

Predation mortality allometries

Predator mortality rate

We next explore the effect of predator mortality on an herbivore population, taking into account carnivore-specific growth and energetic rates. Without explicitly taking into account the dynamics of a predator population, we can account for the effects of an implicit predator P with mass M_P on the population of the consumer C with mass M_C , where we will for now assume that the predator population exists at some steady state P^* . The effect of the predator on the consumer's population is given by

$$\begin{aligned}\frac{d}{dt}C &= -bP^*C, \\ b &= \frac{\lambda_P}{Y_P k_C^{\max}},\end{aligned}\tag{1}$$

where b is the capture efficiency of the predator on the consumer, P^* is the steady state density of the predator population, λ_P is the maximum growth rate of the predator, k_C^{\max} is the density of the consumer population that maximizes this predator growth, and Y_P is the yield coefficient for the predator. As we are not tracking dP/dt , we assume a constant predator population density given by Damuth's Law, but where the slope and intercept consider only measured densities of predatory mammals. If P is g/m^2 , the density of individuals/ m^2 then follows $(1/M_P)P^*(M_P) \propto M_P^{-0.88}$.

The predator's yield Y_P is calculated

$$Y_P = \frac{M_P E_C}{\int_0^{t_{\lambda_P}} B_0^P m_P(t)^\eta dt},\tag{2}$$

where $m_P(t)$ is the ontogenetic mass of an individual predator as it grows over time to an adult mass M_P . The parameters t_{λ_P} and B_0^P are the timescale associated with reaching reproductive maturity and the metabolic coefficient for predatory mammals, respectively, and $\eta = -3/4$ is the metabolic exponent. In words, the predator yield scales proportionally with the individual mass of the predator (g) and the energy density of prey E_C (J/g), normalized to the lifetime energetic needs of a predator reaching maturity (J). Accordingly, the predator yield coefficient describes the grams of predator produced per gram of prey consumed.

We assume that predators consume all non-skeletal mass of prey. Because the amount of consumable tissues with different energy densities within an herbivore varies allometrically, so too should the energy density E_C . We consider four primary tissue groups: a consumable set composed of muscle, fat, and *other* tissues, and a non-consumable set composed only of skeletal tissues. If the scalings associated with fat, muscle, and skeletal tissues are $M_C^{\text{fat}} = f_0 M_C^{1.19}$, $M_C^{\text{musc}} = g_0 M_C^{1.00}$, and $M_C^{\text{skel}} = h_0 M_C^{1.09}$, the scaling of the *other* tissue (gut tissue, organ tissue, etc) is given by $M_C^{\text{other}} = M_C - (M_C^{\text{fat}} + M_C^{\text{musc}} + M_C^{\text{skel}})$. The energy density of fat is $E_{\text{fat}} = 37700$ J/g, whereas the energy density of muscle is $E_{\text{musc}} = 17900$ J/g. If we assume that gut and organ tissues have roughly the same energy density as muscle, the attainable energy density for an herbivore of size M_C is given by

$$E_C(M_C) = E_{\text{fat}} \frac{M_C^{\text{fat}}}{M_C} + E_{\text{musc}} \left(\frac{M_C^{\text{musc}}}{M_C} + \frac{M_C^{\text{other}}}{M_C} \right).\tag{3}$$

Another important consideration is that we have assigned k_C^{\max} to represent the consumer density maximizing predator growth λ_P . Because predator growth is proportional to prey growth, and prey growth is responding to a logistically growing resource R , we assume that predator growth is maximized when prey growth is maximized, which occurs when the resource reaches its half-saturation point $R = k_R/2$ g/ m^2 , where we assume $k_R = 23000$ g/ m^2 . The translated available consumer biomass represented by this half-saturation point is then given by $k_C^{\max} = Y_C k_R/2$ (consumer g/ m^2) where Y_C is the consumer yield coefficient, giving the grams of consumer per grams of resource and calculated analogously to Y_P , such that

$$Y_C = \frac{M_C E_R}{\int_0^{t_{\lambda_C}} B_0^C m_C(t)^\eta dt},\tag{4}$$

where $m_C(t)$ is the ontogenetic mass of an individual herbivorous consumer as it grows over time to an adult mass M_C . The parameters t_{λ_C} and B_0^C are the timescale associated with reaching reproductive maturity and the metabolic

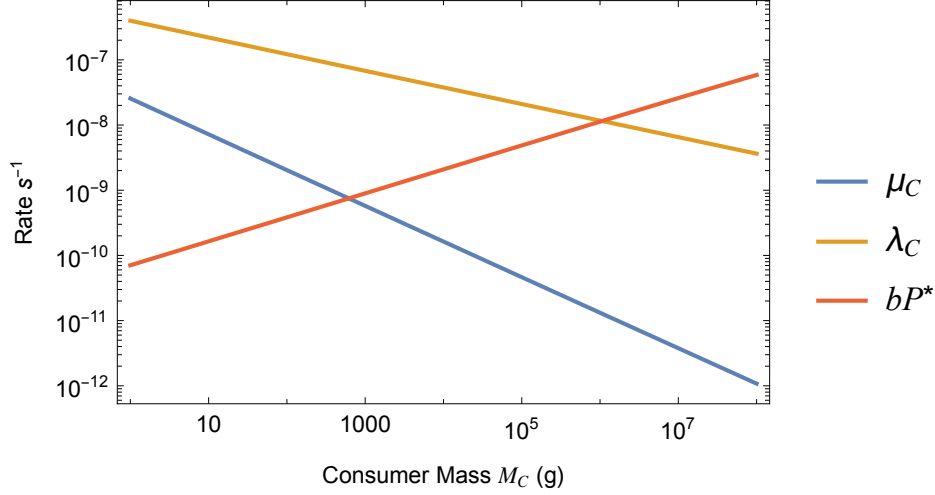


Figure 1: An herbivore consumer's life-history mortality rate μ_C , reproductive rate λ_C , and predation rate bP^* as a function of its mass M_C (g).

coefficient for herbivorous mammals, respectively, and $\eta = -3/4$ is the metabolic exponent. Moreover, we assume a resource energy density that approximates graze, such that $E_R = 18200$ J/g.

Because predator-prey relationships tend to be determined largely by the body sizes of predator and prey, the mortality of a prey consumer due to predation requires us to assume a consumer with mass M_C has a predator with body mass M_P . The probability of a trophic interaction between predators and prey $\ell_{C,P}$ as a function of the body sizes of both follows a logit relationship, where

$$\log \left(\frac{Pr(\ell_{C,P} = 1)}{Pr(\ell_{C,P} = 0)} \right) = q_0 + q_1 \log \left(\frac{M_C}{M_P} \right) + q_2 \log^2 \left(\frac{M_C}{M_P} \right). \quad (5)$$

and the parameters $\mathbf{q} = (q_0, q_1, q_2)$ are fitted to an adjacency matrix describing empirical interactions between predators and prey of different body sizes within a community. The result for diverse terrestrial mammalian communities such as that in the Serengeti results in a Gaussian-shaped distribution in log body mass space, where for a particular predator mass there is a range of prey masses for which the linking probability is high, and below or above which the linking probability is low. We describe this peak of this linking probability as the optimal prey size for a particular predator, which can be algebraically manipulated to provide the optimal predator size associated with a particular consumer prey, such that

$$M_P^{\text{opt}} = M_C e^{\frac{q_1}{2q_2}}. \quad (6)$$

Given best-fits of \mathbf{q} for interactions in the Serengeti, one of the few remaining diverse terrestrial mammalian communities, we observe that $\log(M_P^{\text{opt}}) < \log(M_C)$, meaning that predators are smaller than their prey. We note that in aquatic systems the reverse relationship is observed, given those predators tend to be gape-limited. If we operate under the assumption that - on average - a consumer with mass M_C will suffer mortality by a predator with mass M_P^{opt} , we obtain a mortality rate $-bP^*$ that varies only as a function of consumer mass M_C .

Even without exploring directly the consumer-resource dynamics, we can gain insight into the potential effects of predation mortality by comparing the mortality rate to the consumer's population growth rate λ_C as a function of consumer mass M_C . While the consumer's reproduction rate scales $\lambda_C \propto M^{-0.25}$, the predation mortality rate is shown to scale $bP^* \propto M^{0.37}$, meaning there is a consumer mass M_C where these rates intersect. For smaller consumer masses, the predation mortality rate is lower than the consumer's reproductive rate, suggesting that these populations can sustain a predator population. However, as consumer mass increases, the predation mortality rate crosses λ_C , at which point the predation mortality rate becomes larger than the consumer reproductive rate. This suggests that, given the optimal predator:prey mass scaling observed in diverse terrestrial communities (Eq. 6), there is a consumer mass threshold M_C^{crit} above which the consumer population can no longer sustain itself in the presence of such predative load.

While the analytical expression of bP^* is not tractable, numerical assessment of this critical consumer mass gives $M_C^{\text{crit}} = 1064$ Kg. Our analysis suggests that a consumer mass above this threshold cannot sustain a predator

population with a predator:prey mass ratio observed for lower body masses, and with densities predicted by Damuth's Law. Intriguingly, this corresponds to the body size of herbivores in the Serengeti that effectively escape predation due to their large size. Cape buffalo have a mass $M_C \approx 450$ Kg, where predation accounts for roughly 23% of mortality, whereas giraffes with mass $M_C \approx 800$ Kg suffer $\approx 5\%$ mortality due to predation. The next largest herbivore in the Serengeti are rhinoceros, which weigh ≈ 1200 Kg and suffer 0% mortality due to predation (Sinclair et al. 2003), a threshold remarkably consistent with our estimated M_C^{crit} of 1064 Kg.

Previous efforts have evaluated the maximum sustainable terrestrial mammalian carnivore size to be roughly 700 – 1100 Kg based on the energetic constraints of assimilated energy gain. Here we provide an alternative perspective: that carnivore body size may be additionally limited by instabilities that the act of predation introduces to their herbivorous prey. As our predicted allometric predator mortality rate crosses the consumer's reproductive rate at M_C^{crit} , the populations of herbivore species larger than 1064 Kg are expected to collapse, an effect that would be expected to cascade into the predator population. Because we assume that predator mass is dependent on prey mass, we can estimate the predator mass that would destabilize its prey population, for which we obtain $M_P^{\text{crit}} = 802$ Kg. This estimate corresponds closely to the largest observed terrestrial apex carnivores: the Hyaenodontid *Megistotherium osteothlastes* ranged between 500-800 Kg (Rasmussen 1989, Sorkin 2008), while the Oxyaenodont *Sarkastodon mongoliensis* weighted ≈ 800 Kg. Other large mammalian predators are known to have existed, though their body mass is less well known due to a dearth of fossil specimens: *Andrewsarchus* is famously thought to be the largest terrestrial predator (800 – 1000 Kg), while a recent skull of *Smilodon populator* indicates that some individuals may have attained body sizes up to 900 Kg.

[Because our framework is constructed based on underlying energetic relationships, we can now ask: how do variations in less constrained model parameters alter these estimated mass thresholds?]

[Pleistocene implications]