Peer Community In
Evolutionary Biology

A population biological modeling approach for life history and body size evolution

Wolf Blanckenhorn *based on reviews by Frédéric Guillaume and 2 anonymous reviewers*

A recommendation of:

Density dependent environments can select for extremes of body size

Tim Coulson, Anja Felmy, Tomos Potter, Gioele Passoni, Robert A Montgomery, Jean-Michel Gaillard, Peter J Hudson, Joseph Travis, Ronald D Bassar, Shripad D Tuljapurkar, Dustin Marshall, Sonya M Clegg *(2022), bioRxiv, 2022.02.17.480952, ver. 3 peer-reviewed and recommended by Peer Community in Evolutionary Biology* ***https://doi.org/10.1101/2022.02.17.480952***

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Recommendation

Body size evolution is a central theme in evolutionary biology. Particularly the question of when and how smaller body sizes can evolve continues to interest evolutionary ecologists, because most life history models, and the empirical evidence, document that large body size is favoured by natural and sexual selection in most (even small) organisms and environments at most times. How, then, can such a large range of body size and life history syndromes evolve and coexist in nature?

The paper by Coulson et al. lifts this question to the level of the population, a relatively novel approach using so-called integral projection (simulation) models (IPMs) (as opposed to individual-based or game theoretical models). As is well outlined by (anonymous) Reviewer 1, and following earlier papers spearheading this approach in other life history contexts, the authors use the well-known carrying capacity (K) of population biology as the ultimate fitness parameter to be maximized or optimized (rather than body size per se), to ultimately identify factors and conditions promoting the evolution of extreme body sizes in nature. They vary (individual or population) size-structured growth trajectories to observe age and size at maturity, surivorship and fecundity/fertility schedules upon evaluating K (see their Fig. 1). Importantly, trade-offs are introduced via density-dependence, either for adult reproduction or for juvenile survival, in two (of several conceivable) basic scenarios (see their Table 2). All other relevant standard life history variables (see their Table 1) are assumed density-independent, held constant or zero (as e.g. the heritability of body size).

The authors obtain evidence for disruptive selection on body size in both scenarios, with small size and a fast life history evolving below a threshold size at maturity (at the lowest K) and large size and a slow life history beyond this threshold (see their Fig. 2). Which strategy wins ultimately depends on the fitness benefits of delaying sexual maturity (at larger size and longer lifespan) at the adult stage relative to the preceeding juvenile mortality costs, in agreement with classic life history theory (Roff 1992, Stearns 1992). The modeling approach can be altered and refined to be applied to other key life history parameters and environments. These results can ultimately explain the evolution of smaller body sizes from large body sizes, or vice versa, and their corresponding life history syndromes, depending on the precise environmental circumstances.

All reviewers agreed that the approach taken is technically sound (as far as it could be evaluated), and that the results are interesting and worthy of publication. In a first round of reviews various clarifications of the manuscript were suggested by the reviewers. The new version was substantially changed by the authors in response, to the extent that it now is a quite different but much clearer paper with a clear message palatable for the general reader. The writing is now to the point, the paper's focus becomes clear in the Introduction, Methods & Results are much less technical, the Figures illustrative, and the descriptions and interpretations in the Discussion are easy to follow.

In general any reader may of course question the choice and realism of the scenarios and underlying assumptions chosen by the authors for simplicity and clarity, for instance no heritability of body size and no cost of reproduction (other than mortality). But this is always the case in modeling work, and the authors acknowledge and in fact suggest concrete extensions and expansions of their approach in the Discussion.

References

Coulson T., Felmy A., Potter T., Passoni G., Montgomery R.A., Gaillard J.-M., Hudson P.J., Travis J., Bassar R.D., Tuljapurkar S., Marshall D.J., Clegg S.M. (2022) Density-dependent environments can select for extremes of body size. bioRxiv, 2022.02.17.480952, ver. 3 peer-reviewed and recommended by Peer Community in Evolutionary Biology. https://doi.org/10.1101/2022.02.17.480952

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Reviews

Evaluation round #1

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Author's Reply, 20 Jul 2022

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Please find attached a response to reviewers plus a file comparing the changes between the new and old document. Best wishes, Tim

Decision by Wolf Blanckenhorn, 18 May 2022

Body size evolution is a central theme in evolutionary Biology. Particularly the question of when and how smaller body sizes can evolve is of continuing interest within the field evolutionary ecology, because most life history models, and the empirical evidence, document that large body size is favoured by natural and sexual selection in most organisms and environments at most times.

The paper by Coulson et al. lifts this question to the level of the population, a novel approach, by using so-called integrated projection models (IPMs). As well outlined by (anonymous) Reviewer 1, the authors assume the well-known carrying capacity (K) of population biology as the fitness parameter to be maximized (rather than body size per se), and observe density-dependent (as well as density-independent), size-structured population growth trajectories in terms of age and size at maturity (including also other standard life history traits). Importantly and interestingly, life-history trade-offs are not assumed, as happens frequently in life history models, but emerge as a property from the modelling approach taken here. The authors find that often large body size indeed evolves, but under some (not overly rare) parameter combinations small size can also evolve, while yet other combinations lead to disruptive selection on body size. These results may ultimately explain the evolution of smaller body sizes from large body sizes at least under some environmental circumstances (despite common selection favouring larger individual body sizes).

All reviewers agree that the approach taken seems technically sound (as far as it can be evaluated), and that the results are interesting and worthy of publication after some revision. Nevertheless, at various places clarification and justification of e.g. some assumptions need to be provided as suggested by the reviewers.

Criticism centers on the often too technical descriptions of the model and its assumptions, especially if the targeted readership are general evolutionary ecologists. This should be changed in a revision of the manuscript, and especially reviewers 1 & 2 have made multiple concrete suggestions. One solution is to write the entire manuscript for a more general audience, and to relegate some of the more technical descriptions and justifications for the modelling specialists to an appendix (or the Methods).

In general, and related to the previous criticism of being to technical in writing, the precise focus of the paper needs clarification in the Introduction (again referring to reviewer 1s & 2s comments).

Reviewer 2 additionally points out the necessity of connecting the action of natural selection, in terms of mechanistic selection coefficients, to this overall phenomenological approach. This would help reconcile any differences in the results between this type of population biological model and the more traditional life history models.

Finally, all reviewers made some more specific, minor suggestions on how to improve the paper even further that should be addressed in a revision.

I am looking forward to seeing a revised version of this manuscript in light of the reviewer comments.

Wolf Blanckenhorn, University of Zürich

May 2022

Reviewed by anonymous reviewer, 07 Apr 2022

In this manuscript, the authors study body size evolution, with a particular focus on identifying what promotes the evolution of extremes in body size. They build a size-structured integral projection model (IPM), use carrying capacity as fitness, assume no a priori life history trade-offs, and model some life history traits as density-dependent and others as density-independent. They show that 1) some parameter combinations and scenarios can result in disruptive selection and lead to the evolution of extreme body sizes, 2) under disruptive selection, if the cost of delaying maturity is compensated by a benefit to adults (increased reproduction or lifespan), large bodies will be favoured, otherwise small bodies will evolve, and 3) life history trade-offs can emerge without any a priori trade-off assumptions, simply due to the fact that (negative) density-dependence leads to minimization of density-dependent traits, while density-independent traits are maximized.

General comments:

Overall, I think the topic of body size evolution is very interesting. Body size is a fundamental trait linked to various life history traits, evolutionary dynamics, and ecological interactions, and I think it is always fascinating to read a new study that approaches body size evolution from a different angle. Although I am a theoretician and study life history evolution, I do not have expertise in IPMs, having never used them myself, but it seems to be an adequate framework to tackle the questions the authors study. These said, I do have some suggestions for improvement and some questions.

One of my main problems with this manuscript was that I found it very difficult to identify what the main question was. Is it studying body size evolution under density-dependence? Is it looking at what promotes the evolution of body size extremes? Is it how life history trade-offs can emerge when body sizes evolve under density-dependence? Is it how these trade-offs can affect selection for body size extremes? Is it the demographic patterns that result from these body sizes and life histories? There are some suggestions throughout the manuscript (e.g. lines 59-61, 187-189), but it was very difficult to pinpoint where the main emphasis was. At times, it seemed like the authors were more interested by the methodology and wanted to study what happens when one constructs a size-structured IPM and includes density-dependence, without any specific question in mind. In sum, while I found the results quite interesting, I think the main question(s) should be clearer and the manuscript can be more focused. As it is, it feels unorganized, and at times, it was difficult to read.

I found the emergence of life history trade-offs quite interesting as a result, and it was great to see how these trade-offs can result in different life histories and population structures. However, I wonder whether the fact that density-dependent rates are minimized whereas density-independent ones are maximized is rather trivial. Showing that these trade-offs emerge, and that different population dynamics and life histories can result from them is important and very interesting, but I think it is also important to acknowledge that these trade-offs are rather intuitive based on the modelling approach and assumption, particularly because the authors use carrying capacity as fitness. But perhaps I am missing something.

On a similar vein, I found the emphasis on disruptive selection a little too strong. If I understood correctly, at least in the scenario 1, disruptive selection occurs only at a specific part of the parameter space, which coincides with the parameters that the authors use (see Figure 6). It is not a limited part of the parameter space, and the results are nevertheless very interesting, but I think this could be acknowledged more clearly in the manuscript. Now, it looks like disruptive selection is the main result from their model. They could say that depending on the parameterization of the survival function, one can observe directional selection for large sizes or small sizes, as well as disruptive selection. The former cases might be too "obvious" to discuss at length and I understand opting for leaving them out and focusing on the parameter space where both extremes can occur. However, I think it is important to acknowledge this choice of focusing on one particular set of parameters, and do it earlier in the results section than at the very end. Also, on a related note, if the idea is to look at when extreme body sizes evolve, showing when there is directional selection for large or small sizes is also an answer the authors' question, or am I wrong?

A mix between being very accessible and very technical persists throughout the paper. For instance, I found the Introduction very clear and accessible, until it suddenly became a bit more technical (~line 71). This made me wonder what the target audience of the paper is. Sometimes it read like a paper written for a general (life history) evolution audience, whereas some bits seemed more oriented towards those who are specifically interested in demography and modelling. I wouldn't necessarily say it is bad to do both in one paper per se, but at times the technical explanations came before those that are less jargon-y, which made the paper difficult to read, at least for myself. Several times I found myself looking at the description of what happens in the model and trying to get a biological intuition, only to realize that it followed soon after (e.g. lines 306-328). I think the manuscript would benefit from rethinking a little bit how to present the model and the results, as to make sure the readers are not stuck trying to think what do increasing rates and derivatives mean biologically.

A little more specific comment, but since it is related to my confusion about what the paper is about and who the target audience is: the section about carrying capacity at the Discussion also made me wonder what the aim and audience of the paper is. I think it was interesting to read from a methodological point of view, and to see how this approach can be used or adapted to study interactions between conspecifics, interspecific interactions, responses to environmental change in communities, coexistence etc. But I think if the main goal of the paper is studying body size evolution and life history evolution (?), this section derails it from that goal. For instance, I would have liked the next section that is about the empirical considerations and body size evolution to have a more prominent place in the discussion, possibly with more discussion about how the four functions that the authors used might vary interspecifically and be linked to different sizes we observe in different lineages. There could also be more discussion about how to use existing data or collect data to see how these functions in the nature are. And, perhaps more speculatively, there could also be a more concrete mention of eco-evolutionary dynamics, and how these functions might change when a species responds to environmental change. I particularly liked the discussion of different rules related to body size evolution and the example of sauropods, but I just wished there was more of that; a more prominent and extensive discussion of body size evolution, which to me seems to be the main question of this paper, rather than carrying capacity as fitness, which seems more methodological. And if the paper is indeed a methodological paper inspired by a biological question (instead of vice versa: a novel approach used to study a biological question), then this is not clear and it should be.

More specific comments:

I wonder whether the manuscript would benefit from a figure that explains different scenarios and shows the model structure. I found it difficult to constantly remember what was density-dependent and what was body-size dependent, and what was not, in two different scenarios. Not sure if this is a good idea, but maybe even making a big figure showing the model structure, and inserting the density-independent plots in Fig 1 in there, to show how these functions behave.

The authors refer to slow and fast life histories, but I think they don't really define what they are or explain what rates and what values of them are associated with "slowness" or "fastness" of life histories, which I think would be useful in general, but particularly in the context of their model.

Although it is clear from the context, I think it would be good if the authors clarified earlier on that they talk about "negative density dependence".

Line 149: This mathematical notation is incorrect. Survival is not equal to beta, but beta is different in juveniles and adults.

I found that the results and methods were written in a way that it is not clear what is a method and what is a result obtained from the model (e.g. lines 206-215).

Line 271: typo, "adult reproduction"?

Line 276: Figure ref for adult reproductive rate?

In scenario 2, larger body sizes and slower life histories performed much better compared to smaller body sizes and fast life histories, compared to scenario 1. Could this be discussed, and overall, would it make sense to compare these scenarios a little more?

Line 306: It should be made clearer in the text that this is the point at which fitness is minimum, just like in the figure caption.

Lines 357-370: A very lengthy discussion and presentation of Fig 6 might not be essential for the manuscript text, which is already complicated and long, especially since these parameters were not explored. I would suggest acknowledging the variety of results that can be obtained based on different parameterization of the survival function more clearly in the text (as I suggested above), but moving the non-essential bits to the supplementary material.

Line 361: intercept instead of (or in addition to) elevation?

Line 388: Again here, for instance, it seems to me that the authors completely ignore the fact that their models can also be used to show directional selection for either extreme in size.

Line 391-393: Where is this shown?

Simulation code:

I had a brief look at the code used in the model. The comments in the scripts were quite helpful, but it would be really nice if there was also more explanation on how to use the code, if possible (e.g. a “readme” text explaining which files lead to which figures).

Figures and tables:

Figure 1: Figure 1 was not very easy to understand during a first read. It is more accessible after reading through the manuscript once and after having seen the other figures. For instance, it is not necessarily clear what fitness is (it becomes clearer later) and the reader could be reminded in the caption. In A), what are the bars and are they necessary? In C), would it be possible to place the dots elsewhere, e.g. at the end of the curves, instead of on the part of the curves where life histories start to differ from each other in terms of growth?

Figure 2: I found Figure 2C and D really complicated to unpack; there are two axes, showing three and two different things for scenarios 1 and 2, respectively, two colours for size-distribution of each life history, which are then overlayed creating even more colours. In C, dark colours are reproduction rate, whereas in D they are survival. In the size distribution, adults and juveniles are separated by a vertical line and different colours, whereas for the rates shown with dots, one needs to infer that they are mean rates for juveniles and adults by the positioning of the dots along the x-axis, which is not very consistent. Also, regarding the points showing density-dependent rates (figure caption); aren’t all points solid? Do the authors mean lighter vs darker colours? Also the panels are so close that right y-axis label of C and left y-axis label of D are merged to become essentially one label. And what is the dashed line on panel C? The survival function from 1D? It should be explained. What do the lines that connect darker dots represent in panels C and D? Overall, I was very confused when I saw this figure for the first time, and I think this figure and its caption needs some work to make it easier for the readers to understand it.

Figure 3: Should have a figure main title and say this is scenario 1 in the caption.

Figure 4: What is a_s? Is it age at maturity, and if so, why is it not a_m as before? What the polygons are is not explained clearly. Which axis shows which curve is not very clear. In general, I find figures with two y-axes very complicated and would avoid them if possible. I see why they are useful in this case, but everything should be very clearly explained.

Figure 6: Maybe I am missing something, but why do blue lines end in the middle of x-axis? Does the carrying capacity stay the same after that point or does values were not looked at? If they were not looked at, why are they on the plots?

Figure S1: The caption lacks what the green dot represents (the strategy with minimum fitness I assume)

Table 2: It would be helpful to have the symbols of what these parameters are. In this table, do growth parameters represent 20 different life history scenarios? I am a little confused. And also, of the survival parameters, which ones are for juveniles and which are for adults? To my understanding, in scenario 2, only juvenile survival is density-dependent, whereas both juvenile and adult survival are a function of body size. I expect these to be reflected by non-zero body size and density slopes, but then this means, density slope should be zero for adults and non-zero for juveniles, right? Or am I missing something?

Reviewed by Frédéric Guillaume, 21 Apr 2022

This manuscript addresses the key question of how body size co-evolves with pace of life when some demographic rates are density-dependent. They show how density-dependence generates disruptive selection on body size by maximizing carrying capacity at equilibrium. The outcome of the model is thus the evolution of extreme body sizes and life-histories: small-fast or large-slow. One key interesting aspect of the model is the non-imposition of a trade-off between demographic rates. Instead, a linear trade-off between reproduction and offspring survivorship emerges from the model dynamics. The approach used is a size-structured model called IPM. The topic is complex and so is the methodological approach. I found the model and results descriptions hard to follwo because rather abstract and technical. Certain aspects of the model must be clarified. The manuscript discusses in length some of the key model assumptions, namely fitness defined as carrying capacity and addresses theoretical and empirical implications.

The manuscript will gain by being shortened and streamlined, especially in the Results. Authors should strive to provide more biological intuitive understanding of the outcomes, especially when describing figures in the Results. My general feeling was that it is addressed to IPM specialists more than to a general audience.

Authors should improve the description of the simulation approach implemented, in relation to IPMs. In particular, it is unclear how simulations help in computing a life-history strategy's carrying capacity and whether any evolutionary dynamics are involved in the simulations. No description of the simulation procedure is provided. This should be improved.

One key aspect of the approach not well delineated is whether a polymorphic population (ie containing multiple competing strategies) would actually evolve towards the strategy(ies) having the highest K identified in the IPM analysis and whether they may coexist. The manuscript misses a link between long term evolution as predicted from K-maximization principle à la Lande et al 2009 and per-generation rate of change in average population trait values (eg. body size) provided by a selection gradient. Authors should clarify how such selection gradients, based on a K-definition of fitness can or cannot be derived. It wouls help link with more classical neo-Darwinian thinking about evolutionary dynamics.

In addition, it is assumed that carrying capacity is fitness and thus maximized by evolution but it is not demonstarted that it is indeed the case in the present model. A derivation of a selection gradient emerging from the model definition might clarify this point.

Discussion on carrying capacity as fitness is great but hard to follow. It would gain by being reduced, for instance by focusing on inter-specific interactions. As of now, a large part of that discussion is disconnected from the main subject of the paper. Moreover, a good part of the discussion consists in a verbal description of mathematical models from the literature, which is hard to follow without knowing them. Limiting the discussion to more intuitive arguments would ease the reading by a fair amount.

One key asumption leaves me unsure as whether the model is correct. On L167 (and Figure 1A) the distribution of the offspring size is independent of the adult phenotype. It is fine when considering the variance of the distribution but not when considering the mean. As stated, there is not inheritance of the parental traits in the offspring if the offspring size is invariant as shown in Figure 1A. Is this really the case? (h^2 = 0)? please clarify, provide a justification and explain how the model outcomes depend on that assumption. I would very much doubt that body size evolves in the model if offspring do not inherit their parental size.

L89: clarify that the demonstration of "fitness is carrying capacity" is provided in Lande et al 2009, but not in the other references.

L96/111: provide clarification and a definition of "asymptotic representation" and "asymptotic size".

L98-105: clarify if a demonstration exists or is this only a verbal argument? also clarify if it applies only to a monomorphic starting population, looking at invasion fitness or also applies to polymorphic populations?

L219-220: please provide necessary details about calculations from model predictions.

L325: "ever-earlier size" -> ever-smaller size?

L369: sentence needs correction. The reasons for this comment on linearization are unclear. Please provide more details on why it is necessary.

L411-413: It is unclear where such negative correlations can be directly observed. Please clarify.

table 2: please add symbols to relate to model definition (which are the rho's etc.)

Reviewed by anonymous reviewer, 11 May 2022

The authors investigate one of the problems of life-history evolution, the evolution of extreme body sizes. For this, the authors develop a size-structured integral projection model. Within this approach, the body size is associated with other life-history traits, such as survival, development, reproductive rate, and heredity of body size trait. What I find interesting in the paper is using a carrying capacity as a proxy for the fitness of a particular life-history strategy. Because the used model is density-dependent, the authors split the analysis into two scenarios. The first one, where density-dependence works on reproduction, and the second, where juvenile survival was density-dependant.

As a result, the authors showed conditions under which either body-size extremes evolve (small-bodied or large-bodied). For example, fast life-history evolves when delayed age at maturity leads to increased size at maturity, as well as an elevated mortality rate. In general, this paper adds an understanding of the conditions why a particular body size is selected. There are some assumptions and simplifications made, that the authors state clearly. At the same time, there are several comments I believe would help to improve the manuscript and make it easier to understand.

The authors can see my comments in the PDF file attached

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