**Review of:**

Manuscript title: Extrinsic mortality and senescence: a guide for the perplexed

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**TO THE EDITOR/authors:**

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.

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.

**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.

- 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.

- Lines 56-59: This sentence sounds quite clunky and is somewhat convoluted. I recommend rewriting and simplifying.

- 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.

- 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).

- 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.

- 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?

- Lines 171-173: Long sentence which is hard to follow.

- 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.

- 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.

- 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.

- 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.

- Lines 266-272: This is a very long sentence. Consider shortening or breaking into multiple sentences.

- "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.

- 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?

- 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?

- Line 352: What do you mean by equilibrium?

- Line 377-379: I believe that there is a word missing in this sentence

- 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.

- Lines 448-459: This is a great summary.

- 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.

- 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.
- Lines 531-537: Could you explain why this observation is at odds with the models' predictions?

I hope my comments will help the authors to further strengthen their paper.

Kind regards,

Nicole Walasek