

Dear Nature Communications editorial committee,

We thank the reviewers for the valuable insight, suggestions, and critiques of our prior submission to *Nature Communications* (MS. NCOMMS-17-14602). We have carefully considered the feedback supplied by the Reviewers, have addressed all of the Reviewer's concerns and suggestions, and believe that the revisions made greatly increase the value of our manuscript. Importantly, the suggested changes do not alter our results, but provide better context and clarity. We thank the Reviewers for their insights and hope that our changes and clarifications satisfy their concerns. Our responses to Reviewer comments are detailed below (Comments are in **BLACK** and our responses are in **BLUE**). Please let us know if any clarification is required.

Sincerely,

Justin Yeakel  
Christopher Kempes  
Sidney Redner

Reviewer #1 (Remarks to the Author):

In this paper the authors introduce a population dynamics model (nutritional state-structured model; NSM) where mortality and reproduction of a consumer are linked to the underlying dynamics of body mass growth and body fat gain and loss. These starvation and recovery dynamics determine the rates at which individuals move between the 'full' state, where individuals reproduce, and the 'hungry' state, where individuals can die. One of the nice features of this approach is that state changes are driven by a mechanistic depiction of energy gain and loss in individuals, which are then transformed into the rate parameters in the model.

The authors use the NSM model to investigate multiple questions. They use it to describe variation in population dynamics in terms of starvation and recovery rates, to show that mammalian herbivores generally reside in an 'extinction refuge' that is smaller for larger species, to show that steady-state abundances decline with body mass and that this aligns with the idea of the energetic equivalence rule, to show that there is a maximal size attractor that is consistent with the observed largest size of land mammal, and to suggest that increased body fat suggests greater persistence for larger species, which might be a mechanism driving Cope's rule.

Comment 1.1) OK so there's a lot in this paper. I think it's a strong point to introduce a model and to provide a deep list of predictions that the model makes and that are consistent with observations. The downside is that it is very dense and doesn't take much time with any one of these observations. Also, I noticed that new results just kept coming through the discussion. Perhaps the authors could consider a structure to clarify the different NSM vignettes they are working through?

Response 1.1) We agree that there are many results in this paper and in response to the referee's comments and to better serve the reader we made the following changes:

- We rewrote the last paragraph of the introduction to summarize our new results in a straightforward way.
- We added several section subheadings.

- We've reorganized the discussion section and moved several new results earlier in the ms.

Comment 1.2) My biggest concern with the paper has to do with the extinction risk and invasion analyses. In both of these sections, the authors use a community assembly process (i.e., relative competitive ability through  $R^*$ ) to infer a 'within-lineage' (e.g., lines 385 and 455) process of evolution. As presented, the process invoked is that a whole population of individuals of the invader genotype with more fat reserves could outcompete a whole population of the non-invader genotype, due to the invader's lower  $R^*$ , and thus persist while the non-invader goes extinct. It is argued that this is a within-lineage mechanism, but it really is not. A within-lineage mechanism would be one in which a rare invader to a population would have higher individual fitness than the rest of non-invader population and thus grow and become a larger component of the population.  $R^*$  is not an individual-level fitness metric and does not tell you whether that individual invader will be successful. Rather, it is a population-level metric of competitive ability. Thus, the authors are conflating a competitive process among populations for a within-population process of a mutant growing when rare. Similarly with the extinction risk analysis, the authors use population-level extinction risk to imply selection within a population, but selection drives changes in gene frequencies within a population and is not a process picking among different populations which goes extinct and which doesn't. Importantly, I think this is just a matter of rephrasing the sections to more precisely indicate what their analysis actually does, not that there is anything wrong with the analysis itself.

Response 1.2) We agree that  $R^*$  is not designed to consider the detailed mutation/invader dynamics of a population of single species. We used the "within lineage" terminology to match the Cope's rule literature, however, this literature is actually referring to a fairly wide diversity of species when describing "lineages", for example all mammals. In our case the population perspective of  $R^*$  is appropriate because we are comparing competition abilities of populations that do not interbreed. We have revised our description of the selective mechanism for Cope's Rule, and have re-casted the problem in terms of two closely related competing species, which more accurately captures the framework of  $R^*$  theory. We have clarified our terminology in the text to reflect these subtleties: the 'invader population' is now described as the 'competing species'.

Lines 380-385: "However, the above resource relationships do not offer a mechanism for how body size is selected. We directly assess competitive outcome between two closely related species: a resident species of mass  $M$ , and a competing species (denoted by  $'$ ) where individuals have a different proportion of body fat such that  $M' = M(1 + \chi)$ ."

Lines 403-408: "To assess the susceptibility of the resident species to competitive exclusion, we determine which consumer pushes the steady-state resource density  $R^*$  to lower values for a given value of  $\chi$ , with the expectation that a population capable of surviving on lower resource densities has a competitive advantage."

Also see changes to [Figure 5](#).

Comment 1.3) The authors might want to look at Carbone, Teacher & Rowcliffe (2007). These authors use scalings of energetics to predict the maximum size of mammals and get the approximately right answer as well. They do so without having to account for starvation and recovery dynamics. Can you say what advantage the NSM has relative to the simpler approaches?

Response 1.3) As the referee points out, while our model is simple, there are still simpler models that predict a subset of our results. For example, the simple algebra of the metabolic theory of ecology predicts Damuth's law, given the assumption of equal energy partitioning. The Carbone et al. reference offers another important example, and we now discuss their findings in relation to our results. Importantly, our approach is able to predict Damuth's rule, Cope's rule, and a maximum herbivore size all within a single framework, and also makes detailed predictions about dynamics and population stability. We have added the following text that compares and contrasting our results to existing work, including that of Carbone et al. We have also added text highlighting the multiple features that can be explained within a single framework.

Lines 62-71: "Our model makes several basic predictions: (i) the dynamics are typically driven to a refuge far from cyclic behavior and extinction risk, (ii) the steady-state conditions of the NSM accurately predict the measured biomass densities for mammals described by Damuth's law 26–29, (iii) there is an allometrically constrained upper-bound for mammalian body size, and (iv) the NSM provides a selective mechanism for the evolution of larger body size, known as Cope's rule 30–33."

Lines 297-312: " While the previous metabolic studies supporting Damuth's law provided arguments for the value of the exponent 27 , these studies are only able to infer the normalization constant ( $0.01 \text{ g}^{1.78} \text{ m}^{-2}$  in the above equation) from the data (see SI for a discussion of the energy equivalence hypothesis related to these metabolic arguments). Our model predicts not only the exponent but also the normalization constant by explicitly including the resource dynamics and the parameters that determine growth and consumption. It should be noted that density relationships of individual clades follow a more shallow scaling relationship than predicted by Damuth's law 29 . In the context of our model, this finding suggests that future work may be able to anticipate these shifts by accounting for differences in the physiological parameters associated with each clade."

Lines 336-346: " It has also been shown that models that incorporate the allometry of hunting and resting combined with foraging time predicts a maximum carnivore size between  $7 \times 10^5$  and  $1.1 \times 10^6$  (g) 51,52 . Similarly, the maximum body size within a particular lineage has been shown to scale with the metabolic normalization constant 53 . This complementary approach is based on the balance between growth and mortality, and suggests that future connections between the scaling of fat and muscle mass should systematically be connected with  $B_0$  when comparing lineages."

Lines 430-449: "An optimal size for mammals at intermediate body mass was predicted by Brown et al. based on reproductive maximization and the transition between hungry and full individuals 54. By coupling the NSM to resource dynamics as well as introducing an explicit treatment of storage, we show that species with larger body masses have an inherent competitive advantage for size classes up to  $M_{\text{opt}} = 1.748 \times 10^7$  based on resource competition. Moreover, the mass distributions in Ref. 54 show that intermediate mammal sizes have the greatest species diversity, in contrast to our efforts, which consider total biomass and predict a much larger  $M_{\text{opt}}$ . Compellingly, recent work shows that many communities can be dominated by the biomass of the large 61. While the state of the environment as well as the competitive landscape will determine whether specific body sizes are selected for or against 33, we propose that the dynamics of starvation and recovery described in the NSM provide a general selective mechanism for the evolution of larger body size among terrestrial mammals."

Lines 458-463: “We found that incorporating allometrically-determined rates into the NSM predicts that: (i) extinction risk is minimized, (ii) the derived steady-states quantitatively reproduce Damuth’s law, and (iii) the selective mechanism for the evolution of larger body sizes agrees with Cope’s rule.”

Minor points:

Minor Comment 1.1) No line numbers given – In the abstract, it indicates there is a trade-off between reproduction and ‘dynamics’. How can such a trade-off occur, when dynamics are a pattern and not something organisms can allocate to by allocating less to reproduction?

Minor Response 1.1) We thank the referee for pointing this out. To avoid semantic confusion, we replaced the word tradeoff with interplay.

Minor Comment 1.2) Lines 48-51 – As indicated in the previous sentence above these lines, unicellular organisms depend on nutrition. But they also have no real distinction between somatic growth and reproduction. Thus, perhaps it’s not quite right to say that the somatic growth-reproduction trade-off is universal. Rather it may be more precise to say that nutritional state influences all organisms by determining whether they can grow to a reproductive state.

Minor Response 1.2) We agree with the referee and have modified the phrasing in the text.

Lines 42-44: “In the extreme case of unicellular organisms, nutrition directly controls growth to a reproductive state 3,21.”

Minor Comment 1.3) Lines 60-63 – I would argue that LV models actually do explicitly include resource availability for reproduction. It’s right there in the terms that transform resource consumption (based on availability through the functional response) into new consumers. So that’s not the right deficiency for LV models. Perhaps you want to say that they assume that all individuals have the same nutritional state and reproduce or die at the same rate as a result. But there may be consequences for not allowing variation in nutritional state because this should influence who reproduces and who dies. Not sure if this gets more precisely at what you are intending, but it’s a try.

Minor response 1.3) We thank the referee for pointing out our imprecise language. We’ve rewritten this section and attempted to make the text more precise. Some of this material addresses Comment 1.1.

Lines 50-62: “A common simplifying approach is the classic Lotka-Volterra (LV) model, which assumes that consumer population growth rate depends linearly on resource density. Here, we introduce an alternative approach—the Nutritional State-structured Model (NSM)—that accounts for resource limitation via explicit starvation. In contrast to the LV model, the NSM incorporates two consumer states: hungry and full, with only the former susceptible to mortality and only the latter possessing sufficient energetic reserves to reproduce. Additionally, we incorporate allometrically derived constraints on the timescales for reproduction, starvation, and recovery.”

Minor Comment 1.4) Line 84, 117 – Evolve doesn't seem to be the right word here. Evolve implies evolution – this is after all biology! I think maybe you are referring to population growth.

Minor Response 1.4) We thank the referee for pointing out that our use of “evolve” in a dynamic sense is confusing. We replaced the word “evolve” with a clearer description of the dynamics.

Lines 79-82: “The dynamics of the underlying resource R are governed by logistic growth with an intrinsic growth rate  $\alpha$  and a carrying capacity C.”

Minor Comment 1.5) Line 92 – Not sure what ‘fully mechanistic’ means. You have a mechanism for every part of everything in this model? Might be overstating it a bit.

Minor Response 1.5) We replaced “fully” with the more specific “physiological and energetically”, now on Line 87 of the revised manuscript.

Minor Comment 1.6) Line 98 – So R has to be  $< 1$ , right, because if it is not then the term is negative, which then keeps full individuals full? It seems from 478 that K is 1. But then on line 139  $R \gg 0$ ? Should it say  $R \sim 1$ ?

Minor Response 1.6) We thank the referee for pointing out our lack of clarity regarding these points. We have clarified our description of the carrying capacity and conditional statements regarding resource density, some of which have been deleted from the text as they lacked accuracy and did not aid interpretation of the dynamics in the NSM.

Line 94: “(the maximum resource density has been non dimensionalized to 1; see SI)”

Lines 114-129: “This system of nondimensional equations follows from a set of first-principle relationships for resource consumption and growth (see the SI for a full derivation and the dimensional form). Notice that the total consumer density  $F + H$  evolves according to  $F^* + H^* = \lambda F - \mu H$ . This resembles the equation of motion for the predator density in the LV model, except that the resource density does not appear in the growth term. The rate of reproduction is independent of resource density because the full consumer partitions a constant amount of energy towards reproduction, whereas a hungry consumer partitions no energy towards reproduction. Similarly, the consumer maintenance terms ( $\delta H$  and  $\beta F$ ) are also independent of resource density because they represent a minimal energetic requirement for consumers in the H and F state, respectively.”

Minor Comment 1.7) Lines 102-104 – Why do you account for growth and maintenance when modeling the rate of eating resources?

Minor Response 1.7) Both hungry and full individuals have a requirement for repair of tissue and some fraction of metabolism is dedicated to these purposes. Thus the requirement for resource consumption, which is based on total metabolic rate, will be determined in part by maintenance purposes. In the supplement we have included a detailed explanation of these dynamics. The main feature of maintenance is that it is proportional to overall body size both during growth and after maturation. Please see for example references 6, 7, and 1 (and the review therein) of the supplement.

Supplementary Lines 29-34.

Minor Comment 1.8) Lines 327-329 – Note that those other models are simpler yet also predict the intercepts of the scaling patterns. What advantage does the NSM have in describing this scaling pattern?

Minor Response 1.8) We now include comparisons of our results with those mentioned by the Reviewer, and detail our inclusion of these comparisons in Response 1.3.

Lines 297-312: “ While the previous metabolic studies supporting Damuth’s law provided arguments for the value of the exponent 27 , these studies are only able to infer the normalization constant ( $0.01 \text{ g}^{1.78} \text{ m}^{-2}$  in the above equation) from the data (see SI for a discussion of the energy equivalence hypothesis related to these metabolic arguments). Our model predicts not only the exponent but also the normalization constant by explicitly including the resource dynamics and the parameters that determine growth and consumption. It should be noted that density relationships of individual clades follow a more shallow scaling relationship than predicted by Damuth’s law 29 . In the context of our model, this finding suggests that future work may be able to anticipate these shifts by accounting for differences in the physiological parameters associated with each clade.”

Minor Comment 1.9) Lines 337-340 – No one has actually shown that mammals show energetic equivalence. This would require population-level estimates of energy use, which do not exist. The mere canceling of abundance and metabolic rate scaling exponents only suggests it is possible. Also see Pedersen, Faurby & Svenning (2017), who show that most clades have shallower scaling, indicating that even using the exponent-cancelling approach, energetic equivalence may not really exist.

Minor Response 1.9) We agree with the referee and have made several major changes: 1.) we have moved the main discussion of the energy equivalence hypothesis to the supplement; 2.) In the now supplementary section we have reworked the prose to highlight that energy equivalence is a hypothesis based on the simple algebraic cancellations described by the referee and we have noted that this hypothesis has not been explicitly measured at the whole population level; 3.) In the main text we have focused the presentation on density relationships and noted that these relationships shift across clades per Pedersen, Faurby & Svenning (2017) and typically have shallower scaling relationships for individual clades. 4) We have moved the figure demonstrating model predictions of energetic equivalence (previously subfigure 4b) to the supplement as an independent figure.

Lines 297-312 quoted immediately above.

Supplementary Lines 180-194: “The energy equivalence hypothesis is based on the observation that if one assumes that the total metabolism of an ecosystem  $B_{\text{tot}}$  is equally partitioned between all species ( $B_i$ , the total metabolism of one species, is a constant), then the abundances should follow  $N(M)B(M)=B_i$  implying that  $N(M) \propto M^{-\eta}$ , where  $\eta$  is the metabolic scaling exponent 19,20. As  $\eta \approx 3/4$  this hypothesis is consistent with Damuth’s law 19. However, the actual equivalence of energy usage of diverse species has not been measured at the population level for a variety of whole populations. Figure S2 recasts the results of the NSM in terms of this hypothesis and shows that  $F * B$  is nearly constant over the same range of mammalian sizes up to the asymptotic behavior for the largest terrestrial mammals.”

Minor Comment 1.10) Line 366-370 – It sort of seems here like the implication is that the upper asymptote is independent of resources. It might be good to clarify that the scalings of body composition – that is the actual observed scalings from body composition measurements – depend directly on the resources those animals had available. So resources matter to this outcome, but here they are embedded and implicit.

Minor Response 1.10) We have been more specific in describing that the resource parameters cancel from the steady state equations, and we have clarified that although resources are driven to zero that there is a growth of resource that is entirely consumed by the population. For example, we have pointed out that in Equation 2 of the main text if the resource growth rate ( $\alpha$ ) equals zero, then the consumer abundances go to zero.

Lines 328-331: “We emphasize that the asymptotic behavior and predicted upper bound depend only on the scaling of body composition and are independent of the resource parameters.”

Supplementary Lines 111-116: However, two points are important to note here: first, our framework predicts the overall scaling of  $F^*$  and  $H^*$  independently of  $\alpha$  and this correctly matches data, and second, both the asymptotic behavior and slope of  $F^*$  and  $H^*$  are independent of  $\alpha$ , such that our prediction of the maximum mammal size does not depend on  $\alpha$ .

Minor Comment 1.11) Lines 510-513 – This is not clear through here. Perhaps there is a detail or two that could be added to clarify how this happens.

Minor Response 1.11) We added several sentences clarifying that equation 4 is used to determine a variety of timescales and that for growth this is used to determine the rate of population increase. We have explicitly included the derivation between timescales and overall specific growth rates.

Lines 496-511: “For example, the rate of reproduction is given by the timescale to go from the birth mass to the adult mass. The time to reproduce is given by Equation 4 as  $t_{\text{lambda}} = \tau(\epsilon_{\text{lambda}})$ , where  $\epsilon_{\text{lambda}}$  is the fraction of the asymptotic mass where an organism is reproductively mature and should be close to one (typically  $\epsilon_{\text{lambda}}=0.95$ – $0.99$ ). Our reproductive rate,  $\lambda$ , is a specific rate, or the number of offspring produced per time per individual, defined as  $dF/dt = \lambda F$ . In isolation this functional form gives the population growth  $F(t) = F_0 e^{\lambda t}$  which can be related to the reproductive timescale by assuming that when  $t = t_{\text{lambda}}$  it is also the case that  $F = \nu F_0$ , where  $\nu - 1$  is the number of offspring produced per reproductive cycle. Following this relationship the growth rate is given by  $\lambda = \ln(\nu)/t_{\text{lambda}}$ , which is the standard relationship (e.g., 67) and will scale as  $\lambda \propto M^{\eta-1}$  for  $M \gg m_0$  for any constant value of  $\epsilon_{\text{lambda}}$  3,63–66.”

Figure 2: The different proportions of asymptotic mass  $M$  that determine the different timescales in the NSM are now explicitly identified in the figure.

Minor Comment 1.12) Line 464 – Seems more like a gradient than ‘distinct’ regimes.

Minor Response 1.12) We have rewritten the final paragraph of the discussion to summarize the primary results that we map out in the introduction.



[Lines 458-466](#): “We found that incorporating allometrically-determined rates into the NSM predicts that: (i) extinction risk is minimized, (ii) the derived steady-states quantitatively reproduce Damuth’s law, and (iii) the selective mechanism for the evolution of larger body sizes agrees with Cope’s rule. The NSM offers a means by which the dynamic consequences of energetic constraints can be assessed using macroscale interactions between and among species.”

#### References:

Carbone, C., Teacher, A. & Rowcliffe, J.M. (2007) The costs of carnivory. PLoS Biol, 5, e22.  
Pedersen, R.Ø., Faurby, S. & Svenning, J.-C. (2017) Shallow size–density relations within mammal clades suggest greater intra-guild ecological impact of large-bodied species. Journal of Animal Ecology, 86, 1205–1213.

#### Reviewer #2 (Remarks to the Author):

This manuscript proposes a new demographic model that divide the population of consumers into those that have acquired resources and thus can reproduce (Full state), and those individuals that are in a hungry state. Time scales and rates are taken from known allometric relationships, following a well established tradition in population modelling, and used as constraints for the rates of transitions between states. Based on this model the authors reproduce the energetic equivalence rule, show that the rates of transitions between the hungry and the full state are tuned to a particular range, outside of which population extinction is likely. Further, by performing and adaptive dynamics on the equilibrium state (another well established method in population modelling) the authors show that there is an optimum body size at the largest end of the body size spectra.

In general the manuscript is novel and provocative; it predicts a lot with little, but I think it can be improved. My major concerns are the lack of clarity and some hidden assumptions that somehow may underlie some counter intuitive results.

Comment 2.1) The presentation of the model could be improved by including a table of parameters, their description and units.

[Response 2.1\)](#) We included an expanded table of parameters along with their values, units, and definitions in the supplement. This table cannot be fit in the main text because of space constraints. Also, note that the parameters in the main text are nondimensionalized and we have also explained this procedure and definitions in the supplement.

#### [Supplementary Table 1](#)

Comment 2.2) Resources should be important in affecting extinction, as they modulate the magnitude of the transition rates, but this is not mentioned in the extinction analysis.

[Response 2.2\)](#) Though resource fluctuations can certainly increase extinction risk, in the parameter space that we examine, resource densities do not swing far from the carrying capacity, and the primary determinant of extinction is the collapse of the consumer population due to mismatched



starvation/recovery rates that shunt biomass to the hungry class, lowering reproduction and increasing mortality. We anticipate that resource densities should play a larger role in extinction dynamics once explicit space is included, and we aim to investigate these issues in a following manuscript.

Comment 2.3) There is a fundamental problem with using grams per square meter, as units for F and H. Living matter, comes packed into discrete individuals and this can make a huge difference. Indeed, per gram, an elephant requires less energy than a mouse, but a functional elephant is much larger, and requires more energy (resources) per individual. This distinction is not trivial as per gram the optimum size is a large one but per individual the optimum may well be shifted to medium sizes where density is larger, a major component of extinction risk. This may explain why the model predict a large optimum while most organisms (mammals in particular) are small or medium size. Indeed the model by brown et al (ref 41) predict exactly this and use the same idea of distinguishing full and hungry individuals with transitions between states governed by allometric relationships, this should be acknowledged.

Response 2.3) We thank the referee for this comment, and highlight that our model is tracking biomass density in an area much larger than an individual. This biomass density takes into account the different energetic demands for organisms of different sizes by incorporating metabolic scaling, and the consequences of this are observed in the predicted decrease in steady state biomass density with increasing individual body size. We also agree with the referee that optimal body sizes (such as that predicted by Brown et al.) will depend on many more variables than we include in our model (e.g. predation risks, etc). We have added a discussion highlighting these other effects in addition to contrasting the type of optima predicted by our model and Brown et al.

Lines 430-449: “An optimal size for mammals at intermediate body mass was predicted by Brown et al. based on reproductive maximization and the transition between hungry and full individuals<sup>54</sup>. By coupling the NSM to resource dynamics as well as introducing an explicit treatment of storage, we show that species with larger body masses have an inherent competitive advantage for size classes up to  $M_{opt} = 1.748 \times 10^7$  based on resource competition. Moreover, the mass distributions in Ref.<sup>54</sup> show that intermediate mammal sizes have the greatest species diversity, in contrast to our efforts, which consider total biomass and predict a much larger  $M_{opt}$ . Compellingly, recent work shows that many communities can be dominated by the biomass of the large<sup>61</sup>. While the state of the environment as well as the competitive landscape will determine whether specific body sizes are selected for or against<sup>33</sup>, we propose that the dynamics of starvation and recovery described in the NSM provide a general selective mechanism for the evolution of larger body size among terrestrial mammals.”

Comment 2.4) The model assumes that only hungry individuals are likely to die. They may be more likely to die but full individuals are assumed to be immortal. This implies that may be useful to distinguish an intrinsic death rate, common to both types, and a state dependent one larger in hungry individuals.

Response 2.4) We agree that death not associated with nutrition was not directly modeled in our original manuscript. We now note that adding a constant death term does not adjust the functional form of our model, but only adjusts the values of  $\lambda$  and  $\mu$ . We have now included an additional analysis where we subtract an additional death rate,  $d$ , from  $\lambda$  and  $\mu$  based on allometric survivorship curves. We find that this additional rate is small compared with  $\lambda$  and  $\mu$  and does not alter our predictions (e.g. our prediction for Damuth's law does not change within our numerical confidence).

See Supplementary section “Sensitivity to additional death terms” and Figure S2.

Supplementary Lines 152-161: “It should be noted that our set of dynamics (Equations 1 and 3) could include a constant death term of the form  $-dF$  and  $-dH$  to represent death not directly linked to starvation. Adding terms of this form to our model would simply adjust the effective value of  $\lambda$  and  $\mu$ , and we could rewrite Equation 3 with  $\lambda' = \lambda - d$  and  $\mu' = \mu - d$ . These substitutions would not alter the functional form of our model nor the steady-states and qualitative results, however the quantitative values could shift based on the size of  $d$  relative to  $\lambda$  and  $\mu$ .

A small excerpt of a longer derivation and discussion from Supplementary Lines 161-178: “In figure 2 we compare the value of  $d$  to the reproductive,  $\lambda$ , and starvation-based mortality,  $\mu$ , rates. The values of  $d$  are orders of magnitude smaller than these rates at all scales, and thus, adding this non-starvation based death rate to our model does not shift our results within numerical confidence.”

Comment 2.5) I would appreciate if the authors clearly state what is their explanation for the energetic equivalence according to their model.

Response 2.5) Because there is no direct evidence for energetic equivalence in nature (just indirect evidence inferred from Damuth's law), we now focus nearly exclusively on how our model predictions are in line with Damuth's law. We provide a brief description of predictions of energetic equivalence in the supplement.

Minor Comment 2.1) There are some issues with the literature cited. Some abbreviations are not standard (Philos. instead of Phil. in 23 and the initials of authors in refs 39, and 41

Minor Response 2.1) We thank the referee for spotting these errors. We have corrected the abbreviation for Ref. 23. We fixed the erroneous author initials in Ref. 39, among others.

Reviewer #3 (Remarks to the Author):

This manuscript presents a novel model of consumer-resource dynamics that examines the effects of incorporating two metabolic states (starved vs nutritionally replete and reproducing) on population dynamics. As many of the parameters are functions of body size, derivable using basic principles, and affect the stability and extinction probability of consumer populations, they explore the implications of the model for the evolutionary ecology of body size. Based on their analysis, they suggest that their framework provides a basis (essentially, a theory) for understanding constraints on the evolution of large body size, Cope's rule, Damuth's rule, and extinction risk. The strength of the paper is their approach: the development of a nutritional state-structured population model and linkages to allometric scaling theory, which allows the authors to raise and address difficult questions at the nexus of ecology, evolution, and physiology and can inspire future theoretical and macroecological work. Thus, although some aspects of their conclusions can certainly be disputed and will require more evaluation from multiple theoretical and empirical angles, I found the paper highly worthwhile. I have only a few minor comments that, if addressed, may help augment the impact of the paper.

Comment 3.1) Their coverage of the energetic equivalence rule was the least compelling part of the paper for me. It was unclear to me how their theory gives support to the energy equivalence rule, as it seemed like energy equivalence necessarily follows from the assumptions of their model rather than being a surprising, non-trivial result. I recommend either more explanation on the subject, toning down statements regarding the work's contribution to understanding the energy equivalence rule, or even removing most of that material. The paper is already quite involved, running the risk of scaring off readers due to it having both high breadth and depth, so removing some material may be beneficial. The energetic-equivalence rule is a controversial and slippery concept, often misunderstood, so the authors may want to reconsider whether it's worth getting into here (it may be better instead to devote an entire paper to the subject).

Response 3.1) As stated above in response to referee #1 and 2, we have moved all of the discussion of the energy equivalence to the supplement, where we have also added additional subtlety and discussion. In particular, we have highlighted that energy equivalence is an inferred hypothesis without explicit population-level measurements. We have chosen to keep this result in the supplement because many individuals from the metabolic community will expect a discussion of energy equivalence given our interaction with Damuth's law, but we agree that it distracts from the main text.

Supplementary Lines 180-194: "The energy equivalence hypothesis is based on the observation that if one assumes that the total metabolism of an ecosystem  $B_{\text{tot}}$  is equally partitioned between all species ( $B_i$ , the total metabolism of one species, is a constant), then the abundances should follow  $N(M)B(M)=B_i$  implying that  $N(M) \propto M^{-\eta}$ , where  $\eta$  is the metabolic scaling exponent<sup>19,20</sup>. As  $\eta \approx 3/4$  this hypothesis is consistent with Damuth's law<sup>19</sup>. However, the actual equivalence of energy usage of diverse species has not been measured at the population level for a variety of whole populations. Figure S2 recasts the results of the NSM in terms of this hypothesis and shows that  $F * B$  is nearly constant over the same range of mammalian sizes up to the asymptotic behavior for the largest terrestrial mammals."

Comment 3.2) The authors should address to what degree the choice of distributions for the initial densities for  $F$  and  $H$  affects results, and why the uniform distribution was chosen (L257). Population sizes tend to exhibit more log-normal like distributions so the choice of a uniform distribution isn't immediately apparent.

Response 3.2) We thank the reviewer for their suggestion. Our goal was to consider the range of possible dynamics within the model and this can effectively be done by covering the full range of initial conditions for those dynamics. Thus, our choice of a uniform distribution was simply to cover the range of values equally and we didn't want to bias our sampling of initial conditions by implementing a particular distribution. Our choice of a uniform distribution should be seen as varying initial conditions along the full range of values, and this could be done using a random selection (as we have implemented) or sequentially across values within the range without altering results.

Comment 3.3) The authors may want to briefly address similarities/differences between their work and Okie et al. (Okie et al. 2013). Conceptually, this work shares some similarities with theory developed in Okie et al. and appears complementary to it (rather than conflicting). Okie et al.'s more coarse-grained theory and macroecological empirical analyses suggest that the evolution of large body size is constrained by ability of taxa to have sufficiently high rates of individual productivity (i.e., growth and reproduction) in order to sufficiently and consistently offset background rates of loss. In both Okie et al. and Yeakel et al., larger mammals are suggested to be more sensitive to variability in factors affecting

physiological and life history rates. Yeakel et al. provide a complimentary more detailed analysis of the population dynamical ways by which these kinds of physiological ecology constraints might constrain maximum evolvable body size, including adding the starvation rates as an important factor to consider.

Response 3.3) We thank the reviewer for this reference, and now address the results of Okie et al. in the text. We note that we have - in general - included more comparisons and contrasts with existing work that explores similar energetic constraints in different contexts. We detail lines in the manuscript where these comparisons are made in Response 1.3.

Lines 340-346: “Similarly, the maximum body size within a particular lineage has been shown to scale with the metabolic normalization constant  $B_0$ . This complementary approach is based on the balance between growth and mortality, and suggests that future connections between the scaling of fat and muscle mass should systematically be connected with  $B_0$  when comparing lineages.

Small suggestions/comments

Minor Comment 3.1) L52: “General dynamic implications”: Perhaps too vague.

Minor Response 3.1) We agree that this sentence is a bit vague and have simply removed it.

Minor Comment 3.2) L126-132. Perhaps add a clarifying phrase or few words. I found these sentences confusing at first read as you first said the rate of reproduction is independent of resource density and then went on to say that the rate of reproduction for the total consumer density is dependent on resource density.

Minor Response 3.2) We agree that this was confusing, and have clarified with the following revisions to the text:

Lines 121-129: “The rate of reproduction is independent of resource density because the full consumer partitions a constant amount of energy towards reproduction, whereas a hungry consumer partitions no energy towards reproduction. Similarly, the consumer maintenance terms ( $\delta H$  and  $\beta F$ ) are also independent of resource density because they represent a minimal energetic requirement for consumers in the H and F state, respectively.”

Minor Comment 3.3) L271. “Allometrically constrained values”. Clarify briefly how these values were allometrically constrained as it is not clear from the main text (requires going to the Methods, which breaks reading flow).

Minor Response 3.3) We now explain that each represents different trajectories along the ontogenetic curve and point the reader to figure 2. Specifically, we now briefly summarize our allometric approach:

Lines 193-199: “Because we aim to explore the starvation-recovery dynamics as a function of an organism’s body mass  $M$ , we parameterize these rates in terms of the percent gain and loss of the asymptotic (maximum) body mass,  $\epsilon M$ , where different values of  $\epsilon$  define different states of the consumer (Fig. 2; see Methods for derivations of allometrically constrained rate equations).”

Minor Comment 3.4) SOM: L61. Should say “known” instead of “know”.

Minor Response 3.4) We thank the Reviewer for catching this error. It is now fixed.

#### Reference

1.

Okie, J.G., Boyer, A.G., Brown, J.H., Costa, D.P., Ernest, S.K.M., Evans, A.R., et al. (2013). Effects of allometry, productivity and lifestyle on rates and limits of body size evolution. *Proc R Soc B*, 280, 20131007.