Below we give point-by-point replies to the reviewer comments (in green).

Reviewer 1 (Nicole Walasek)

William's prediction states that reduced age-independent extrinsic mortality selects for delaying senescence. At present their exists an abundance of theoretical studies outlining cases in which William's prediction holds, cases in which we observe 'anti-Williams' patterns where reduced extrinsic mortality leads to faster life-histories, and cases in which extrinsic mortality has no effect on senescence ('null-pattern'). While these studies often outline the conditions which might give rise to these specific patterns, the overarching literature is chaotic and there exists no single piece of work which tells the whole story. In this manuscript the authors attempt to systematically explore and highlight conditions which give rise to Williams-like patterns, anti-Williams patterns, and the null-pattern. To this end the authors present 10 variations of a model which compares slow and fast senescing populations while considering different mechanisms of population regulation. In their interpretation the authors lean on the intuitive explanation of considering the relative importance of placing offspring into a population earlier than later. The authors replicate previous theoretical results and find that the null-pattern arises in the absence of density-regulation, or in the presence of density-regulation that depresses survival at all ages. We should expect Williams-like patterns whenever density dependence affects juveniles more so than adults. Lastly, we should expect anti-Williams like patterns when juveniles are shielded from the effects of density-dependence and density-dependence therefore disproportionally affects older individuals.

Although the presented models are simple, they cover key variables and systematically explore a range of realistic scenarios. The results are supplemented with extremely helpful and visually appealing figures. Lastly, the authors do a great job of first providing a basic intuition using a very simple trade-off free model before diving deeper into the main models of the paper.

Thank you for your kind words, and for all the useful feedback below!

My biggest concern regarding the paper is that the language is still quite complex across large parts of the paper. I find this especially problematic because the goal of the authors is to provide an intuitive understanding of the 'chaotic' literature related to William's prediction. I believe that the paper can achieve this goal and reach a wider audience by heavily simplifying the language. Reading the paper, I often felt that I would need to first read all of the previous theoretical studies on William's prediction to fully understand the present work. As I am not an expert in that specific literature and on that specific topic, I find it difficult to provide concrete suggestions for simplifying the language while conveying the depth of the argument. In what follows I try to point to passages that I found especially hard to understand and make concrete suggestions for improvement where I see fit.

The authors may consider reading this blogpost (https://www.danielnettle.org.uk/2022/02/18/live-fast-and-die-young-maybe/) by Daniel

Nettle which discusses their preprint in a manner that is easy to follow. This may give the authors some concrete ideas of how to rephrase some parts of the paper.

Thank you for this useful feedback, and for the link to Daniel Nettle's blog! Like you, we have found the blog text very useful – but we also would like to avoid plagiarizing his work that is very helpfully disseminating our work's content to others. We have been inspired by his clarity of writing when providing this new version.

Comments

- *- In its current form the paper assumes a reader that is already familiar with the literature. In my opinion a reader outside this specific literature will have a hard time following the paper. This is unfortunate as the goal of this work is to order and structure the existing literature related to William's prediction.*

  One way to help a naïve reader is to better explain key concepts, such as selection gradients. These concepts reoccur throughout the entire paper and form a foundation for understanding the present study. Relatedly, the paper seems to be referring to a few key studies (e.g. Caswell 2007 or Day & Abrams' 2020). It would be very helpful for a reader that is not already familiar with these key studies to get a brief and easy introduction to them.

  We have taken this advice seriously, see below for details.

- *- Abstract: After reading the entire paper the abstract seems like a good summary of the paper. Before reading the paper, the abstract was a bit complex and overwhelming. This is true especially for the second half starting with 'Our first examples show ...'. I would advise to revise the second half of the abstract by simplifying the language and reducing the amount of content that is being discussed.*
  - It is indeed difficult to put all the clarification effort of this whole paper into the abstract – but we tried our best.
- *- Lines 56-59: This sentence sounds quite clunky and is somewhat convoluted. I recommend rewriting and simplifying.*
-
  - Thank you for pointing this out, we hope you like our attempt to de-clunk it (now on lines 60-63).
- *- 67-79: This is hard to follow. It seems important and I think it can be explained better. For example, I suggest to briefly explain the concept of selection gradients and to break the sentence into shorter sentences.*
  - Thank you, we expanded this section and we hope it works now (now lines 71-85).
- *- Lines 80-87: I think it would be helpful to more explicitly state that you are contributing actual models which you have developed to explore under what conditions William's prediction holds. I think this whole paragraph would benefit from slight rewriting. Additionally, a reader may wonder how your models are similar or different from previous work (e.g. Day & Abrams 2020).*

    - Thank you for this suggestion, we have rewritten this section quite dramatically. Day & Abrams 2020 do not make use of Gompertz-Makeham survival, but we do not highlight that specifically, as we'd like to avoid giving the impression that their choice is a flaw (it isn't); we simply mention here what we do in our model (new lines 86-104).
- *- Lines 103-106: This sentence is very long and hard to follow. Here, I was expecting to get a brief overview over the conducted work using terms that have already featured in previous parts of the introduction. Instead, there are a lot of new terms (regulation via fecundity, recruitment, or declining survival) that remain unexplained.*
    - Thank you for pointing this out, we rewrote the sentence to make it simpler and shorter. We now only use words/terminology that we had previously already used.
- *- Lines 110-121: Please, explain explicitly how the trade-offs work. For example, you mention reproductive effort trading off with senescence but don't elaborate further. Could you explain in more detail how they trade off and what are other trade-offs?*
    - We explain trade-offs better now, but we put this into a little earlier (intro lines 97-100), as this particular section is about the trade-off-free model.
- *- Lines 171-173: Long sentence which is hard to follow.*
    - We rewrote this section, and also combine the paragraphs in a slightly different way to make the flow better.

- *- Table 3: I understand the function of table 3 in conjunction with table 2. However, I find table 3 in its current form quite unappealing and it is tedious for a reader to go back and forth between the two tables. I suggest that the authors add a few keywords to table 3 which remind the reader of which cells in table 2 the letters in table 3 are referencing.*
    - Done. Thank you for this suggestion!
- *- Lines 216-218: It is very hard to follow this sentence. The explanation for 'canceling out' is important for equipping the reader with some intuition. The authors should rewrite this explanation and elaborate more.*
    - Thank you, this has been rewritten (new lines 229-231, and sentences after it).
- *- Line 219: 'selection to have' does not sound grammatical in the context of the sentence. However, I am not a native English speaker and therefore not sure. Consider rewriting.*
    - This phrase disappeared in the rewrite.
- *- Lines 218-239: this is important and I appreciate that the authors attempt to convey the intuition as easily as possible. However, I believe that there is still quite some scope for simplifying the writing.*
    - We have done our best (new lines 231-249).
- *- Lines 266-272: This is a very long sentence. Consider shortening or breaking into multiple sentences.*
    - We agree. It's now 3 shorter sentences (new lines 276-282).
- *- "beyond the null: what cancels out under density dependence, what does not" I think that the first paragraph in this section does a good job at transmitting information in an intuitive way.*
    - Thank you ☺

- *- Lines 316-320: This is an important intuition which I think could be phrased even clearer. For example, who are the 'remaining individuals'? Why did those remaining individuals respond with improved survival?*
    - We rewrote for added clarity that hopefully exposes the logic more clearly than before (new lines 326-332).
- *- Lines 332-334: This is the key message and well phrased. Perhaps the section could be shortened and start with this message and then provide the intuition in a shorter and more concise way?*
    - Thank you. The request to shorten seems to conflict with the general message (above) that we should clarify more, and we did not really want to risk erring on the too succinct side.
- *- Line 352: What do you mean by equilibrium?*
    - We rephrased (new line 364).
- *- Line 377-379: I believe that there is a word missing in this sentence*
    - We edited this sentence (new line 391-394).
- *- Perhaps first explain the standard procedure in one standalone section called standard procedure and then outline the different scenarios? Also add more subheadings. For example, lines 426-447 could be labeled 'model outcome'. Introducing these additional breaks might make it easier for a reader to follow the overall structure.*
    - Thank you for this suggestion, we agree that some extra subheaders are an improvement.
- *- Lines 448-459: This is a great summary.*
    - Thank you!
- *- The first page of the discussion is well written. I think that the rest of the discussion would benefit from some shortening. Some passages feel quite repetitive. I was also expecting to read more about the practical implications of this current paper. What has the literature gained from this work? How will this work inform future work? However, I also want to stress that the authors already cover these topics to some extent. To me the limitations of the current study got buried somewhere in the discussion. All of my issues might be resolved by restructuring and shortening the discussion section. By removing redundancies with the main text, the practical implications and limitation might shine through more.*

    Thank you for this suggestion, we shortened the discussion on a sentence by sentence basis, and did a fair bit of reorganizing. Both reviewers also wanted additional material, so as a whole it is not shorter, but the previous content has been shortened. In our experience, readers often expect the most major findings to be written about in a re-cap sense in the Discussion, and if we only considered the limitations and extensions of what was found, the discussion would not really manage to serve as a re-cap. We now point to more future work than before.

- *- The authors may consider discussing the implications of their current findings for the human literature (especially psychology and more generally the social sciences) which typically assumes that higher extrinsic (i.e., uncontrollable) mortality favors faster life histories. The current paper provides a valuable overview of the limitations*

of this claim. It may therefore be useful to explicitly connect this current paper with this body of work in the social sciences.

- We have added a paragraph about this, with plenty of pointers to recent literature (lines 582-600).

- *- Lines 531-537: Could you explain why this observation is at odds with the models' predictions?*
  - We have revised this part and we hope it works now.

Reviewer 2:

Dear authors,

Please find my review of the manuscript, "Extrinsic mortality and senescence: a guide for the perplexed".

General comments:

The authors firstly present examples focusing on the occurrence of a null result (where extrinsic mortality has no effect) and the importance of the presence/absence of density-dependence. They then investigate 10 differing scenarios that incorporate density-dependent effects on either age-independent survival, survival at old ages or recruitment. This is in addition to also considering three different forms of density-dependence (deterministic, stochastically or continuous). Ultimately, the authors show that under these different conditions, three scenarios can occur, namely, the null model, the Williams prediction (where increasing extrinsic mortality leads to the evolution of faster senescence) and the anti-Williams model (where increased extrinsic mortality leads to the evolution of slower senescence).

Overall, I believe this to be an important and well-written paper and really only have comments regarding the need for additional clarification and increasing the interpretability of some of the figures, mainly Figure 5 (where the results from the ten different scenarios are shown).

Thank you for your kind words, and for all the useful feedback!

Specific comments:

Keywords: is it worth also adding density-dependence and slow-fast continuum keywords here?

That's a good idea, thank you.

L22: Here and elsewhere: keep with either numerical numbers or written numbers e.g., "ten" – so it matches L86 or for instance on L176 - "one".

Replaced all the 10s with tens.

L24: Possibly worth changing, "that vary along the fast-slow continuum".

In addition, could this be simplified to "favour life histories that vary along the fast-slow continuum", as it is implied that they must either be slow or fast?

The abstract has been rewritten a little bit more than just this, we hope it is now clearer in the current form.

L25-28: "could suggest" sounds odd here. I would consider trying to rewrite this sentence for clarity and possibly end with more of a summarising sentence to this abstract.

We now discuss what we meant: that this is indirect evidence, and we say we "discuss" it in the paper, which we believe hits the tone right: we don't claim we're 100% correct on this, but it's a very intriguing possibility. We actually do think this is a good way to end the abstract. One could add something like "in any case, population regulation is key to everything" but we believe that should be clear from the preceding sentences already.

L58: Could this be reworded to something simpler: i.e., "prediction made by Williams holds and also scenarios when it doesn't hold? – or something similar".

Edited to make this sentence simpler, thanks (new line number 61-63)!

L77: Slight reword to: "by instead focusing explicitly".

Done

L85: Does the use of Gompertz-Makeham survival curves need a very brief explanation? I guess this is discussed on L375 but might be useful here too when it's first introduced.

Good idea; done. (New lines 95-97)

L117: Comma after "we are" and after" in this first exercise".

Done

L124: Is it worth making clear that the bat and mouse can be both fast or slow. Currently the way it is worded could sound like both species have competing life histories (at least to me). For instance - "Both the bat and the mouse are able to be either one of two competing life histories that differ…".

Changed (new line 140-143).

L128-129: What does "The sign of selection is therefore clear" mean. Possibly reword.

Reworded (new lines 144-145)

L158-159: This is a really important point to make.

We agree!

L173: Here you might want to reiterate that fast senescers only breed once which is why you're focusing on slow senescers and the ability to breed twice.

Reworded (new lines 187-189)

L218-221: Not sure I follow this sentence, potentially worth rewriting for clarity.

Rewritten, hopefully clearer now (new lines 231-234).

L230: Unless I'm mistaken, should this be 0.6/3.51? Should the notation be SM or SB?.

You're right, apologies! This equation disappeared in the rewrite with the aim to simplify.

L371-372: Could this be rephrased to: "we contrasted the success of a fast life history that senesces, with a slow life history that does not experience senescence".

Done (new lines 385-386)

L378: (Not a comment, just a thought) I wonder what would happen if fecundity was allowed to change either instead of survival or at the same time, i.e., followed an age-specific reproductive schedule with peak reproduction in midlife followed by a senescent decline?

Interesting question, would be fun to model ☺ In the scenario with density-dependence acting on old age survival, the answer would presumably depend on whether the reproductive peak sits before or after the age classes that suffer from density-dependence. Also, there is the question of whether the peak 'exists' a priori or arises via evolution (trade-offs). It is a much more complicated setting in any case.

L379: Worth reiterating that these are 3A-D in Tables 2/3.

Done (new line 394)

L381: If these are indeed steps - would it be more appealing to place them in a numbered order and then also link them to the life cycle on Figure 4. So the readers know which section describes what part of the standard procedure.

We gave this some thought, but started worrying that they would confuse, as we use a combination of numbers and letters for the scenarios already.

L430: Here and elsewhere: density-dependence/dependent with or without a hyphen. Keep consistent.

There is actually some logic here that we tried to adhere to: 'density-dependent something' (e.g. regulation) versus 'density dependence'.

448-459: This is a very important paragraph. It would be good if this section could directly refer to Figure 5. i.e., when discussing 1A-1C, you could say exactly why the lines represent the null result with reference to values of F0 and F1? This could make it a bit easier to follow. Same with the Williams and anti-Williams mentions.

Good idea, thank you, done (new lines 468-483).

L481-495: This is also an important paragraph that helps readers understand why a Williams pattern is seen, perhaps you could also add some further explanation about 2A-C and why anti-Williams might be seen?

Added a paragraph to explain the anti-Williams result (new lines 503-515).

Figure 1-2: Could there be an indication on the graph that the width of line indicates payoff.

We appreciate the suggestion but we struggled to find a solution that does not look cluttered. We hope the explanation in the Figure legend suffices to make this clear.

I would keep with the notation of time in both figures (Figure 1 preferably), just for consistency.

We added the time axes to all figures now.

Figure 3: What does a and d represent here (I realise it's mentioned earlier, but worth making it obvious in the legend)

Done (green text in figure legend)

Figure 4: "take the same amount of time" rather than "takes equally much time".

Done

Reword "to allow mortality rates the appropriately long time to apply before the next year".

Done

Figure 5 is an important graph. I think it could do with some adjustments as currently it's a tad confusing (though could be a personal preference). For instance:

- *In the legend, reiterate that slow = F0 and fast = F1.*

Edited to this effect.

- *The lines could do with some better explanation and could be clearer. Something like "threshold fecundities for the slow type to win when F1 fecundity differs" or something similar.*

Done

- *Also, you could probably remove some of the axis labels as they are repeated row/column wise, which may reduce clutter?*

Done

- *3C also needs to include 1 as an axis limit as currently it looks to be a bigger increase than the others but really could be a scaling issue.*

Done

- *Also, perhaps it could be easier to move the legend to below the graph, so it doesn't look like its related to the "competition for territories" column, unless you place the title directly over 3D.*

Placed the title directly over 3D

- *Also, unless I missed this, what was the justification for these values of F1 fecundity and for the a/d parameters of the Gompertz-Makeham (i.e., had 5 possible values and d had 2)? Just some additional clarification could be useful (in text and possibly legend would be ideal).*

There is no strong justification for the chosen parameters, similarly shaped graphs can be made with different values. Note that e.g. the example of Table 1 shows that F does not matter at all. We believe that it is more strongly relevant to point out (as we do in the MS) that similarly shaped graphs can be made with an entirely different survival function (a survival function inspired by increasing cancer risk with increasing cell divisions, from Kokko and Hochberg, 2015), which we had used for an earlier version of the manuscript, and for which code and figures can be found at https://doi.org/10.5281/zenodo.6705180). The general shape of these curves (flat, decreasing, or increasing for the 3 types of density-dependence) seems to be quite insensitive to the model details. We hope that the gist of the entire MS makes it clear.