS, Dimakatso T, du Toit JT, et al. The return of the giants: ecological effects of an increasing elephant population. *Ambio*. 2004; 33:276–282. [PubMed: 15387059]
- Smith C, Reay P. Cannibalism in teleost fish. *Rev. Fish Biol. Fish.* 1991; 1:41–64.
- Szwabiński J, Pekalski A, Bena I, Droz M. Food web model with detritus path. *Phys. A*. 2010; 389:2545–2556.
- Turchin, P. *Complex Population Dynamics*. Princeton University Press; Princeton, NJ: 2003. p. 450
- Turner WC, Fox MT, Getz WM. Seasonality and demographic patterns influencing gastrointestinal parasitism of ungulates of Etosha National Park. *J. Wildl. Dis.* 2010; 46:1108–1119. [PubMed: 20966262]
- Ulanowicz RE. Quantitative methods for ecological network analysis. *Comput. Biol. Chem.* 2004; 28:321–339. [PubMed: 15556474]
- Williams RJ, Martinez ND. Simple rules yield complex food webs. *Nature*. 2000; 404:180–183. [PubMed: 10724169]
- Wilmers CC, Crabtree RL, Smith DW, Murphy KM, Varley JD, Getz WM. Intra-trophic subsidies: gray wolf foraging and resource flow to scavengers in Yellowstone National Park. *J. Anim. Ecol.* 2003; 72:909–916.
- Wilmers CC, Getz WM. Simulating the effects of wolf-elk population dynamics on resource flow to scavengers. *Ecol. Model.* 2005; 177:193–208.
- Winemiller, KO.; Polis, GA. Food webs: what they can tell us about the world. In: Polis, GA.; Winemiller, KO., editors. *Food Webs: Integration of Patterns and Dynamics*. Chapman and Hall; New York: 1996. p. 1-22.

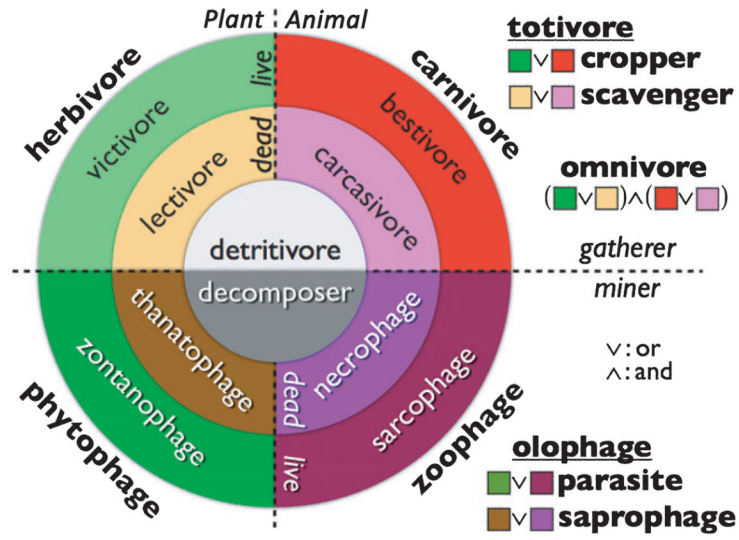


Figure 1. Consumer categories (see Appendix S1 and Table S1 for more details).

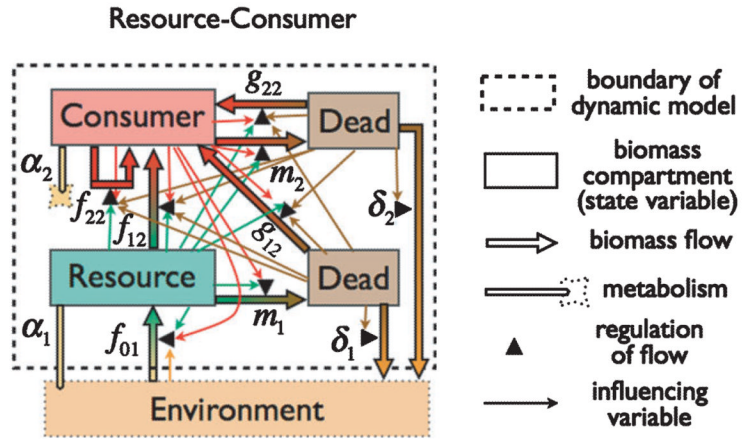


Figure 2. A biomass flow diagram of a general resource–consumer system modelled by eqn 6 in which the consumer, but not the resource population, may be subject to cannibalism. For simplicity, the diversion functions θ_{12} and θ_{22} are not illustrated.

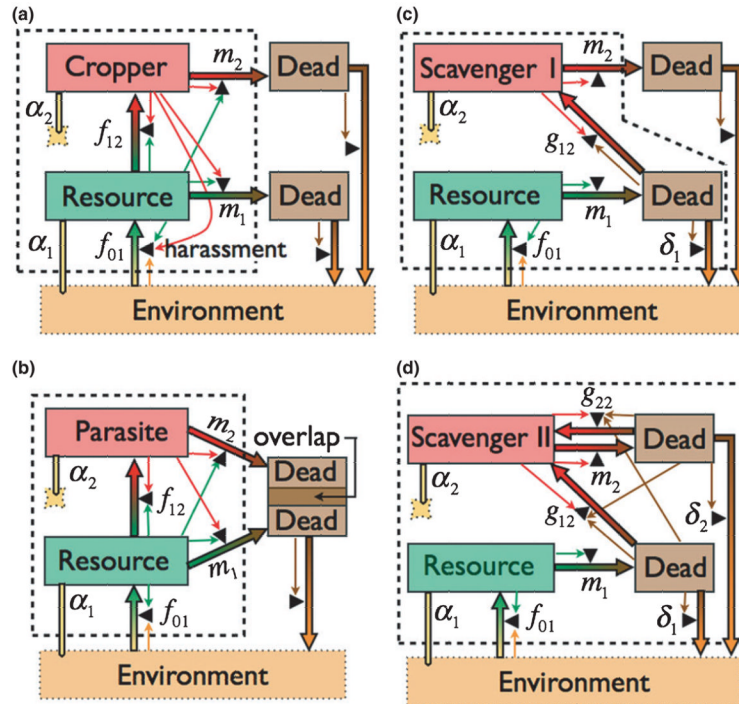


Figure 3. Specific cases of the biomass flow diagram illustrated in Fig. 2 (same legend applies), with flow and influence structures detailed in Table 2, for (a) a cropper, with the link that corresponds to the influence of harassment specifically labelled; (b) a parasite, with the overlapping death compartments indicated; (c) scavengers that feed only on dead resources and (d) scavengers that feed both on dead resources and cannibalistically on their own dead biomass.

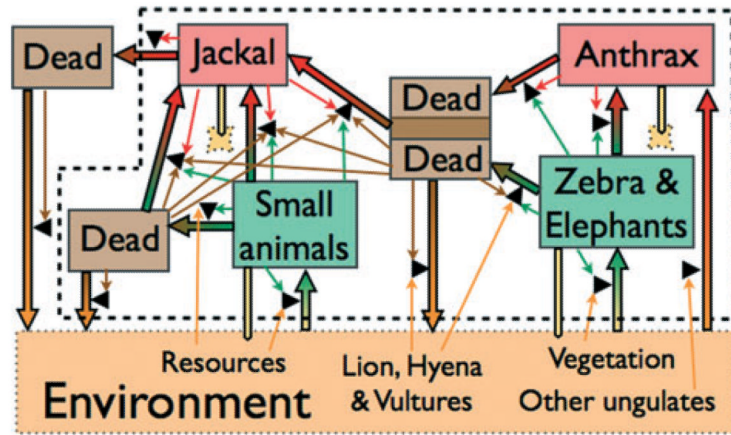


Figure 4. A simplified anthrax-centred biomass transformation web in Etosha National Park, Namibia. See Appendix S4 for equations modelling this system.

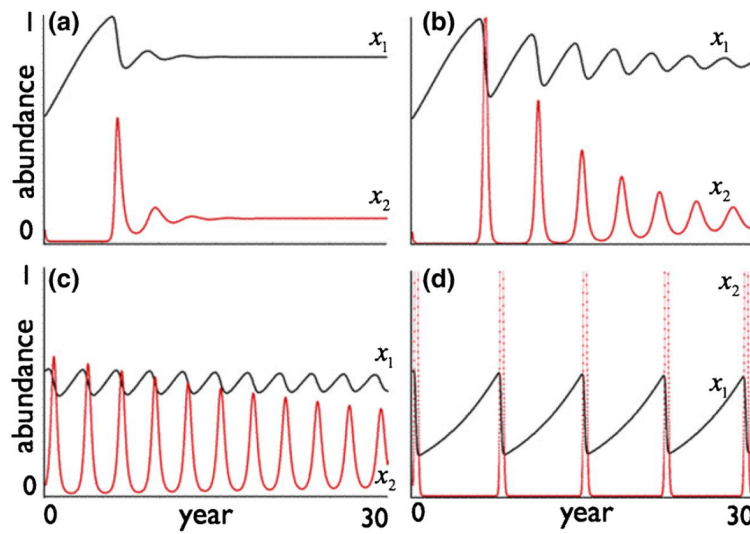


Figure 5.

The zebra/elephant biomass abundance $x_1(t)$ (Scale 1 = 18 000 metric tons) and anthrax spore abundance $x_2(t)$ (Scale 1 = 200 unspecified units) solutions to eqn 12 are plotted over a 30-year period for the parameter values given in Table S2 (Appendix S5), except as noted: (a) $a_2 = 0.5$ and $\mu_{22} = 0.0001$, (b) $a_2 = 0.5$ and $\mu_{22} = 0$, (c) $a_2 = 0.8$ and $\mu_{22} = 0$, and (d) $a_2 = 1.2$ and $\mu_{22} = 0$.

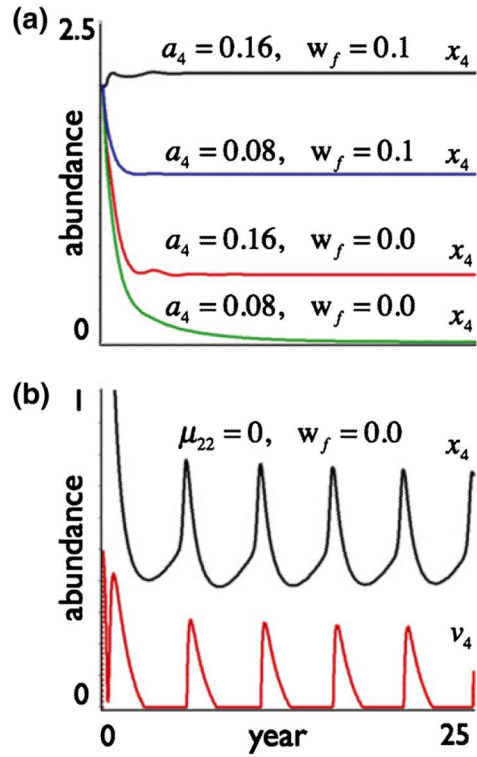


Figure 6.

Jackal biomass abundance $x_4(t)$ (Scale 1 = 20 metric tons) solutions to eqn 12 are plotted over a 25-year period for the parameter values given in Table S2 (Appendix S5), except as labelled in (a) for the four illustrated cases. The same applies to (b), except here the deficit stress variable v_4 (Scale 1 = 10^{-1}) is also plotted for the labelled case.

Table 1

A summary of functions and description of parameters appearing in the model

Symbol	Description	Equations
t	Time: the independent variable	
State variables		
x_i	Live biomass of population i	Equation 2
y_i	Dead biomass of population i	Equation 2
v_i (v)	Deficit stress in population i	Equation 2 (eqn 3)
z, x	Live consumer biomass x feeding on resource input z	Equations 3 and 4
Processes		
$\tilde{F}(t)=F(\mathbf{x}(t), \mathbf{y}(t), t)$	Representing F purely as a function of time for all functions below	
f_{ij} (f)	Live i biomass extraction to j	Equations 1 and 2 (eqn 4)
g_{ij}	Dead i biomass extraction to j	Equations 1 and 2
θ_{ij} (θ)	Live i to dead j biomass diversion	Equations 1 and 2 (eqn 4)
K_{ij}^f and K_{ij}^g (κ)	Conversion of live and dead i , respectively, to j	Equation 1 (eqn 4)
ϕ_i (ϕ)	Per unit i biomass incorporation	Equations 1 and 11 (eqn 4)
α_i (α)	Per unit i metabolism	Equation 2 (eqn 3)
$m_i(\cdot)$ (m)	Per unit i senescence (mortality other than extraction)	Equations 2 and 10 (eqn 5)
δ_i	Per unit i dead biomass decay	Equation 2
V_i	Deficit stress accumulation rate	Equation 2
w_i	Deficit stress accommodation over time	Equation 2
$\mu(x)$	Density-dependent component of $m(x,v)$	Equation 5
Parameters		
a (a_1)	Maximum extraction rate in f (in f_{01})	Equation 4 (eqn 9)
a_2	Rate at which diseased carcass produces spores	Equation 11
b (b_1)	Resource density at which extract rate is $a/2$ in f (in f_{01})	Equation 4 (eqn 9)
c (c_1, c_{12})	Weakness = inverse-of-strength of competition in f (in f_{01})	Equation 4 (eqn 9)
γ	Abruptness in onset of competition in f	Equation 4
$v^s \left(v_1^s \right)$	Starvation level for deficit stress variable v (v_1)	Equation 5 (eqn 7)
μ_i, μ_{ij}	Parameters in μ and μ_i , $i = 0, 1, 2, j = 1, 2$	See text and Equation 10
$a_i, b_i, c_i, V_i^S, \gamma_i, w_f, w_g, h_{\text{index}}$	are specific to anthrax model in Appendix	Equation 21

Table 2

A selection of ideal consumer types as denned by the arguments of BTW functions f , g , θ and m , CN CR, DV, HR, PS and SC

Extracted live resource $f_{21}(\bullet, \bullet)$	Diverted live resource $\theta_{21}(\bullet, \bullet)$	Extracted dead resource $g_{21}(\bullet, \bullet)$	Cannibalism: Live $f_{22}(\bullet, \bullet)$	Diverted live cannibalism $\theta_{22}(\bullet, \bullet)$	Cannibalism: dead $g_{22}(\bullet, \bullet)$	Resource mortality $m_1(\bullet, \bullet)$	Consumer mortality $m_2(\bullet, \bullet)$	Selection of functional types
x_1, x_2	0	0	0	0	0	ϕ_1	ϕ_2	CR only (e.g. many frugivores)
x_1, x_2	0	0	0	0	0	$\phi_1, \mu_1(x_2) \frac{d\mu_1}{dx_2} > 0$	ϕ_2	CR-HR (e.g. leopards*)
x_1, x_2	0	0	0	0	0	$\phi_1, \mu_1(x_2) \frac{d\mu_1}{dx_2} > 0$	$\phi_2, m_1 \frac{dm_2}{dm_1} > 0$	PS (endo- and ectoparasites)
x_1, x_2, y_1	x_1, x_2, y_1	0	0	0	0	ϕ_1	ϕ_2	CR-DV (e.g. some grasshoppers [†])
x_1, x_2, y_1	x_1, x_2, y_1	0	0	0	0	$\phi_1, \mu_1(x_2)$	$\phi_2 \frac{d\mu_1}{dx_2} > 0$	CR-DV-HR (elephants [‡] , cheetahs [§])
0	0	x_2, y_1	0	0	0	ϕ_1	ϕ_2	SC Type I (necro-, saprophages and decomposers)
0	0	x_2, y_1, y_2	0	0	0	ϕ_1	ϕ_2	SC Type II (e.g. some vultures [¶])
x_1, x_2, y_1	x_1, x_2, y_1	x_1, x_2, y_1	0	0	0	$\phi_1, \mu_1(x_2) \frac{d\mu_1}{dx_2} > 0$	ϕ_2	HR-CR-SC Type I (e.g. lions ^{**})
x_1, x_2, y_1, y_2	x_1, x_2, y_1, y_2	x_1, x_2, y_1, y_2	0	0	0	ϕ_1	ϕ_2	CR-SC Type II (possibly wild dog ^{††})
x_1, x_2, y_1	x_1, x_2, y_1	0	x_1, x_2, y_1	x_1, x_2, y_1	0	ϕ_1	ϕ_2	CR-DV-CN (e.g. some fish ^{‡‡})
x_1, x_2, y_1, y_2	x_1, x_2, y_1, y_2	x_1, x_2, y_1, y_2	x_1, x_2, y_1, y_2	x_1, x_2, y_1, y_2	x_1, x_2, y_1, y_2	ϕ_1	ϕ_2	CR-DV-CN-SC (e.g. some crabs ^{§§})

CN, cannibal; CR, cropper; DV, diverter; HR, harasser; PS, parasite; SC, scavenger.

* Leopards generally are able to feed on their kills in trees to protect against diverting dead biomass to scavengers.

[†] Gandar 1982.

[‡] Skarpe *et al.* 2004.

[§] Marker *et al.* 2003.

[¶] Bearded vulture chicks will sometimes be fed their dead siblings, Mangalida *et al.* 2004.

** Hopcraft *et al.* 2006.

^{††} Scavenging is rare (Creel & Creel 1995) and cannibalism could be related to infanticide and hence more complex (Robbins & McCreery 2001).

^{‡‡} Smith & Reay 1991.

^{§§} McKillup & McKillup 1996.