

## Appendix A: Consumer categories

Throughout most of the mid-20<sup>th</sup> 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: <i>phagos</i> =eat)	Gatherer (Latin: <i>vorus</i> =swallow)	
<b>A. <u>Whole or particulate</u></b>	animal OR plant	<b>olophage</b> <sup>1</sup>	<b>totivore</b> <sup>2</sup>	
	Whole or identifiable part	zoophage	carnivore (including cannibals)	
	plant ONLY	phytophage	herbivore	
	animal AND plant	N/A <sup>3</sup>	omnivore	
<b>Particulate</b>	organic	<b>decomposer</b>	<b>detritivore</b>	
<b>B. <u>Live or Dead</u></b>	animal, plant, OR microbial	<b>parasite</b>	<b>cropper</b>	
	Live biomass	sarcophage (e.g. <i>hematophages</i> , <i>parasitoids</i> )	bestivore <sup>4</sup> (e.g. <i>sanguivores</i> , <i>piscivores</i> , <i>insectivores</i> )	
	plant ONLY	zontanophage <sup>5</sup> (e.g., <i>xylem feeders</i> )	victivore <sup>6</sup> (e.g. <i>frugivores</i> , <i>folivores</i> , <i>graminivores</i> , <i>nectivores</i> )	
	microbial ONLY	bacteriophage (e.g. <i>phages</i> )	microbivore (e.g. <i>some amoebas</i> )	
	Dead biomass	animal OR plant	<b>saprophage</b>	<b>scavenger</b>
		animal ONLY	necrophage (e.g. <i>carrion flies</i> )	carcasivore <sup>7</sup> (e.g. <i>some vultures</i> )
plant ONLY		thanatophage <sup>8</sup> (e.g. <i>pill bugs</i> )	lectivore <sup>9</sup> (e.g. <i>some termites</i> )	

<sup>1</sup>Greek: *olos*=whole; <sup>2</sup>Latin: *totus*=whole; <sup>3</sup>Not applicable: an organism cannot eat intact parts of animals and plants without moving around unless doing so in different life stages <sup>4</sup>Latin: *bestia*=animal; <sup>5</sup>Greek: *zontanos*=alive; <sup>6</sup>Latin: *victus*=living; <sup>7</sup>Latin: *carcasium*=carcass; <sup>8</sup>Greek: *thanatos*=death; <sup>9</sup>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  $w_i(t-s) \rightarrow \infty$ , as  $s \rightarrow \infty$ . 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:

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

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

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

## 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:

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

where  $\phi_1$  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

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

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

$$f_{12} = \frac{a_2}{b_1 \left(1 + \left(\frac{x_2}{c_2}\right)^{\gamma^2}\right) + x_1 + wy_1} \quad \text{and} \quad g_{12} = \frac{a_2 w}{b_1 \left(1 + \left(\frac{x_2}{c_2}\right)^{\gamma^2}\right) + x_1 + wy_1}. \quad (16)$$

## 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 carcassivore 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), carcassivore (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

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

where we recall that  $y_{01}$  are the resources that zebra and elephant extract from the environment and  $\kappa_1$  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  $\frac{\mu_{12}x_2v_1^s}{v_1^s - v_1}$  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

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

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

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

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

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

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  $\theta$  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

$$\begin{aligned}
\text{Live zebra \& elephant: } \frac{dx_1}{dt} &= \left( \phi_1 - \alpha_1 - \frac{(\mu_1 + \mu_{12}x_2)v_1^s}{v_1^s - v_1} - h_{x_1} \right) x_1 \\
\text{Dead z. \& e.: } \frac{dy_1}{dt} &= \left( \alpha_1 + \frac{(\mu_1 + \mu_{13}x_3)v_s}{v_1^s - v_1} + (1 - \theta)h_{x_1} \right) x_1 - \left( g_{14}x_4 + \delta_1 + h_{y_1} \right) y_1 \\
\text{Deficit stress z. \& e.: } \frac{dv_1}{dt} &= \max \left\{ 0, \left( \tilde{\alpha}_1(t) - \tilde{\phi}_1(t) \right) \right\} - \max \left\{ 0, \left( \tilde{\alpha}_1(t - t_1^s) - \tilde{\phi}_1(t - t_1^s) \right) \right\} \\
\text{Infectious } B. anthracis: \frac{dx_2}{dt} &= \left( a_2 \frac{\mu_{12}x_1v_1^s}{v_1^s - v_1} - \alpha_2 - \mu_2 - \mu_{22}x_2 \right) x_2 \\
\text{Live small animals: } \frac{dx_3}{dt} &= \left( \phi_3 - \alpha_3 - f_{34}x_4 - \frac{\mu_3v_3^s}{v_3^s - v_3} - h_{x_3} \right) x_3 \\
\text{Dead small animals: } \frac{dy_3}{dt} &= \left( \alpha_3 + \frac{\mu_3v_3^s}{v_3^s - v_3} \right) x_3 - \left( g_{34}x_4 + \delta_3 + h_{y_3} \right) y_3 \\
\text{Deficit stress small an.: } \frac{dv_3}{dt} &= \max \left\{ 0, \left( \tilde{\alpha}_3(t) - \tilde{\phi}_3(t) \right) \right\} - \max \left\{ 0, \left( \tilde{\alpha}_3(t - t_3^s) - \tilde{\phi}_3(t - t_3^s) \right) \right\} \\
\text{Live jackal: } \frac{dx_4}{dt} &= \left( \phi_4 - \alpha_4 - \frac{\mu_4v_4^s}{v_4^s - v_4} \right) x_4 \\
\text{Deficit stress jackal: } \frac{dv_4}{dt} &= \max \left\{ 0, \left( \tilde{\alpha}_4(t) - \tilde{\phi}_4(t) \right) \right\} - \max \left\{ 0, \left( \tilde{\alpha}_4(t - t_4^s) - \tilde{\phi}_4(t - t_4^s) \right) \right\}
\end{aligned} \tag{21}$$

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



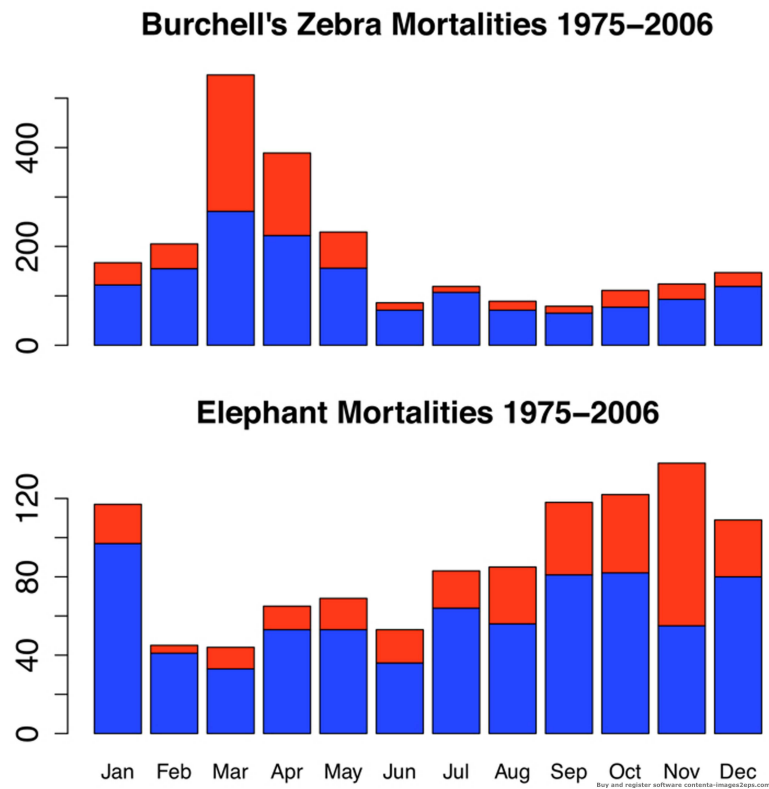


Figure 7: Deaths of zebra and elephant from anthrax (red) and other causes (blue) by month in ENP. (This graph is courtesy of Steve Bellan, UC Berkeley, 2010)

## 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 an 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 preyed upon by jackal are the lagomorph, *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	<i>B. Anthracis</i>	Small Animal	Jackal
Max extract rate <sup>†</sup>	$a_1 = 0.02$	$a_2 = 1$	$a_3 = 0.05$	$w_f = 0.1$ $a_4 = 0.16$ $w_g = 1$
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

<sup>†</sup> 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  $\gamma$  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  $\gamma_4 = 2$ .