To the PNAS editorial board,

We wish to resubmit our manuscript #2016-14116 to PNAS. While both reviewers found our submission thought provoking, it was rejected, primarily due to concerns of Reviewer 2 about the model itself. While we were not invited to resubmit, there are two compelling reasons for doing so. First, we made a simple blunder in the original model so that it was dimensionally wrong, as properly criticized by referee 2. We now start with a fully justified, mechanistic and dimensional model, from which we obtain the consistent non-dimensionalized rate equations (1), which differs only slightly from what appeared in our original submission. Second, we extended our model in several important ways, including: (i) an explicit treatment of biosynthesis and maintenance metabolism, (ii) a clear discussion of resource growth rates and density, (iii) an explicit carrying capacity for the resource dynamics, and (iv) saturating dynamics for resource consumption and consumer reproduction. These elements integrate fundamental concepts from ontogenetic growth, resource dynamics, and growth physiology.

Crucially, the predictions of our model are qualitatively similar to those in our original submission. Moreover, because of the connection between the rate coefficients of our present model with allometric constraints, we are able to make quantitative predictions for data. We therefore believe that this revision makes substantial contributions to understanding the physiological constraints that drive mammalian species population dynamics, as well as the forces that influence changes in body size over evolutionary time. Specifically:

(i) Across the observed body size range, terrestrial mammals occupy a region of parameter space where sustained cyclic dynamics are not permitted.

(ii) We identify a "refuge" in parameter space where the extinction probability is minimized. Further, mammals have allometrically constrained rates of starvation and recovery that place them clearly within this refuge.

(iii) Steady-state populations in the NSM support the energy equivalence hypothesis (equal energy use across species populations with different individual body size) for a wide range of body sizes. Our model accurately predicts both observed steady-state population densities of mammals, as well as the energy equivalence rule (we have included a comparison of the model's prediction with interspecific data) .

(iv) By investigating the dynamics of a steady-state population with respect to the invasion by a species with altered endogenous energetic reserves, we obtain a fundamental stability criterion that provides a within-lineage mechanism for the evolution of larger body size among terrestrial mammals, namely, Cope's rule.

Thank you for considering this request,

Justin Yeakel, Chris Kempes, Sidney Redner

Responses to the Reviewers' Comments:

Reviewer Comments:

Reviewer #1:

Suitable Quality?: Yes
Sufficient General Interest?: Yes
Conclusions Justified?: Yes
Clearly Written?: No
Procedures Described?: Yes

Comments :

This is a remarkable contribution to the understanding of ecological allometries. It does seems to be an step in the right direction, as the proposed Nutritional models accomplish a lot with rather little in therms of assumptions. However, there are a couple that may be important to discuss in a more explicit way in the manuscript. First, the model assumes that only hungry individuals die, while allometric data shows that mortality rate (e.g. Azbel 1994 PNAS 91, Brown et al 2004). More importantly, however, the authors assume that reproductive rate is independent of resources, and that reproducing individuals require less energy than that required to recover from the starving state. In part this generates the odd result that when there are no resources then (lambda > sigma) the population of well nourished individuals grows exponentially (lines 149-153).

Our revised model clarifies the dependency of the system on the lambda < sigma criterion. By accounting for the added maintenance term for individuals in the hungry state as well as individuals in the full state, which we developed in our revised model, biologically plausible values for both consumers and the resource (such that all have densities > 0) is dependent on the condition that lambda < sigma. The lambda=sigma condition now represents a true transcritical bifurcation, not dissimilar from many other consumer-resource models, such that (R*,H*,F*)<0 if lambda > sigma.

In lines 410-415. In relation to the ecological constraints upon body size and how resources in particular can limit extreme sizes see (Marquet and Taper 1998 Evolutionary Ecology, 12(2), 127-139.). This result and a later paper by Burness in PNAS highlight that area exerts important constraints upon persistence, since energy and resources area spatially distributed.

The Reviewer correctly notes that area is an important determinant of body-size

constraints. We now account for resource limitation via an explicit resource density and specific resource growth rate in the dimensional formulation of the model and show that the resulting steady states of the consumer match nearly perfectly against empirical data.

Lines 440-452. Although R* theiry predicts that those species able to maintain populations under low resource concentrations will out-compete those with higher R* it is important to realize that as populations decrease in size several other factor affect viability (e.g demographic and genetic stochasticity) such that thresholds (e.g.Allee effects) are common.

We agree with the Reviewer, and have investigated the effects of stochastic extinction due to lower steady states and cyclic dynamics in the paper (illustrated in Fig. 5).

Minor comments

Line 80. delete "many"

Line 460 change linneage to lineage

Several references need amendment (initial for authors in 36, 38 incomplete in 42 etc.

All corrected.

It would be interesting to see what the model can say regarding the scaling of extinction risk.

We agree that exploring additional issues regarding mass-specific extinction risks would be fruitful, but beyond the scope of this work. However, to address the question of extinction risk as dependent on size, we show, in Fig. 5, the extinction likelihood based on sigma and rho for three different body sizes that span the range of mammals considered. This plot shows that the parameter space where extinction is unlikely is shrinking in area with increased body size.

Figure 5: "Probability of extinction for a consumer with (A) M = 10^2g, (B) M = 10^4g, and (C) M = 10^6g as a function of the starvation rate sigma and recovery rate rho, where the initial density is given as (XF_*,XH_*,R_*), where X is a random uniform variable in [0,2]. Note the change in scale for M = 10^4 and M = 10^6g. Extinction is defined as the population trajectory falling below 0.2x the allometrically constrained steady state. The white points denote the allometrically constrained starvation and recovery rate. "

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Reviewer #2:

Suitable Quality?: No
Sufficient General Interest?: No
Conclusions Justified?: No
Clearly Written?: Yes
Procedures Described?: Yes

Comments:

This paper proposes a nutritional-state structured model of consumer-resource interaction and uses the scaling rules resulting from metabolic theory to make inferences about expected types of population dynamics, the risk of extinction as well as the outcome of an evolutionary process in maximum body size. The paper is overall written with a lot of enthusiasm and a clear use of language and therefore has quite a bit of appeal. However, a more careful and critical read of the manuscript shows me that the starting point of the model development and analysis is seriously flawed when considered form a biological point of view. I therefore do not think this is a publishable paper.

• To start with, I fail to see how the proposed model is related to the authors motivation of the study as explained in the introduction. The motivation centers around the trade-off between investment in maintenance and growth on the one hand and reproduction on the other hand, as also emphasised in the significance statement. However, in my opinion the model that the authors propose has little or nothing to do with maintenance and certainly not with somatic growth.

We now include a more complete treatment of maintenance as detailed below, and agree that the original model was lacking on this topic. The goal of the original model was to describe the simplest dynamics for starvation, recovery, and reproduction. However, this original formulation lacked an explicit treatment of important biological processes. We now include an explicit dimensional and mechanistic model which we non-dimensionalize into a form that is only slightly different than the original rate equations. Our updated model gives new quantitative predictions and allows us to confront interspecific data.

> Lines 121-129: "The rate at which consumers transition between states and consume resources is dependent on their overall abundance, the abundance of resources, the efficiency of converting resources into metabolism, and how that metabolism is partitioned between maintenance and growth purposes. In the supplementary information (SI) we provide a fully mechanistic model for each of these dynamics and constants, and show that the system produces a simple non-dimensional form which we describe below."

• However, my most fundamental problem with the model is not its motivation but its formulation. The authors model a consumer class that is hungry or starving and a consumer class that is full, satiated and reproducing. Both classes of consumers feed on the resource. The resource grows via a logistic growth equation and the authors off-handedly mention that its carrying capacity equals 1. This innocuous remark has huge implications as it means the resource density has to be interpreted as a scaled resource density. In turn, the authors assume that the transition from a full state to a hungry state is proportional to the absence of resource, which they identify with $1-R$, where R is resource density. To define the difference between current resource density and its carrying capacity as "absence of resource" is in my opinion not correct, but biologically it is also an absurd assumption as in an unscaled version of the model (where the carrying capacity is not set equal to 1 and hence the term $1 - R$, would read $K - \tilde{R}$ with K the carrying capacity of the resource and $\tilde{R}$ the unscaled density) it would imply that an individual consumer would more quickly end up in a hungry state if the maximum density of its resource increases. This makes no sense to me. I have tried to see whether there is some magic scaling of the resource density that would justify this choice of functional form. I failed, so I have come to the conclusion that the term $\sigma(1-R)F$ describing the rate at which consumer transition from the full to the hungry state is not based on any sensible biological mechanism. It is a mathematical construct that has little or no connection with

biological realism.

In our treatment of the dimensional model we have added an explicit treatment of carrying capacity and the saturation of the resource to an upper bound, thus including terms of the form (1-R_d/C). We also show that within our dimensional system there is a choice of non-dimensionalizations that leads to a form for resource dynamics that depends on (1-R) where R is the non-dimensionalized resource that has been rescaled by the carrying capacity. We agree that the non-dimensional model is not complete without a presentation of the fully dimensional form that we have now added to the supplement along with our explicit non-dimensionalization procedure. Again, it should also be noted that the adjusted mechanisms of the dimensional model lead to a non-dimensional form that differs from the original model for the resource dynamics (dR/dt) equation.

See Supplement Lines 8-57.

• A second issue arising from this assumption has to do with dimensions: the authors completely overlook the problem of dimensionality that results from the assumption about the starvation rate $\sigma(1-R)F$ as well as the recovery rate ρRH. In a later section they derive estimates for the parameters σ and ρ, which they give the dimension time^{-1}. This derivation, however, totally ignores that the parameters σ and ρ represent proportionality constants in terms that also involve the resource density. Again in an unscaled version of the model the product ρR should have the dimension time^{-1} when we only consider the ODE for H, which would suggest that ρ should have a dimension time^{-1} . resource^{-1}. However, if in an unscaled version of the model we consider the ODE for R, it can be inferred that the product ρH should have the dimension time^{-1} and hence that ρ should have a dimension 1 time^{-1} . consumer^{-1}. In short, considering the dimensions of the different terms the model does not make much sense either.

Much of the referee's criticism correctly points out our naïve errors in the initial formulation of the model. Now we explicitly account for the carrying capacity and resource saturation in the dimensional model. We then show that there is a non-dimensionalization that leads to a form for resource dynamics that depends on (1-R) where R is the non-dimensionalized resource density (rescaled by the carrying capacity). We now provide the fully dimensional model in the supplementary material, together with our non-dimensionalization procedure. Our reformulation also allows us to incorporate a greater number of measured values for specific biological rates laws, such as consumer maintenance metabolism, and this in turn allows us to make quantitative predictions of population density and an asymptotic limit on mammalian size. This newer nondimensional model differs from the previous version in the dR/dt equation where the last two terms are (rho R + delta)H + beta F instead of the previous R(rho H + beta F).

• Further biological issues with the model formulation are more subtle. For example, implicit in the model formulation is that the changes between the hungry and satiated state are taking place at the same time scale as consumer and resource population growth. In my opinion, this assumption is not very convincing as reproduction takes place at a lifetime scale, but individuals are hardly ever hungry for their entire life. It is for this difference in time scale that classic models usually involve a consumer functional response to account for the difference in time scale of the process of hungry/satiated switches and population dynamics.

The rates controlling starvation and reproduction operate on different timescales as stated explicitly in the manuscript. This disparity is evident in the graph of reproduction rate and starvation rate as a function of body mass (Fig. 3). In the model, individuals can transition back and forth between hungry and full states - on average - many times within an average lifespan.

• Apart from the biological issues with the model, there are also mathematical issues with its analysis. The authors report that for $\sigma = \lambda$ a transcritical bifurcation occurs, but this statement is evidently wrong. A transcritical bifurcation indeed involves a real eigenvalue turning positive, as the authors explain, but apart from that a transcritical bifurcation involves 2 different fixed points, one that turns from stable to unstable, while the other turns from unstable to stable. Two different equilibria are hence necessarily involved in a transcritical bifurcation. Inspection of the expressions for the consumer and resource density in the internal equilibrium (equations [2]) shows however that neither the (0, 0, 0,) nor the (0, 0, 1) equilibrium is involved in the TC. Although for $\lambda \uparrow \sigma$ R* approaches 0, F* and H*do not. What happens around $\sigma = \lambda$ is therefore mathematically unclear.

Our original manuscript had a condition that we mistakenly identified as a transcritical bifurcation. However, our reformulated model makes this transition point clear and consistent with other consumer-resource models. Accordingly the condition $\sigma = \lambda$ is now a true transcritical bifurcation where the internal steady state crosses (0,0,0), as the factor $(\sigma - \lambda)$ appears in the numerator for the steady state equations of R, H, and F. This added factor is due to the modifications of the dR/dt equation.

• Along the same lines, in figure 1 it is shown that a parameter region with cycles is bordering the line where $\sigma = \lambda$, where a real eigenvalue turns from negative to positive. From a mathematical point of view I do not understand the dynamics in this region, as the real eigenvalue turning positive relates to the already unstable non-trivial equilibrium. What happens at that border to the limit cycle? It should be explained for which parameter values the limit cycle is stable or unstable, the fact that the already unstable equilibrium becomes infeasible is unrelated to the fate of the limit cycles. Because of the more fundamental problems with the underlying model I will only shortly comment on the later sections, which deal with the parameterisation of the model based on the scaling rules from metabolic

theory and with evolution of body size.

Our reformulated model avoids the mathematical issues of the original, but shows again that there are three regions with distinct dynamics. Holding the recovery rate constant, and increasing the starvation rate starting from a small value, the interior fixed point moves from being unstable to a cycle (as the transcritical bifurcation is crossed), and then to being stable (as the Hopf bifurcation is crossed).

• The authors derive estimates for the recovery rate ρ from the ontogenetic growth model. Implicitly, the authors equate here the process of fattening up following starvation to the process of body size growth after birth. I find this also a questionable assumption, the latter has to do with developing body tissues and structures, whereas the former is a process of replenishing storage compartments. I hence disagree with the starting point that recovery from-starvation parameters can be deduced from the ontogenetic growth model.

We did not make this point clear in the original manuscript, but we do in fact employ different energetics for the recovery, which only accounts for replenishing fat storage. This dynamic is encapsulated in a' (which is energetically different than a), which we employ for recovery along the ontogenetic curve. The ontogenetic growth curve encapsulates a wide variety of shapes that are largely controlled by a, and so, a' leads to replenishment along a different trajectory. We didn't draw this in the original growth curve schematic (Figure 2) because we felt that it was confusing to the reader, but we have altered the figure to represent the altered recovery trajectory due to the different energetics of a'.

See Lines 254-276.

• In the last section on evolution of body size, the authors identify the ESS with the consumer body size with the highest steady-state density of consumers. This assumption is in contrast to any other theory in consumer-resource interaction, in which it invariably holds that the consumer type with the lowest equilibrium resource density is the winner over evolutionary time. Unfortunately, in the model that the authors develop this is the non-sensical consumer with σ = λ as is made clear in figure 6 of the paper. In summary, I can only conclude that I am not at all convinced by this manuscript, which involves a lot of (mathematical) reasoning, but is founded on a flawed biological basis. I apologise for this harsh judgement, but I fail to see an alternative.

We reformulated our analysis of competitive advantage (or invasibility) by comparing the steady states of the resource for both resident and invading populations. According to R-star theory, the consumer that can push its resource to the lower steady state will have a competitive advantage. Moreover, we avoid ESS terminology to prevent confusion of our analysis with game-theoretic methods, and focus instead on addressing potential competitive advantages/

disadvantages of an invading consumer with modified body mass. We also note that although starvation rates are modified by changing the body mass of the invading consumer, the extent to which mass can be added or removed are strictly constrained by (i) at the small end, the proportion of body mass that is fat (chi = -f_0*M^(gamma-1), and (ii) at the large end, the reproductive body mass (which we assume is 0.95 the asymptotic mass, such that chi cannot be greater than 0.05). Because of these constraints, the $\sigma > \lambda$ condition always holds, and our analysis does not disobey the fundamental laws dictated by our formulation. This revised approach (comparing R-star's of the invader and resident population) indicates that the maximum size of mammalian body mass is 1.748×10^7g, which is very close to the observed maximum mammalian body size of 1.74×10^7g value reported by Smith et al. (Science) 2010.

See Lines 507-536