IDEA AND PERSPECTIVE

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

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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.

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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 (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; Jörgensen & 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 seemlessly 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 ith ($i = 1, \ldots, n$) 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 ith 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 $v_i(t) = v_i^f$ are 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 $\mathbf{x}(t) = (x_1(t), \ldots, x_n(t))'$, $\mathbf{y}(t) = (y_0(t), y_1(t), \ldots, y_n(t))'$ and $\mathbf{v}(t) = (v_1(t), \ldots, v_n(t))'$ (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^f 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.
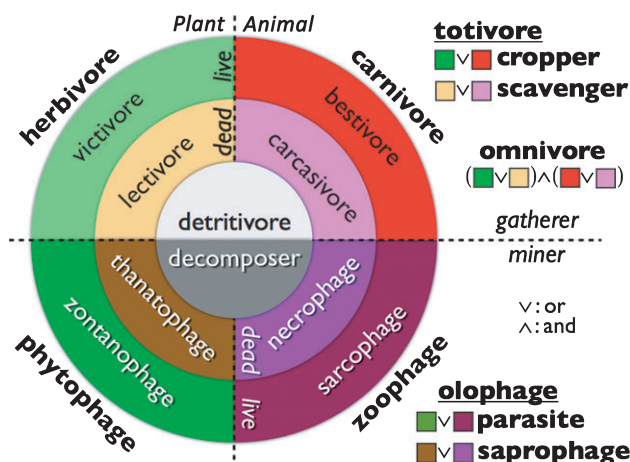
Figure 1 Consumer categories (see Appendix S1 and Table S1 for more details).

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		
$\bar{F}(t) = F(\mathbf{x}(t), \mathbf{y}(t), t)$	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)
κ_{ij}^f and κ_{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^f (v_1^f)	Starvation level for deficit stress variable v (in 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
$a_i, b_i, c_i, v_i^f, \gamma, w_f, w_g, b_{index}$ are specific to anthrax model in Appendix		Equation 21

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 $\kappa_{ji}^f(\mathbf{x}, \mathbf{y}, t)$ and $\kappa_{ji}^g(\mathbf{x}, \mathbf{y}, t)$, 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)

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

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 $m_i(\cdot, v_i) \to \infty$ as $v_i \to v_i^s$, 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),

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

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 $V_i(\tilde{\alpha}_i(t) - \tilde{\phi}_i(t), v_i(t))$ 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 $\log_{10}$ 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 $\tilde{V}(s) = \max\{0, (\tilde{\alpha} - \tilde{\phi}(t))\}$, it follows from eqn 2 (Box 1) that the equations for the variables $x(t)$ and $v(t)$ satisfy the closed system

$$\frac{dx}{dt} = (\phi(z, x) - m(x, v) - \alpha)x,$$
$$\frac{dv}{dt} = \max\{0, (\alpha - \tilde{\phi}(t))\} - \max\{0, (\alpha - \tilde{\phi}(t - t_s))\}. \tag{3}$$

Once $x(t)$ and $v(t)$ have been found, then the dead compartment can be generated from the 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 κ and the θ, respectively, that the form of biomass incorporation function $\varphi(z, x) = \kappa\theta f(z, x)z$ 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

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

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

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 $x \to 0$) 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

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

This form implies $m(x, v) \to \infty$ as $v \to v^s$, 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
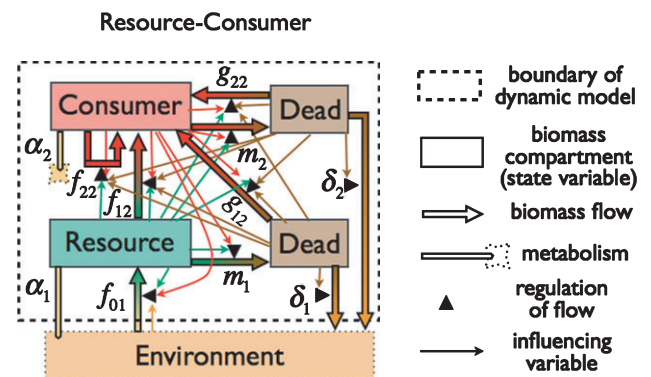
Resource-Consumer

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.

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 κ_r. 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):

$$\frac{dx_i}{dt} = (\phi_i - \alpha_i - m_i - f_{i2}x_2)x_i,$$
$$\frac{dy_i}{dt} = (\alpha_i + m_i)x_i + (1 - \theta_{i2})f_{i2}x_ix_2$$
$$\quad - (g_{2}x_2 + \delta_i)y_i, \quad i = 1, 2,$$
$$v_i(t) = \int_{-\infty}^{t} w_i(t-s)V_i(\tilde{\alpha}_i(s) - \tilde{\phi}_i(s), v_i(s))ds,$$

(6)

where

$$\phi_1 = \kappa_{01}^f f_{01}y_0, \quad \text{and}$$
$$\phi_2 = \kappa_{12}^f \theta_{12}f_{12}x_1 + \kappa_{22}^f \theta_{22}f_{22}x_2 + \kappa_{12}^g g_{12}y_1 + \kappa_{22}^g g_{22}y_2.$$

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 that 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 κ_{12}^f and κ_{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 $m_i(v_i) = \frac{\mu_i v_i^f}{v_i^f - v_i}$. 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:

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

(7)

where

$$\phi_1 = \kappa_1 \theta_1 f_{01}y_0 \quad \text{and} \quad \phi_2 = \kappa_2 f_{12}x_1.$$

(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

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

(9)

sufficesfor 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:

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

(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

Table 2 A selection of ideal consumer types as defined 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	$\phi_1, \mu_1(x_2) \frac{d\mu_1}{dc_2} > 0$	ϕ_2	CR-HR (e.g. leopards*)
x_1, x_2	0	0	0	0	0	$\phi_1, \mu_1(x_2) \frac{d\mu_1}{dc_2} > 0$	$\phi_2, m_1 \frac{dm_2}{dm_1} > 0$	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	$\phi_1, \mu_1(x_2)$	$\phi_2 \frac{d\mu_1}{dc_2} > 0$	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	x_2, y_1, y_2	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	$\phi_1, \mu_1(x_2) \frac{d\mu_1}{dc_2} > 0$	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	x_1, x_2, y_1, y_2	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, Margalida 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).
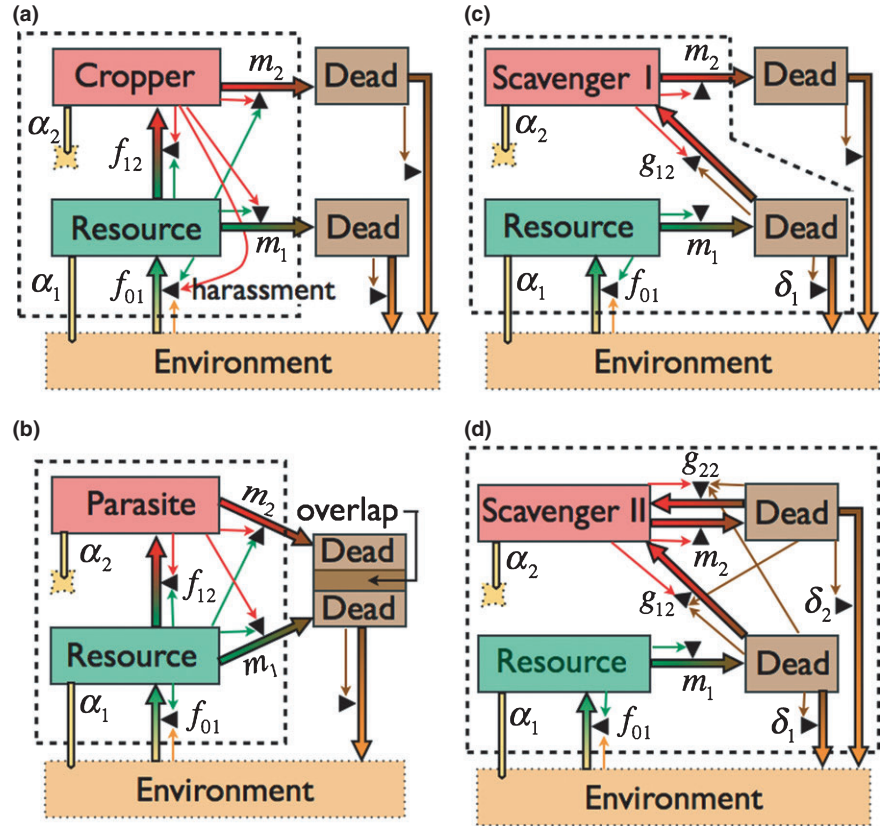‡‡Smith & Reay 1991.
§§Mckillup & Mckillup 1996.

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.

$$
\begin{aligned}
m_2 x_2 &= \frac{\mu_2 v_1^s}{v_1^s - v_1} x_2 + \mu_{21} \frac{x_2}{x_1} m_1 x_1 \\
&= \left((\mu_2 + \mu_{21}\mu_1) + \mu_{21}\mu_{12}x_2 \right) \frac{v_1^s x_2}{v_1^s - v_1},
\end{aligned}
$$

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 $\frac{\mu_{12}x_2 v_1^s}{v_1^s - v_1}$. Thus, it follows that

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

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:

$$
\frac{dx_1}{dt} = \left(\frac{\kappa_1 a_1 y_{01}}{b_1\left(1 + \left(\frac{x_1}{c_1}\right)^{\gamma_1}\right) + y_{01}} - \alpha_1 - (\mu_1 + \mu_{12}x_2) \right) x_1, \tag{12}
$$

$$
\frac{dx_2}{dt} = (a_2\mu_{12}x_1 - \alpha_2 - \mu_2 - \mu_{22}x_2)x_2,
$$

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 carcasivores (several kinds of vultures) and carnivores (hyenas and lions), but especially black-backed jackals (*Canis mesomelas*) that are both carcasivores 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 ecystem (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 km^2 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
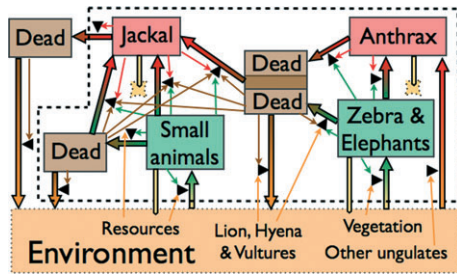
Figure 4 A simplified anthrax-centred biomass transformation web in Etosha National Park, Namibia. See Appendix S4 for equations modelling this system.
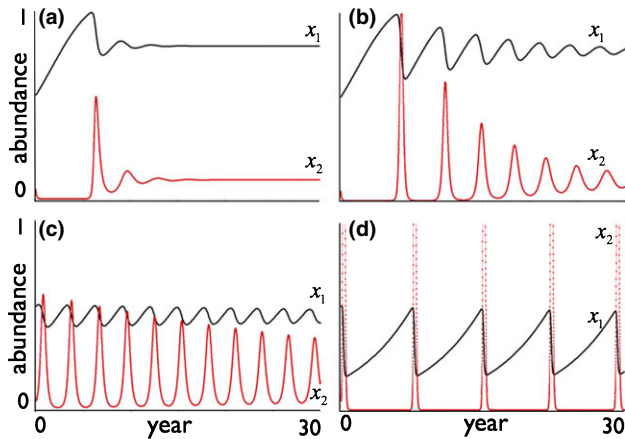

Figure 5 The zebra/elephant biomass abundance $x_1(t)$ (Scale 1 = 18 000 metric tons) and anthrax spore abundance $x_2(t)$ (Scale 1 = 200 unspecified units) solutions to eqn 12 are plotted over a 30-year period for the parameter values given in Table S2 (Appendix S5), except as noted: (a) $a_2 = 0.5$ 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.

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 subdecadel and decadel 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 ball-park 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
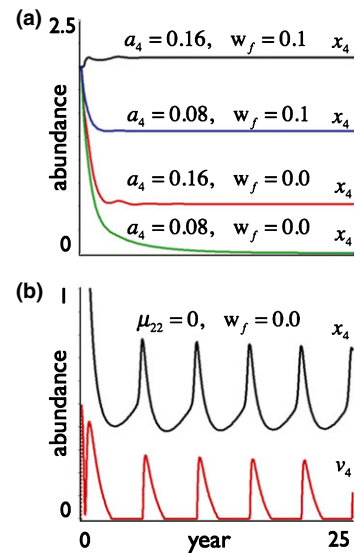
appropriate given that current abundance estimates are rather crude and, in particular, jackal abundances are not known within a factor of two of real levels, while the distribution of anthrax spores across the landscape is unknown.

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) $(\hat{x}_1, \hat{y}_2, \hat{x}_3, \hat{y}_3, \hat{x}_4)' = (7437, 70.0, 31.2, 2351, 3.49, 57.6)'$ (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 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 $w_f = 0$), 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.

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Appendix A: Consumer categories

Throughout most of the mid-20th Century, the separation of biological organisms into plant, animal, protist and prokaryote kingdoms, fostered by traditional discipline-oriented biology departments at universities, led to the development of discipline-specific technical ecological language. This has created some difficulties for a modern integrated perspective, exacerbated by the use of both Latin and Greek etymologies for technical words. For example, the adjectives herbivorous (Latin etymology) and phytophagous (Greek etymology) both mean "feeding on plants," although phytophagous is almost never used to describe plant-eating mammals, but is predominantly used to describe plant-eating insects.

A scheme for naming consumers, motivated by the BTW framework developed in the main text, is based on

1. differences between eating live and dead biomass

2. distinguishing among consumers of animal, plant and microbial biomass

3. distinguishing between consumers of whole/integral-parts of organisms (e.g. leaves, blood) versus feeding on nondescript organic particulate matter (i.e. detritus)

4. differences in the way organisms exploit resources on a *miner-gatherer spectrum*, where miners are relatively sessile in locally exploiting a resource mass larger than themselves and gatherers are relatively mobile in searching out and consuming or sequestering packets of resources typically smaller but sometimes larger (e.g. a tiger killing a water buffalo) than themselves.

To name all the basic categories in Fig. 1 and Table A1—that is, the 4-fold symmetry of each of the two outer circles plus the two-fold symmetry of the inner circle, I propose several new technical terms using Greek etymology for the miners and Latin etymology for the gatherers (since this convention appears to be the most consistent with current terminology). Beyond the basic categories are the following compound categories:

Parasites and Croppers. Respectively these are miners and gatherers of whole or specific parts of live biomass of any type.

Saprophages and Scavengers. Respectively these are miners and gatherers of whole or specific parts of dead biomass of any type.

Decomposers and Detritivores. Respectively these are miners and gatherers of particulates arising from the breakdown of organic material from any source.

In addition, parasites and saprophages together constitute olophages, which can be broken down by animal or plant consumers into zoophages and phytophages respectively, while croppers and scavengers together constitute totivores, which can be broken down by animal or plant consumers into carnivores and herbivores respectively (Fig. 1). The various consumer categories apply by life stage, since individuals can change strategies from one life stage to another. Of course, the various categories are idealizations and some animals may not fit either category particularly well, as in omnivores that are both carnivorous and herbivorous. Categories apply to the primary rather than secondary feeding behavior of individuals. Thus an ungulate remains an herbivore even though individual ungulates may be seen chewing bones for specific nutrients.

Table A1: A proposed scheme for organizing consumer life-stage feeding types in BTW theory (new terms have footnotes describing their etymology, general terms are in boldface, and a partial selection of specializations within animal or plant categories are italicized in parentheses).

| Resource | | Feeding Type | |
State	Material	Miner (Greek: *phagos*=eat)	Gatherer (Latin: *vorus*=swallow)
A. <u>Whole or particulate</u>	animal OR plant	**olophage**[1]	**totivore**[2]
Whole or identifiable part	animal ONLY	zoophage	carnivore (*including cannibals*)
	plant ONLY	phytophage	herbivore
	animal AND plant	N/A[3]	omnivore
Particulate	organic	**decomposer**	**detritivore**
B. <u>Live or Dead</u>	animal, plant, OR microbial	**parasite**	**cropper**
Live biomass	animal ONLY	sarcophage (*e.g. hematophages, parasitoids*)	bestivore[4] (*e.g. sanguinivores, piscivores, insectivores*)
	plant ONLY	zontanophage[5] (*e.g., xylem feeders*)	victivore[6] (*e.g. frugivores, folivores, graminivores, nectivores*)
	microbial ONLY	bacteriophage (e.g. *phages*)	microbivore (*e.g. some amoebas*)
	animal OR plant	**saprophage**	**scavenger**
Dead biomass	animal ONLY	necrophage (*e.g. carrion flies*)	carcasivore[7] (*e.g. some vultures*)
	plant ONLY	thanatophage[8] (*e.g. pill bugs*)	lectivore[9] (*e.g. some termites*)

[1]Greek: *olos*=whole; [2]Latin: *totus*=whole; [3]Not applicable: an organism cannot eat intact parts of animals and plants without moving around unless doing so in different life stages [4]Latin: *bestia*=animal; [5]Greek: *zontanos*=alive; [6]Latin: *victus*=living; [7]Latin: *carcasium*=carcass; [8]Greek: *thanatos*=death; [9]Latin: *lectus*=bed → Middle English: *litere* → litter.

Appendix B: Differential equation for deficit stress variable

Consider the deficit stress variable equation

$$\int_{-\infty}^{t} w_i(t-s) V_i \left(\tilde{\alpha}_i(s) - \tilde{\phi}_i(s), v_i(s) \right) ds.$$

Assume that V is bounded and that $w_i(t-s) \to \infty$, as $s \to \infty$. By the fundamental theorem of integral calculus we have for all $s \leq t$:

$$\frac{dv_i}{dt} = \frac{d}{dt} w_i(t-s) V_i \left(\tilde{\alpha}_i(s) - \tilde{\phi}_i(s), v_i(s) \right).$$

If V_i is simply a function that draws upon resources whenever basal metabolic needs are not meet—that is, $\tilde{V}_i(s) = \max \left\{ 0, \left(\tilde{\alpha}_i(t) - \tilde{\phi}_i(t) \right) \right\}$, and if w_i is an exponential decay function—that is, $w_i(s) = e^{-\omega_i s}$, then for all $s \leq t$ the above equation becomes:

$$\frac{dv_i}{dt} = \begin{cases} 0 & \text{if} \quad \tilde{\alpha}_i(s) \leq \tilde{\phi}_i(s) \\ \omega_i e^{\omega_i(t-s)} \left(\tilde{\alpha}_i(s) - \tilde{\phi}_i(s) \right) & \text{otherwise} \end{cases}$$

On the other hand, if we simply assume that if individuals do not eat for T units of time they die, otherwise they internalize the deficit through weight loss at any point that they eat before this period is up then $w_i(s) = 1$ for $s \in [t - t_s, t]$ and is 0 for $s < t_s$. In this case, using Heaviside calculus (i.e. $\frac{dw_i}{ds} = 1$ at $s = 0$ and $s = t_s$ and is 0 elsewhere), it follows that

$$\frac{dv_i}{dt} = \max \left\{ 0, \left(\tilde{\alpha}_i(t) - \tilde{\phi}_i(t) \right) \right\} - \max \left\{ 0, \left(\tilde{\alpha}_i(t - t_s) - \tilde{\phi}_i(t - t_s) \right) \right\}. \tag{13}$$

Appendix C: Cropping and scavenging

Consumption of dead biomass is a very important life style. The many species that have come to adopt this life style include carrion feeders across taxa as diverse as mammals, birds, reptiles, insects, and crustaceans, saprophages (notably fungi), coprophages (e.g. dung eating beetle and fly larvae, as well as coprophytes which are plants that grow on dung), lectivorous termites and detritivorous crabs, as well as a whole host of bacterial species responsible for the decomposition of dead organic animal and plant material into nutrients that are then recycled back into the ecosystems.

Scavengers, as gatherers of dead biomass, particularly facultative scavenger, are perhaps much more widespread in the vertebrate community than currently appreciated (Selva & Fortuna, 2007), and modeling their dynamics has received much less attention in the modeling literature than other kinds of resource-consumer systems. The BTW formulation provides a powerful platform to address such questions as: what fitness advantages might be gained if a cropper on the live biomass of a resource is also able to exploit the dead biomass compartment of the same resource? Of course one expects an evolutionary tradeoff in selection for more efficient croppers versus better cropper-scavenger generalists in a guild of predators. By way of demonstration, we use the BTW to superficially explore the above question, leaving a more thorough analysis to future studies.

To keep the model simple and in line with our early cropper model, we assume $m_i = \frac{\mu_i}{\phi_i}$, $i = 1, 2$. Also we model a type I rather than type II scavenger (Fig. 2, Table 1), which excludes scavengers feeding on their own dead. The resulting interaction process can be modeled using the following five equations:

$$\begin{aligned}
\frac{dx_1}{dt} &= \left(\phi_1 - f_{12}x_2 - \frac{\mu_1 v_1^s}{v_1^s - v_1}\right)x_1 \\
\frac{dy_1}{dt} &= \frac{\mu_1 v_1^s}{v_1^s - v_1}x_1 + \left(1 - \theta\right)f_{12}x_1x_2 - \left(g_{12}x_2 + \delta_1\right)y_1 \\
\frac{dx_2}{dt} &= \left(\phi_2 - \frac{\mu_2 v_2^s}{v_2^s - 2_1}\right)x_2 \\
v_i(t) &= \int_{t_i - t_i^s}^{t} \max\left\{0, \alpha_i - \tilde{\phi}_i(s)\right\}ds. \quad i = 1, 2.
\end{aligned} \tag{14}$$

where ϕ_1 as defined in Eq. 8, but now

$$\phi_2 = \kappa_{12}^f \theta f_{12}x_1 + \kappa_{12}^g g_{12}y_1. \tag{15}$$

As in our previous case we keep f_{01} as defined in Eq. 9 with $1/c_{12} = 0$, but in defining f_{12} and g_{12} we ensure a common intake satiation level applies by using the same denominator in these two functions. Consider the case where resource extraction is Holling type II. Additionally, in the context of an evolutionary tradeoff, we assume that it is $w > 1$ times easier for a consumer to sequester a unit of dead than live biomass when both are at the same density (dead animals don't have to be chased down), but the nutritive value is less, which implies

$$\kappa = \kappa_{12}^f > \kappa_{12}^g = v\kappa \qquad \text{for some} \qquad 0 \le v \le 1.$$

Under this assumption, setting $\gamma = 4$ (Schoombie and Getz 1998), we define

$$f_{12} = \frac{a_2}{b_1 \left(1 + \left(\frac{x_2}{c_2}\right)^{\gamma_2}\right) + x_1 + wy_1} \qquad \text{and} \qquad g_{12} = \frac{a_2 w}{b_1 \left(1 + \left(\frac{x_2}{c_2}\right)^{\gamma_2}\right) + x_1 + wy_1}. \qquad (16)$$

Reference

Selva, N. & Fortuna, M.A. (2007). The nested structure of a scavenger community. *Proc. Royal Soc. B.* 274, 1101-1108.

Appendix D: Anthrax in ENP: Model

The equations for the system are formulated using a combination of the ideas developed to model host-parasite systems for anthrax interactions with zebra and elephant and cropper-scavenger systems for the jackal as primarily a carcasivore augmented by cropping various small animals (e.g. springbok lambs, springhares, ground squirrels, african hares, dung beetles). As, discussed in the main text, this system can be modelled using nine state variables: x_1 (live zebra and elephants), y_1 (dead zebra and elephants), v_1 (zebra and elephant feeding deficit stress), x_2 (live small animals), y_2 (dead small animals), v_2 (small animal feeding deficit stress), x_3 (anthrax spores in LIZs), x_4 (live jackals), v_4 (jackal feeding deficit stress). In addition, four donor-controlled extraction functions h_i, $i = x_1, y_1, x_3, y_3$, are used to represent the flow of extracted biomass respectively from the zebra/elephant live and dead and small-animals live and dead compartments to background carnivore (lion and hyena), carcasivore (primarily vultures) and scavenger (eagles and corvids) populations.

   The equations are formulated subject to the following assumptions:

1. The units of time t are years. Although seasonal factors are important in understanding some of the finer details of the anthrax and jackal dynamics, we will only model the system in terms of annual averages.

2. The zebra/elephant resource extraction and growth rates are

$$\phi_1 = \kappa_1(t) f_{01} y_{01} \quad \text{where} \quad f_{01} = \frac{a_1}{b_1 \left(1 + \left(\frac{x_1}{c_1}\right)^{\gamma_1}\right) + y_{01}(t)} \tag{17}$$

   where we recall that y_{01} are the resources that zebra and elephant extract from the environment and κ_1 is the conversion efficiency. In reality, both zebra and elephants move off the infectious grazing plain at different times of the year to migrate to other areas of ENP to meet their resource needs. From Fig. 7, we infer that seasonal contacts of elephants and zebra with LIZs is somewhat complimentary since the peak number of zebra and elephants dying from anthrax occurs in different seasons. For this reason, annual averages of the effects of anthrax on a joint zebra/elephant compartment is a reasonable and compatible assumption for a model that does not take account of any spatial structure.

3. A pathogen, such as anthrax, needs to be treated differently than a nematode or coccidial parasite that infects almost all hosts to varying degrees, but is not fatal at low infection levels. In the case of anthrax, however, either the live individual contracts a lethal dose and die very rapidly (e.g. within a week), or fight off the infection, in which case the spores in question can be treated as having disappeared at a background decay rate. Thus to first order we do not need to account for the the actual growth of vegetative anthrax cells in the host, but rather assume that the spore population in the environment is replenished by the rate at which host individuals die or contract a lethal dose of anthrax spores from the environment. If x_2 is some measure of the abundance of anthrax in the soil, then we might assume, at least at low to moderate levels of abundance, that anthrax infection rates are proportional to x_3 (at very high levels a saturation effect which we ignore here may be evident). Thus, in the expression $m_1 = \frac{(\mu_1 + \mu_{12} x_2) v_1^s}{v_1^s - v_1}$ (c.f. Eq. 10), the second part $\frac{\mu_{12} x_2 v_1^s}{v_1^s - v_1}$ can be interpreted as the per unit x_1 biomass death rate from anthrax and the first part the non-anthrax death rate.

Consequently, in the anthrax equation, we assume spores are added to the soil at a rate that is proportional to the second part of m_1.

4. As for zebra, the small animal resource extraction and growth rates are

$$\phi_3 = \kappa_3 f_{03} y_{03} \quad \text{where} \quad f_{03} = \frac{a_3}{b_3 \left(1 + \left(\frac{x_3}{c_3}\right)^{\gamma_3}\right) + y_{03}(t)}. \tag{18}$$

Although anthrax may kill some small animals, such as springbok, where jackal are known to hunt young springbok, this level of detail will not be considered here.

5. Jackal are only able to scavenge but not predate zebra and elephant. Thus jackal (x_4) feed on dead zebra and elephant (x_1), and live (x_3) and dead (y_3) small animals with preferences w_f and w_g for live and dead small animals relative to dead zebra/elephant. This implies non-zero extraction functions

$$g_{14} = \frac{a_4}{b_4 \left(1 + \left(\frac{x_4}{c_4}\right)^{\gamma_4}\right) + S}, \quad f_{34} = \frac{a_4 w_f}{b_4 \left(1 + \left(\frac{x_4}{c_4}\right)^{\gamma_4}\right) + S}, \quad \text{and} \quad g_{34} = \frac{a_4 w_g}{b_4 \left(1 + \left(\frac{x_4}{c_4}\right)^{\gamma_4}\right) + S}. \tag{19}$$

where $S = y_1 + w_f x_3 + w_g y_3$. Note that $g_{14} + f_{34} + g_{34} = \frac{a_4 S}{b_4 \left(1 + \left(\frac{x_4}{c_4}\right)^{\gamma_4}\right) + S}$, which implies a common intake satiation level a_4 for all resources. Thus, assuming all dead biomass has the same nutritive value to jackals irrespective of the source, and assuming jackals completely consume all the small animals they crop, it follows that

$$\phi_4 = \kappa_4^g \left(g_{14} y_1 + g_{34} y_3\right) + \kappa_4^f f_{34} x_3. \tag{20}$$

6. Live and dead zebra/elephant and small animals are respectively removed at rates $h_{x_1} x_1$, $h_{y_1} y_1$, $h_{x_2} x_2$ and $h_{y_2} y_2$ by background populations of lions, hyenas and other predators and scavengers, though only a proportion θ of live biomass of zebra is diverted to dead biomass during predation, assuming smaller animals are consumed completely after being killed (which is often the case).

Using the ideas laid out in the text, in Appendices B-D, and in points 1-7. above, the system

equations for the ENP BTW (Fig. 4) are

$$
\begin{aligned}
\text{Live zebra \& elephant:} \quad \frac{dx_1}{dt} &= \left(\phi_1 - \alpha_1 - \frac{(\mu_1 + \mu_{12}x_2)v_1^s}{v_1^s - v_1} - h_{x_1}\right)x_1 \\[2mm]
\text{Dead z. \& e.:} \quad \frac{dy_1}{dt} &= \left(\alpha_1 + \frac{(\mu_1 + \mu_{13}x_3)v_s}{v_1^s - v_1} + (1 - \theta)h_{x_1}\right)x_1 - \left(g_{14}x_4 + \delta_1 + h_{y_1}\right)y_1 \\[2mm]
\text{Deficit stress z. \& e.:} \quad \frac{dv_1}{dt} &= \max\left\{0, \left(\tilde{\alpha}_1(t) - \tilde{\phi}_1(t)\right)\right\} - \max\left\{0, \left(\tilde{\alpha}_1(t - t_1^s) - \tilde{\phi}_1(t - t_1^s)\right)\right\} \\[2mm]
\text{Infectious } B. \text{ anthracis:} \quad \frac{dx_2}{dt} &= \left(a_2\frac{\mu_{12}x_1 v_1^s}{v_1^s - v_1} - \alpha_2 - \mu_2 - \mu_{22}x_2\right)x_2 \\[2mm]
\text{Live small animals:} \quad \frac{dx_3}{dt} &= \left(\phi_3 - \alpha_3 - f_{34}x_4 - \frac{\mu_3 v_3^s}{v_3^s - v_3} - h_{x_3}\right)x_3 \qquad\qquad (21) \\[2mm]
\text{Dead small animals:} \quad \frac{dy_3}{dt} &= \left(\alpha_3 + \frac{\mu_3 v_3^s}{v_3^s - v_3}\right)x_3 - \left(g_{34}x_4 + \delta_3 + h_{y_3}\right)y_3 \\[2mm]
\text{Deficit stress small an.:} \quad \frac{dv_3}{dt} &= \max\left\{0, \left(\tilde{\alpha}_3(t) - \tilde{\phi}_3(t)\right)\right\} - \max\left\{0, \left(\tilde{\alpha}_3(t - t_3^s) - \tilde{\phi}_3(t - t_3^s)\right)\right\} \\[2mm]
\text{Live jackal:} \quad \frac{dx_4}{dt} &= \left(\phi_4 - \alpha_4 - \frac{\mu_4 v_4^s}{v_4^s - v_4}\right)x_4 \\[2mm]
\text{Deficit stress jackal:} \quad \frac{dv_4}{dt} &= \max\left\{0, \left(\tilde{\alpha}_4(t) - \tilde{\phi}_4(t)\right)\right\} - \max\left\{0, \left(\tilde{\alpha}_4(t - t_4^s) - \tilde{\phi}_4(t - t_4^s)\right)\right\}
\end{aligned}
$$

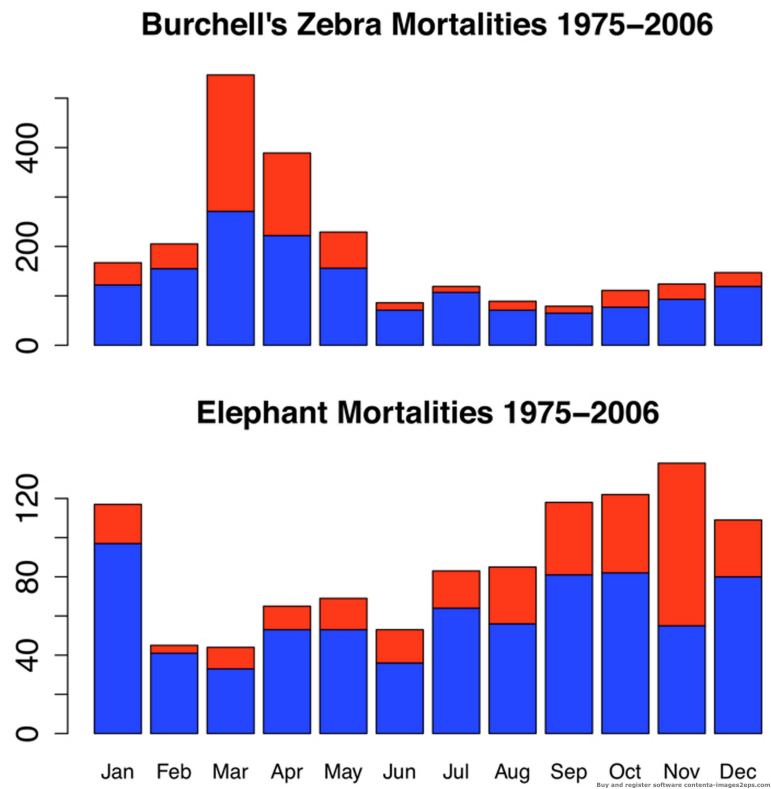where ϕ_i, $i = 1, \ldots, 4$ are given by Eqs. 17 to 20.

Figure 7: Deaths of zebra and elephant from anthrax (red) and other causes (blue) by month in ENP. (This graph is courtesy of Steve Bellan, UC Berkeley, 2010)

Appendix E: Anthrax in ENP: Parameters

As mentioned in Appendix C, as a first cut to exploring the dynamics of an ENP anthrax-zebra-elephant-jackal BTW model, we select parameter values to mostly reproduce annual averages, although the basic time unit is days and rates in Table A2 are per day. A more refined temporal analysis—even if only at seasonal level (e.g. three monthly averages)—would require consideration of spatial structure within ENP to account for seasonal movements of zebra and elephant populations as they migrate around the full 22,000 km extent of ENP.

A 2005 ENP large animal census estimated the size of the zebra and elephant populations to be approximately 13000 and 2500 individuals respectively. Assuming an average zebra biomass of 200 kg (full grown males are 300 kg, females a little less and juveniles reaching adult size at age 2) the standing biomass of zebra is 2,600 metric tons. Assuming an average elephant biomass of 3000 kg per individuals (males range from 4500 to 7000 kg, with females somewhat smaller and juveniles weighing from 100+kg at birth and maturing into full grown males only towards the end of their second decade) the standing biomass of elephant is around 7,500 metric tons. Thus the zebra/elephant compartment has a standing biomass that currently fluctuates around 10,000 metric tons with and elephant:zebra mass ratio of around 1:3.

Using a 1:3 zebra:elephant biomass ratio and the data depicted in Fig. 7, we have that over the 22 years period the average biomass of carcass produced by predators is approximately 115 metric tons and that produced by anthrax is approximately 50 metric tons kg. Since not all carcasses are detected (particularly those of young zebra which will be rapidly consumed and thus not transformed into dead biomass as a resource to be exploited by anyone other than the predator responsible for the death in the first place) and the total carcass weight is only 1.65% of the standing crop, it follows from the roughly 12-15 and 60-70 year longevities respectively of those zebra and elephants that make it to maturity (if it were not for lion predation, then zebra would more likely live for 20+ years) that we would expect in the neighborhood of 10% of the adult zebra population to die each year and about 3% of the adult elephant population to die each year. If we weight these in the ratio 1:3, we expect about 5% of the biomass in each population to be removed each year due both to senescence and predation. We can use the percentage of anthrax-killed carcasses, as indicated in Fig. 5, which is $50/165 \approx 30\%$ to scale the effects of anthrax as part of the total flow that we scale up to represent realistic live-to-death transformation rates in the zebra/elephant compartment. Thus under normal circumstances we expect 5% of the biomass to disappear each year with approximately 3.0% to predators, 1.5% to anthrax and the rest to other causes of senescence (injury, disease, old age).

In terms of small animals, springbok head the list with about 20-30,000 animals averaging about 40 kg each (i.e. standing crop of approximately 1000 metric tons), with a life span of 7-10 years. Other small animals that are predated by jackal are the lagamorph, *Lepus saxatilis* (scrub hare, approx 3 kg), and rodents, *Pedetes capensis* (springhare, about 3 kg), *Xerus spp.* (ground squirrel), *Rhabdomys pumilio* (striped mouse, about 50 g), among several others. Since we have no idea of the average standing crop of these species, we assume a small mammal average standing crop of around 1500 metric tons (i.e about 50% higher than springbok) with an average life span for the combined compartment of around 4 years.

The number of jackals in ENP is not known, but the density appears to be much higher than most other national parks in Africa. It is not unusual to find 50 jackals at one carcass. This is at least 10-20 times the number of hyenas spotted at carcasses. Since the number of hyenas in ENP

is estimated to be 200-300 hyenas in the central and western parts of ENP, we nominal assume on the order of 5000 jackal at average size 8 kg each, which is 40 metric tons of biomass.

We use the above information and many other sources to informally estimate the various parameters listed in Table A2. I do not claim that any of the parameters in Table A2 are reasonable estimates, since many aspects of the general feeding ecology, consumer-resource interaction processes, and mortality processes are insufficiently known to estimate all parameters with reasonable confidence. Further, an assessment of the values of the parameters that reflect our best current knowledge would in itself become a comprehensive literature review and data manipulation exercise. Since the focus of this **Ideas and Perspective** study is to present the Biomass Transformation Web paradigm to modeling population interactions and demonstrating how it can be developed to study a food web such as the ENP system modelled in Appendix D, I do make any pretense that the data in Table A2 is anything other than a set that allows for the demonstration of an ENP anthrax-centered BTW model.

Table A2: Parameter Values used in Eqs. 12 (parameters in red) and Eqs 21 (all parameters).

Parameter	Elephant & Lion	*B. Anthracis*	Small Animal	Jackal
Max extract rate†	$a_1 = 0.02$	$a_2 = 1$	$a_3 = 0.05$	$w_f = 0.1$ $a_4 = 0.16$ $w_g = 1$
Resource half sat.	$b_1 = 200,000$	N/A	$b_3 = 200,000$	$b_4 = 100$
Interference comp.	$c_1 = 20,000$	N/A	$c_3 = 2,000$	$c_3 = 10$
Conversion effic.	$\kappa_1 = 0.15$	N/A	$\kappa_3 = 0.18$	$\kappa_4^f = 0.2$ $\kappa_4^g = 0.1$
Density abrupt.*	$\gamma_1 = 4$	N/A	$\gamma_3 = 4$	$\gamma_4 = 2$
Basal metab.	$\alpha_1 = 0.0016$	$\alpha_2 = 0.001$	$\alpha_3 = 0.003$	$\alpha_4 = 0.004$
Senescence mort.	$\mu_1 = 0.000014$	$\mu_2 = 0.1$	$\mu_3 = 0.0001$	$\mu_4 = 0.0001$
Add. sens. mort.	$\mu_{12} = 0.000014$	$\mu_{22} = 0.0001$	N/A	N/A
Extraction mort.	$h_{x1} = 0.00008$ $h_{y1} = 0.2$	N/A N/A	$h_{x3} = 0.0001$ $h_{y3} = 2$	N/A N/A
Diversion prop.	$\theta = 0.5$	N/A	N/A	N/A
Starvation time	$t_1^s = 30$	N/A	$t_3^s = 20$	$v_4^s = 15$
Starvation point	$v_1^s = 0.05$	N/A	$v_3^s = 0.06$	$v_4^s = 0.06$
Decay rate	$\delta_1 = 0.01$	N/A	$\delta_3 = 0.01$	N/A
Resource input	$y_{01} = 5 \times 10^6$	N/A	$y_{03} = 4 \times 10^6$	N/A
Initial live	$x_1(0) = 10,000$	$x_2(0) = 10$	$x_3(0) = 2000$	$x_4(0) = 40$
Initial dead	$y_1(0) = 50$	N/A	$y_3(0) = 3$	N/A

† In the case of anthrax this is a constant that scales the conversion of a unit biomass infected by anthrax into the number of spores that then enter the soil.

*The most appropriate value for γ is difficult to determine, but it is certainly greater than 1 (Getz, 1996, *Ecology* 77, 2014-2026). Without prior knowledge, the most reasonable value, suggested by an ESS analysis for a herding animal, may be $\gamma = 4$ (c.f. Fig. 4 in Schoombie and Getz, 1998, *Theoretical Population Biology*, 53, 216-235), which is the value we use here for the herbivores, while for territorial carnivores we expect a smaller value and hence use $\gamma_4 = 2$.