

Asymmetric life-history trade-offs shape sex-biased longevity patterns

Corresponding Author: Ms Ella Rees-Baylis

This file contains all reviewer reports in order by version, followed by all author rebuttals in order by version.

Version 0:

Reviewer comments:

Reviewer #1

(Remarks to the Author)

The manuscript develops a two-sex, age-structured model to ask how sex-specific life-history trade-offs shape sex-biased longevity under monogamy. The central idea, how sex-asymmetric life-history trade-offs, under monogamy, can bias evolved longevity and why extrinsic density-dependent mortality potentially obscures sex differences in ageing is interesting.

There are a few issues however, in my opinion. The model assumes independent sex-limited loci and effectively haploid inheritance? Intra-locus sexual conflict and genetic correlations are discussed but not modelled? Not clear how robust the predicted dimorphism is under more realistic scenarios.

As far as I can see, rate of senescence is fixed and identical across sexes, only the onset evolves, unclear why and makes the model less general.

Density dependence seems to be uniform across sex and age, yet the Discussion emphasizes sex/age/condition-dependence of hazards, which is much more realistic.

Perhaps one of the main things that's missing, in my view, is some kind of a serious and quantitative attempt to test this hypothesis using experimental data (or perhaps data from the literature).

Finally, the main issue is that the scope is limited to monogamy. This makes it very narrow indeed.

In summary, the topic is interesting, but the approach - focus on monogamy and lack of empirical tests, makes this manuscript less appealing overall.

(Remarks on code availability)

Reviewer #2

(Remarks to the Author)

This paper seeks to develop a set of models that predict how sex-differences in lifespan will arise within populations in response to trade-offs with different reproductive processes. I agree with the authors that this is an area that lacks formal theoretical modelling in spite of wide-spread current interest and informal predictions about how different factors should influence sex-differences in lifespan and ageing. Therefore, this paper is timely and would be of widespread interest to those working in the field. The results are of interest and to my knowledge fit broadly with the empirical observations of sex differences in adult life expectancy that are observed in nature (and in controlled conditions) under the predicted conditions. With respect to this, I would draw the authors attention to this recently published paper that is the biggest comparison of sex-differences in life expectancy across mammals and birds (Staerk et al 2025; Sexual selection drives sex difference in adult life expectancy across mammals and birds, <https://doi.org/10.1126/sciadv.ady8433>). This shows that monogamy is associated with a male-biased life expectancy, as the models here would predict in most scenarios.

Ultimately, as the authors highlight in the discussion, the models are largely limited to predictions under monogamy, although varying the strength of male costs of mate acquisition reduce male lifespan relative to females. The inferences that could be made from this paper would be improved substantially if the authors could also model a different mating system, for example polygyny, and contrast the evolution of sex-differences in lifespan in this context. The model outcomes of widespread male-biased life-expectancy do not fit with observations in mammals where females typically live longer than males, but this type of mating system is also infrequently found in this taxa. Informal predictions for sex-differences in lifespan often focus on mating system as a key factor, so if this could be shown as a predictive factor that influences sex-differences in lifespan that would be of even greater interest. The authors do highlight this as a next step for future work, but I think the inclusion of this would really increase the impact of the work if possible.

The model assumes monogamy but costs of parental care that occur only in females. I would assume that in most monogamous species there is some form biparental care, and indeed in birds where monogamy is found most frequently males invest in some form of parental care in the majority of species (i.e. Cockburn 2006 Prevalence of different modes of parental care in birds doi:10.1098/rspb.2005.3458). Therefore, we would expect that male investment in parental care would also influence annual offspring per union and entail costs for males in many monogamous mating systems that operate under natural conditions. Are the inferences from the models restricted to systems where only females investment in parental care (maybe I am missing something that can be explained in the paper about relevance to biparental care) or can you incorporate the effects of biparental care?

I found the results that density dependent mortality reduce sex-differences in life expectancy very interesting, and serve as an illustrative example of how sex differences in lifespan may not be fully realized. Sex differences in lifespan do appear to be very variable when comparing populations of the same species. Could the density dependent effect on the magnitude of sex differences in lifespan explain the stronger sex differences in lifespan that are observed in zoos over the wild in Stark et al 2025? Could it also explain the fact that sex differences in lifespan can vary quite dramatically in different populations of the same species in the wild (i.e. Lemaître et al 2020, as cited in the manuscript)? The discussion of this result is cautionary, but there is scope to expand on the potential implications in this section.

(Remarks on code availability)

Reviewer #3

(Remarks to the Author)

REVIEW OF NCOMMS-25-59137

"Asymmetric life-history trade-offs shape sex-biased longevity patterns"
by Ms Rees-Baylis and colleagues

This ms addresses an important question that is receiving a lot of attention these days: the difference in longevity between the sexes. The authors examine a particular explanation for this, that the difference is driven by different sex-specific trade-offs between reproduction and survival. They model a particular implementation: monogamous mating, trade-offs operate via mating probability in males and fecundity (realized production of offspring) in females. They use an ESS approach, aiming to find an evolutionary equilibrium state that is not easily invaded. They find that depending on the strength of the trade-offs, they can generate equilibria with males living longer or vice-versa. They also discuss several possible variants of the analysis and discuss the possible effects of at least (a) how the trade-offs occur, (b) polygamy, (c) density by sex or age, (d) individual quality.

The presentation is well thought-through and arranged, the structure of the model is well-presented, the analysis explained well. This is a strong paper but I do have some questions and comments that should improve the presentation, and possibly even the model. I recommend a (I hope, minor) revision that addresses these comments.

(a) Fig 1b and eqn 1 should clearly define the mortality rate but they do not. Look at eqn 1 (page 13). What happens at age $x < M_i$? Fig 1 suggests that survival is 1, or ?? Please clarify.

(b) How is lifespan defined here? Is it an average age at death? I see that you get it from the fundamental matrix, but since that is the key quantity here, it needs to be clearly defined in words. There is no generally accepted definition of the term.

(c) I understand that the rather messy mating function (eqn 6, page 14) is flexible and presumably cool. But why does it matter here instead of a much simpler function that can be applied age-by-age? After all, why should we have large imbalance in the sex ratio here?

(d) On page 11, line 199-201, you talk about quality, saying: "individual heterogeneity can obscure trade-offs [48, 49]," -- true enough;

and then "with high-quality individuals often exhibiting both higher fecundity and longer lifespans compared to lower-quality ones"

I fail to see why the first statement above leads to the second.

I also fail to why differences in "quality" do not get optimized away.

Please explain. In any case, I don't see how these discussions are at all relevant or useful for the points you aim to make in this ms.

(Remarks on code availability)

The code is available and is in R. I assume it is correct!

Version 1:

Reviewer comments:

Reviewer #1

(Remarks to the Author)

This paper provides a theoretical foundation for the verbal model that sex differences in lifespan and ageing are shaped by sex-specific selection for different optima in life-history traits.

I thank the authors for their careful and constructive response. The revised manuscript is substantially improved. My main concerns have been substantially addressed, and I find the revised manuscript notably stronger in both scope and relevance. In particular, the authors have now broadened the scope beyond strict monogamy by adding model extensions for mating-group composition, variation in monogamy type, and biparental care, which makes the paper more generally relevant and considerably more appealing.

They also clarified the rationale for simplifying assumptions about genetic architecture and fixed senescence rates and strengthened the discussion of how these assumptions may limit the magnitude or generality of the predicted dimorphism. In addition, I appreciate the added connection to recent comparative empirical work (Staerk et al) and the supplementary exploration of density dependence, both of which improve the manuscript's biological relevance.

Some limitations remain of course, e.g the model still does not explicitly incorporate sex-specific ageing rates. However, I now find these acceptable as clearly acknowledged limitations of what is, in my view, a useful, important and timely theoretical contribution.

I would support publication in Nat Comms in its current form.

(Remarks on code availability)

Reviewer #2

(Remarks to the Author)

The authors have made some excellent additions to the paper, particularly the mating system modelling component. I think it is an exciting study that makes an important contribution to the field and will be very helpful in explaining sex-differences in lifespan.

I should highlight that I do not have a background in modelling and so I am unable to review the modelling procedure and how this leads to some of the resulting sex-differences in lifespan due to demographic effects (for example, female demographic dominance). However, the other two reviewers (particularly R3) appear to have a background in this area.

I have provided some minor comments below that the authors could consider when revising this paper:

Demographic dominance and density dependent regulation. If there was a way of providing a brief intro to this it would be helpful. In particular I found it hard to understand how much empirical evidence there is that this is a major population level process influencing demography and the evolution of life-histories. Maybe by expanding from line 37?

In the results it is referred that males outlive females over a broad range of trade-off scenarios/trade-off strengths (lines 81 and 96). From my impression of the figures, the term "broad range" is a little strong. There is clearly an overall bias towards longer male longevity when trade-off strengths are equal, but when the trade-off in males is larger they have a shorter or similar lifespan. Maybe a "wider range" of trade-off strengths would be a more accurate description?

Sometimes I found the varied use of the "trade-off" phrase relating to survival-reproduction trade-offs to be confusing. For the modelling of monogamy, it is concluded that males live longer than females under a broad range of scenarios even when intrinsic trade-off strengths are equal (line 95). Here the authors are referring to reproductive processes being costly for lifespan. But then later in this section it is highlighted that this bias towards male lifespan occurs because female lifespan trades off against offspring production, and when males are given this cost via biparental care, the trade-offs can be easily reversed. Here I believe the authors are saying that the evolution of female lifespan constrains offspring production, and via demographic processes this leads to sex-differences in lifespan. Although connected to the trade-off this seems to be a different process and some more careful explanation may make this more easy to understand.

I feel that the data sources used in Fig 5bandc should be cited within the results section to avoid confusion (line 144). In the methods, you also refer to the this figure as Figure 4bandc, which should be updated.

When introducing the mating system component (either in the introduction or results), adding a couple of references relating to operational sex ratios and intensity of sexual competition might help justify the approach. Currently references are cited for sexual selection intensity and sex-differences in ageing/mortality costs (2,27,28) but a reference or two citing the relationship between OSR and sexual selection etc would be good.

Life-history trade-offs between reproduction and lifespan are often considered in two ways: on a population/species level, and also on an individual level (i.e. intraspecific trade-offs). In the former genetic differences can evolve that mediate the trade-off (and can constrain lifespan even if animals don't actually get the opportunity to reproduce). In the latter changes in reproductive effort within an individual's life-course would have an effect on lifespan. Can it be clarified whether one or both of these types of trade-offs are modelled in this paper? In the discussion the authors talk about empirical evidence for early-late life trade-offs and cite a review on wild animals (ref 38). To my knowledge this article summarizes the trade-offs observable between early and late-life traits that have been observed in wild animals in the absence of any manipulation, and the trade-offs could be a consequence population level factors, rather than intraspecific trade-offs. The authors also highlight the need for manipulative studies of reproductive investment (line 216) to test the importance of trade-offs in causing sex-differences in aging and life-history. A recent paper has shown wide-spread evidence for the trade-off between reproduction and lifespan across vertebrates in the context of sterilization as a manipulation of reproduction. Across all species there is a similar average effect on lifespan in males and females, although the relative effect on lifespan differs dramatically in different species. This may help to justify the variation and parameters for strengths of trade-offs used in your model. Garratt M et al. (2026). Sterilization and contraception increase lifespan across vertebrates. <https://www.nature.com/articles/s41586-025-09836-9>

(Remarks on code availability)

Reviewer #3

(Remarks to the Author)

Good responses to my critiques and the others, thoughtful and clear. The revision is better and acceptable, in my view.

(Remarks on code availability)

NA

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Reviewer #1 (Remarks to the Author):

The manuscript develops a two-sex, age-structured model to ask how sex-specific life-history trade-offs shape sex-biased longevity under monogamy. The central idea, how sex-asymmetric life-history trade-offs, under monogamy, can bias evolved longevity and why extrinsic density-dependent mortality potentially obscures sex differences in ageing is interesting.

There are a few issues however, in my opinion. The model assumes independent sex-limited loci and effectively haploid inheritance? Intra-locus sexual conflict and genetic correlations are discussed but not modelled? Not clear how robust the predicted dimorphism is under more realistic scenarios.

We appreciate the reviewer raising this important consideration about genetic architecture. We agree that intra-locus sexual conflict and genetic correlations are important factors that can constrain the evolution of lifespan dimorphism. The influence of these factors on sex differences in ageing and longevity has been addressed in several empirical studies (e.g., Archer et al., 2012; Berg & Maklakov, 2012; Chen & Maklakov, 2014; Lewis et al., 2011; Maklakov et al., 2008). These studies suggest, intuitively, that stronger genetic correlations and intra-locus sexual conflict constrain the extent of lifespan dimorphism that can evolve – and we therefore explicitly acknowledge in the Discussion that incorporating such genetic architecture in our model would likely reduce the magnitude of the predicted dimorphism (Lines 298-302).

That said, there is also empirical evidence suggesting traits affecting longevity may have some capacity to evolve semi-independently in each sex. The heritability of lifespan can be substantially sex-limited in *Drosophila* (Lehtovaara et al., 2013), several loci with sex-specific associations with longevity have been identified in mice (Jackson et al., 2002) and humans (Zeng et al., 2018), and a lack of intra-locus sexual conflict over ageing was found in crickets (Zajitschek et al., 2007). Whilst the generality of this pattern and its magnitude likely vary across taxa, these examples suggest that the assumption of largely sex-limited loci is not without empirical grounding. We have now also added this to the Discussion (Lines 296-297).

Our decision to not explicitly incorporate more complex genetic architecture in the model also reflects the theoretical focus of this paper. The effects of sex-specific life-history trade-offs on the evolution of sex-biased longevity have not previously been investigated in a theoretical framework. We therefore chose to isolate these mechanisms first, in order to characterise their effects clearly before layering in additional complexity. This is a standard approach in theoretical work: establishing a tractable baseline that can be systematically extended. We believe this contribution stands on its own merits, and we hope it will motivate future work incorporating other genetic assumptions, including genetic correlations and intra-locus conflict.

As far as I can see, rate of senescence is fixed and identical across sexes, only the onset evolves, unclear why and makes the model less general.

The reviewer is correct that we assume fixed ageing rates between the sexes in our model – we appreciate this observation and agree it represents a simplifying assumption. Our decision to focus on longevity (or the age of onset of senescence) reflects the empirical literature we are primarily trying to engage with. Patterns of sex-biased longevity are well-documented and show consistent associations with factors such as the intensity of sexual selection, providing concrete targets for theoretical investigation. In contrast, the direction and magnitude of sex-specific ageing rates is less empirically consistent, making it harder to formulate clear theoretical predictions to test.

For instance, a study in captive ruminants found that the intensity of sexual selection negatively correlates with the age of onset of senescence in males, but shows no relationship with the rate of senescence (Tidière et al., 2015), and a comparative analysis in wild mammals revealed that median lifespan of females is on average longer than that of males, but found no consistent sex differences in ageing rates (Lemaître et al., 2020). We therefore chose to focus on life expectancy differences as a tractable first step, where the empirical grounding is stronger. We agree with the reviewer that extending the model to allow sex-specific rates of senescence would be a natural and valuable next step as the empirical picture better develops. We have made this point clearer in our Discussion (Lines 307-314).

Density dependence seems to be uniform across sex and age, yet the Discussion emphasizes sex/age/condition-dependence of hazards, which is much more realistic.

We thank the reviewer for raising this point and agree that other forms of density regulation merit exploration. In response, we implemented an alternative form of density regulation in which density dependence affects fecundity rather than age-independent survival. For example, competition for mating sites may allow individuals to survive but prevent reproduction in a given season. We have added these results to the Supplementary Information (Lines 754-771; Supplementary Figure 5), and our main conclusion regarding the evolution of male-biased longevity under more scenarios remains robust to this alternative assumption, albeit requiring stronger trade-off strengths for sex differences to emerge clearly.

Regarding age-specific density dependence: how this affects the evolution of senescence has already been investigated in several theoretical studies (e.g., Daňko et al., 2017; Day & Abrams, 2020; de Vries et al., 2023), so we have not duplicated this work here. Regarding sex-specific effects of density dependence: we chose not to implement these as the directional prediction seems intuitive – the sex experiencing stronger density-dependent extrinsic mortality should show a greater reduction in realised life expectancy – though we acknowledge this could be tested explicitly in future work.

Perhaps one of the main things that's missing, in my view, is some kind of a serious and quantitative attempt to test this hypothesis using experimental data (or perhaps data from the literature).

We appreciate this suggestion and agree that stronger empirical connections strengthen the paper. In response, we have made connections with the recently published large comparative dataset of Staerk et al., (2025). Specifically, we changed the metric we use to quantify sex differences in longevity to match that used in Staerk et al., (2025) (Lines 70-74), allowing for more direct comparisons between our theoretical predictions and their empirical patterns, and reference this paper in sections of our Introduction and Discussion. That said, our primary goal in this paper is to develop theory that addresses an important gap in our understanding of how sex-specific life-history trade-offs shape the evolution of sex-biased longevity. We believe this theoretical foundation is a necessary first step that can help motivate and inform empirical tests in the future.

Finally, the main issue is that the scope is limited to monogamy. This makes it very narrow indeed.

We are grateful to the reviewer for highlighting this important limitation. We fully agree that mating systems beyond monogamy are important and deserve investigation, and in response we have substantially expanded the scope of the model. We developed an extended model that explores the effect of group composition – the number of males and females in a group – as a key axis of mating system variation. In this model, the strength of the trade-off between mating and longevity in each sex is determined by the effective reproductive skew. We find, in accordance with empirical findings, that females tend to outlive males in female-biased (e.g., polygynous) groups, whereas males tend to outlive females in male-biased (e.g., polyandrous) groups. We have incorporated this model into the Methods (Lines 440-472) and Results (Lines 147-185; Figure 6), and have revised the Introduction and Discussion accordingly.

We also developed additional model extensions exploring bi-parental care (common in monogamous species; motivated by a comment from Reviewer 2) and variation in monogamy type (lifelong versus sequential), which we have added to the Supplementary Information (bi-parental care: Lines 736-746 and Supplementary Figure 4; monogamy type: Lines 727-735 and Supplementary Figure 3). We acknowledge that mating systems are complex and covary with other factors that plausibly affect sex differences in longevity, such as sex biases in dispersal. A full investigation of all components of mating system is beyond the scope of this paper, but we believe our model extensions (variation in monogamy type, group composition, and parental care assumptions) provide a solid initial framework for better understanding how mating system variation shapes the evolution of sex-biased longevity, and we hope it will motivate further theoretical and empirical work in this direction.

We also retained the baseline monogamous model because monogamy is abundant in nature (e.g., found in most bird species) and encompasses meaningful variation (e.g., sequential versus lifetime monogamy that we

now model explicitly; Supplementary Figure 3). Our results under monogamy are valuable precisely because they help explain how asymmetries in sex-biased longevity can arise under an apparently symmetric mating system.

In summary, the topic is interesting, but the approach - focus on monogamy and lack of empirical tests, makes this manuscript less appealing overall.

We thank the reviewer for their constructive comments, which have substantially improved the manuscript. In response, we have: expanded our theoretical framework beyond monogamy by incorporating variation in monogamy type, group composition, and parental care assumptions; strengthened our engagement with empirical patterns through a direct comparison with the large comparative dataset of Staerk *et al.* (2025); and clarified our theoretical focus and its relationship to existing empirical work throughout the manuscript. We hope these revisions address the reviewer's concerns and that the manuscript is now more compelling in scope.

Reviewer #2 (Remarks to the Author):

This paper seeks to develop a set of models that predict how sex-differences in lifespan will arise within populations in response to trade-offs with different reproductive processes. I agree with the authors that this is an area that lacks formal theoretical modelling in spite of wide-spread current interest and informal predictions about how different factors should influence sex-differences in lifespan and ageing. Therefore, this paper is timely and would be of widespread interest to those working in the field. The results are of interest and to my knowledge fit broadly with the empirical observations of sex differences in adult life expectancy that are observed in nature (and in controlled conditions) under the predicted conditions. With respect to this, I would draw the authors attention to this recently published paper that is the biggest comparison of sex-differences in life expectancy across mammals and birds (Staerk *et al.* 2025; Sexual selection drives sex difference in adult life expectancy across mammals and birds, <https://doi.org/10.1126/sciadv.ady8433>). This shows that monogamy is associated with a male-biased life expectancy, as the models here would predict in most scenarios.

We thank the reviewer for drawing our attention to Staerk *et al.* (2025), which appeared after our initial submission, and we agree that their findings generally align well with our theoretical predictions. As also noted in our response to Reviewer 1, we have now made connections to the dataset in the manuscript, adapting our metric for quantifying sex differences in longevity to match that used by Staerk *et al.* (2025) to allow for more direct comparisons (Lines 70-74), and we reference this paper in our Introduction and Discussion.

Ultimately, as the authors highlight in the discussion, the models are largely limited to predictions under monogamy, although varying the strength of male costs of mate acquisition reduce male lifespan relative to females. The inferences that could be made from this paper would be improved substantially if the authors could also model a different mating system, for example polygyny, and contrast the evolution of sex-differences in lifespan in this context. The model outcomes of widespread male-biased life-expectancy do not fit with observations in mammals where females typically live longer than males, but this type of mating system is also infrequently found in this taxa. Informal predictions for sex-differences in lifespan often focus on mating system as a key factor, so if this could be shown as a predictive factor that influences sex-differences in lifespan that would be of even greater interest. The authors do highlight this as a next step for future work, but I think the inclusion of this would really increase the impact of the work if possible.

We very much appreciate this suggestion, which aligns with a similar comment from Reviewer 1. We agree that extending beyond monogamy would substantially increase the impact of the work, and we have done so. As described in our response to Reviewer 1, we have introduced a divorce parameter to explore variation within monogamy itself (lifelong versus sequential), finding that our main conclusions are robust to the type of monogamy assumed (Supplementary Information Lines 727-735; Supplementary Figure 3). More substantially, we developed an extended model that varies group composition – the number of males and females in a mating group – as a key axis of mating system variation, with the strength of the trade-off between mating and longevity in each sex determined by the effective reproductive skew. This extended model directly addresses the reviewer's point: we find that females tend to outlive males in female-biased (e.g., polygynous) groups, whereas males tend to outlive females in male-biased (e.g., polyandrous) groups, in accordance with empirical patterns in mammals and birds. We have incorporated this model into the Methods (Lines 440-472) and Results (Lines 147-185; Figure 6), and have revised the Introduction and Discussion accordingly.

The model assumes monogamy but costs of parental care that occur only in females. I would assume that in most monogamous species there is some form biparental care, and indeed in birds where monogamy is found

most frequently males invest in some form of parental care in the majority of species (i.e. Cockburn 2006 Prevalence of different modes of parental care in birds doi:10.1098/rspb.2005.3458). Therefore, we would expect that male investment in parental care would also influence annual offspring per union and entail costs for males in many monogamous mating systems that operate under natural conditions. Are the inferences from the models restricted to systems where only females investment in parental care (maybe I am missing something that can be explained in the paper about relevance to biparental care) or can you incorporate the effects of biparental care?

This is an excellent point, and we agree that bi-parental care is common amongst monogamous species, particularly in birds. In response, we developed a model extension in which both sexes trade off survival with offspring production and have added these results to the Supplementary Information (Lines 736-746; Supplementary Figure 4). We find that adding bi-parental care diminishes the male life expectancy advantage that we found previously assuming female-only care, since male as well as female longevity now trades-off with offspring production and the feedback with population size. This confirms the reviewer's intuition about the importance of male parental investment.

I found the results that density dependent mortality reduce sex-differences in life expectancy very interesting, and serve as an illustrative example of how sex differences in lifespan may not be full realized. Sex differences in lifespan do appear to be very variable when comparing populations of the same species. Could the density dependent effect on the magnitude of sex differences in lifespan explain the stronger sex differences in lifespan that are observed in zoos over the wild in Steark et al 2025? Could it also explain the fact that sex differences in lifespan can vary quite dramatically in different populations of the same species in the wild (i.e. Lemaitre et al 2020, as cited in the manuscript)? The discussion of this result is cautionary, but there is scope to expand on the potential implications in this section.

We appreciate the reviewer highlighting these interesting implications of our density-dependence results. We agree there is scope to expand on these patterns, and we have done so. We expanded the Discussion to reflect on the potential role of density dependence in explaining variation in sex difference in lifespan across contexts (Lines 271-277), including the patterns highlighted by the reviewer – namely the stronger sex differences observed in the wild versus in zoos in Staerk *et al.* (2025), and the variation across populations of the same species documented in Lemaitre *et al.* (2020).

In addition, motivated by a comment from Reviewer 1, we implemented an alternative form of density regulation in which density dependence acts on fecundity rather than survival – for example, competition for mating sites may allow individuals to survive but prevent reproduction in a given season. Our main conclusion regarding the evolution of male-biased longevity under more scenarios remains robust to this alternative assumption, albeit requiring stronger trade-off strengths for sex differences to emerge clearly (Supplementary Information Lines 753-771; Supplementary Figure 5). This further supports the general relevance of density-dependent processes in shaping the realised magnitude of sex differences in life expectancy.

Reviewer #3 (Remarks to the Author):

REVIEW OF NCOMMS-25-59137

"Asymmetric life-history trade-offs shape sex-biased longevity patterns"
by Ms Rees-Baylis and colleagues

This ms addresses an important question that is receiving a lot of attention these days: the difference in longevity between the sexes. The authors examine a particular explanation for this, that the difference is driven by different sex-specific trade-offs between reproduction and survival. They model a particular implementation: monogamous mating, trade-offs operate via mating probability in males and fecundity (realized production of offspring) in females. They use an ESS approach, aiming to find an evolutionary equilibrium state that is not easily invaded. They find that depending on the strength of the trade-offs, they can generate equilibria with males living longer or vice-versa.

They also discuss several possible variants of the analysis and discuss the possible effects of at least (a) how the trade-offs occur, (b) polygamy, (c) density by sex or age, (d) individual quality.

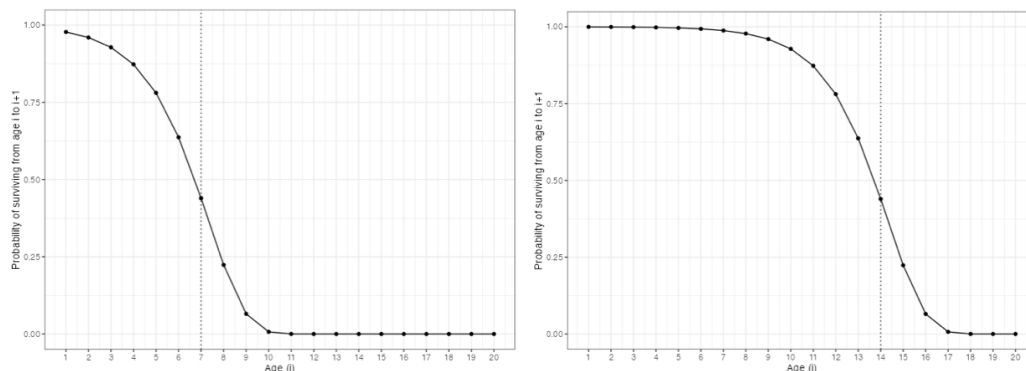
The presentation is well thought-through and arranged, the structure of the model is well-presented, the analysis explained well. This is a strong paper but I do have some questions and comments that should improve the presentation, and possibly even the model. I recommend a (I hope, minor) revision that addresses these

comments.

(a) Fig 1b and eqn 1 should clearly define the mortality rate but they do not. Look at eqn 1 (page 13). What happens at age $x < M_i$? Fig 1 suggests that survival is 1, or ?? Please clarify.

We thank the reviewer for bringing to our attention that this is unclear. In response, we have added a clarifying sentence to the caption of Figure 1 and to the explanation of equation 1 in the Methods (Lines 351-352).

When $x < M_i$, survival is close to 1 (in the absence of density-dependent mortality) but declines gradually, with the rate of decline accelerating markedly at M_i – the age at which senescence begins to strongly limit survival. The exact shape of the function thus depends on the value of M_i . We have kept Fig. 1b as a schematic diagram illustrating the general shape of the function, given the amount of detail already present in this figure. For clarity, we here show two examples of the actual survival function under $M_i = 7$ and $M_i = 14$:



(b) How is lifespan defined here? Is it an average age at death? I see that you get it from the fundamental matrix, but since that is the the key quantity here, it needs to be clearly defined in words. There is no generally accepted definition of the term.

We appreciate the reviewer noting this ambiguity. The output from the model is life expectancy at adulthood – the average age at death, conditioned on survival to adulthood, facilitating comparison with empirical studies that typically use the same definition. In our model, reproduction can become non-zero from age 2, which we therefore define as the age of adulthood, and calculate life expectancy from this point accordingly. This definition is given in the Methods, but for clarity we have now also added it to the model overview section of the Results, where the term is first introduced (Lines 68-70).

(c) I understand that the rather messy mating function (eqn 6, page 14) is flexible and presumably cool. But why does it matter here instead of a much simpler function that can be applied age-by-age? After all, why should we have large imbalance in the sex ratio here?

We appreciate the opportunity to clarify our choice of mating function. In equation 6, we sum over all age classes since we do not explicitly model age-assortative mating – however, in the implementation in the projection matrix it is applied in an age-by-age manner (*e.g.*, an age 3 female mating with an age 4 male) as detailed in the Supplementary Methods (Equations. 46-51).

Regarding the choice of mating function itself: whilst we agree simpler functions might seem preferable, alternatives such as the minimum function and harmonic mean (of which our current function is a combination of) each have well-documented limitations. The minimum function assumes that all individuals of the limiting sex will mate, which can be biologically unrealistic. The harmonic mean was designed for continuous-time models and can be problematic in discrete-time models like ours, where it can produce per-time-step mating probabilities exceeding 1 – an issue that can only be avoided by imposing unrealistically low mating probabilities at balanced sex ratios (mating efficiency). These limitations are discussed in detail by Cachelou *et al.* (2024), who propose the minharmonic mating function as a solution. This function is mathematically sound, ensures that the number of unions never exceeds the number of individuals of the limiting sex, and allows flexible assumptions about mating efficiency – which is why we chose to implement it here. That said, our main conclusions are robust to different

assumptions about mating efficiency (Supplementary Figure. 2), suggesting the specific functional form is not driving our results.

(d) On page 11, line 199-201, you talk about quality, saying: "individual heterogeneity can 200 obscure trade-offs [48, 49], " -- true enough;

and then "with high-quality individuals often exhibiting both higher fecundity and longer lifespans compared to lower-quality ones"

I fail to see why the first statement above leads to the second.

I also fail to why differences in "quality" do not get optimized away.

Please explain. In any case, I don't see how these discussions are at all relevant or useful for the points you aim to make in this ms.

We apologise that our writing was unclear and thank the reviewer for pointing this out – we have revised this passage (Lines 285-290). The connection between the first and the second sentences is as follows: if individual quality is mediated by environmental heterogeneity – for example, whether an individual is born into a resource-rich or resource-poor environment – then high-quality individuals may have sufficient energy reserves to achieve both high fecundity and long lifespan, while low-quality individuals face a harsher trade-off between the two. In this case, the trade-off would be detectable in low-quality individuals but obscured in high-quality ones, hence individual heterogeneity can mask the presence of trade-offs at the population level. Such quality differences need not be optimised away if they reflect persistent environmental variation rather than heritable genetic variation. We include this in the discussion because our model assumes the trade-off operates uniformly across all individuals of a given sex, and we therefore wanted to acknowledge in the Discussion that the empirical detection of the predicted patterns may be complicated by individual and environmental heterogeneity.

Reviewer #3 (Remarks on code availability):

The code is available and is in R. I assume it is correct!

We appreciate the reviewer's trust in our code! All model code and output is available for testing in an online repository, with the link to this found in the main manuscript.

References cited in our responses:

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Reviewer #1 (Remarks to the Author):

This paper provides a theoretical foundation for the verbal model that sex differences in lifespan and ageing are shaped by sex-specific selection for different optima in life-history traits.

I thank the authors for their careful and constructive response. The revised manuscript is substantially improved. My main concerns have been substantially addressed, and I find the revised manuscript notably stronger in both scope and relevance. In particular, the authors have now broadened the scope beyond strict monogamy by adding model extensions for mating-group composition, variation in monogamy type, and biparental care, which makes the paper more generally relevant and considerably more appealing.

They also clarified the rationale for simplifying assumptions about genetic architecture and fixed senescence rates and strengthened the discussion of how these assumptions may limit the magnitude or generality of the predicted dimorphism. In addition, I appreciate the added connection to recent comparative empirical work (Staerk et al) and the supplementary exploration of density dependence, both of which improve the manuscript's biological relevance.

Some limitations remain of course, e.g the model still does not explicitly incorporate sex-specific ageing rates. However, I now find these acceptable as clearly acknowledged limitations of what is, in my view, a useful, important and timely theoretical contribution.

I would support publication in Nat Comms in its current form.

We are pleased to hear that the reviewer's main concerns have been substantially addressed, and we thank them again for providing useful feedback that improved the manuscript.

Reviewer #2 (Remarks to the Author):

The authors have made some excellent additions to the paper, particularly the mating system modelling component. I think it is an exciting study that makes an important contribution to the field and will be very helpful in explaining sex-differences in lifespan.

I should highlight that I do not have a background in modelling and so I am unable to review the modelling procedure and how this leads to some of the resulting sex-differences in lifespan due to demographic effects (for example, female demographic dominance). However, the other two reviewers (particularly R3) appear to have a background in this area.

I have provided some minor comments below that the authors could consider when revising this paper:

Demographic dominance and density dependent regulation. If there was a way of providing a brief intro to this it would be helpful. In particular I found it hard to understand how much empirical evidence there is that this is a major population level influencing demography and the evolution of life-histories. Maybe by expanding from line 37?

We thank the reviewer for this helpful suggestion, and we agree that a brief clarification of the role of population-level processes improves accessibility. We added a sentence to the Introduction when mentioning female life history trade-offs: "Since reproduction is typically limited by female fecundity, female life histories may also be more directly linked to population-level dynamics, although empirical evidence largely focuses on direct survival costs of reproduction." We also expanded a sentence in the Introduction to highlight that current theoretical predictions remain limited when such processes are taken into account: "Current insights have been drawn primarily from empirical studies and meta-analyses, and there remains a lack of formal theoretical predictions to explain how sex-specific life-history trade-offs can shape lifespan evolution, particularly when accounting for feedbacks between individual life histories and population-level processes such as population size, density-dependent regulation, and mating structure." We keep these additions brief to conserve the flow of the Introduction, and provide a more detailed discussion of these processes in relation to our model results in the Discussion.

In the results it is referred that males outlive females over a broad range of trade-off scenarios/trade-off strengths (lines 81 and 96). From my impression of the figures, the term “broad range” is a little strong. There is clearly an overall bias towards longer male longevity when trade-off strengths are equal, but when the trade-off in males is larger they have a shorter or similar lifespan. Maybe a “wider range” of trade-off strengths would be a more accurate description?

We agree with the reviewer and have updated the wording to use “wider range” instead.

Sometimes I found the varied use of the “trade-off” phrase relating to survival-reproduction trade-offs to be confusing. For the modelling of monogamy, it is concluded that males live longer than females under a broad range of scenarios even when intrinsic trade-off strengths are equal (line 95). Here the authors are referring to reproductive processes being costly for lifespan. But then later in this section it is highlighted that this bias towards male lifespan occurs because female lifespan trades off against offspring production, and when males are given this cost via biparental care, the trade-offs can be easily reversed. Here I believe the authors are saying that the evolution of female lifespan constrains offspring production, and via demographic processes this leads to sex-differences in lifespan. Although connected to the trade-off this seems to be a different process and some more careful explanation may make this more easy to understand.

We thank the reviewer for this helpful comment, and agree that our previous wording did not clearly distinguish between the direct effects of the intrinsic survival-reproduction trade-offs and the asymmetry that emerges through their demographic consequences.

In the baseline model, the trade-offs in males and females are mathematically equivalent in form: increasing longevity in either sex reduces a component of reproduction by the same proportional amount. Thus, the asymmetry underlying the bias towards male-biased longevity does not arise directly from these intrinsic trade-offs themselves, but indirectly from how they act on different components of reproduction (offspring production or per union versus the number of unions formed) and how these propagate through population dynamics. To clarify this, added a sentence to the Results: “The key asymmetry does not arise directly from the intrinsic trade-offs themselves, which are symmetric in form, but indirectly from how they act on different components of reproduction and thereby feedback differentially into population-level dynamics.”

We have also clarified the interpretation of the bi-parental care scenario: “In this extension, we apply the survival-offspring production trade-off to both sexes, so that population size and subsequent union formation are jointly determined by male and female life histories. This restores demographic symmetry between the sexes; the model is entirely symmetric with respect to sex when survival-offspring production trade-off strengths are equal, such that the sex with the stronger trade-off evolves a shorter life expectancy (Supplementary Fig. 4). Any remaining bias towards shorter male life expectancy arises due to males incurring additional costs of mating effort.”

We hope these revisions clarify the distinction between the intrinsic trade-offs and their demographic consequences.

I feel that the data sources used in Fig 5bandc should be cited within the results section to avoid confusion (line 144). In the methods, you also refer to the this figure as Figure 4bandc, which should be updated.

We are grateful to the reviewer for bringing these to our attention. We have cited the data sources when referring to Fig. 5 b and c in the Results section, and corrected the typo in the Methods section to refer to this as Figure 5.

When introducing the mating system component (either in the introduction or results), adding a couple of references relating to operational sex ratios and intensity of sexual competition might help justify the approach. Currently references are cited for sexual selection intensity and sex-differences in ageing/mortality costs (2,27,28) but a reference or two citing the relationship between OSR and sexual selection etc would be good.

We appreciate this good suggestion from the reviewer. We now cite a meta-analytical study showing that operational sex ratio predicts the intensity and direction of sexual selection across a wide range of taxa. We use this relationship to motivate our modelling assumption that competition intensity increases as a sex becomes more common in the mating pool, thereby strengthening mating-related survival costs in the model. The relevant addition to the Results is: “Given that operational sex ratio biases are known to influence the direction and

intensity of sexual selection (Janicke *et al.*, 2018) we assume here that trade-off strengths depend on competition intensity, measured as the proportion of each sex that successfully mates: when a smaller fraction mates, competition intensifies and the survival cost of mating effort increases.”

Life-history trade-offs between reproduction and lifespan are often considered in two ways: on a population/species level, and also on an individual level (i.e. intraspecific trade-offs). In the former genetic differences can evolve that mediate the trade-off (and can constrain lifespan even if animals don't actually get the opportunity to reproduce). In the latter changes in reproductive effort within an individual's life-course would have an effect on lifespan. Can it be clarified whether one or both of these types of trade-offs are modelled in this paper? In the discussion the authors talk about empirical evidence for early-late life trade-offs and cite a review on wild animals (ref 38). To my knowledge this article summarizes the trade-offs observable between early and late-life traits that have been observed in wild animals in the absence of any manipulation, and the trade-offs could be a consequence population level factors, rather than intraspecific trade-offs. The authors also highlight the need for manipulative studies of reproductive investment (line 216) to test the importance of trade-offs in causing sex-differences in aging and life-history. A recent paper has shown wide-spread evidence for the trade-off between reproduction and lifespan across vertebrates in the context of sterilization as a manipulation of reproduction. Across all species there is a similar average effect on lifespan in males and females, although the relative effect on lifespan differs dramatically in different species. This may help to justify the variation and parameters for strengths of trade-offs used in your model. Garratt M *et al.* (2026). Sterilization and contraception increase lifespan across vertebrates. <https://www.nature.com/articles/s41586-025-09836-9>

We thank the reviewer for this insightful comment. Our model captures survival-reproduction trade-offs at the genetic (population) level rather than as within-individual plastic trade-offs over the life course. Specifically, the evolving traits determine how individuals allocate investment between survival and reproduction, thereby shaping life-history strategies via selection, even in the absence of within-lifetime changes in reproductive effort. We added a sentence to the Introduction to clarify this ambiguity: “The trade-offs here operate at the level of evolved life-history strategies (i.e. genetic allocation), rather than representing within-individual plastic changes in reproductive effort over the life course.”

We agree that empirical evidence for such trade-offs can arise both from population-level patterns and within-individual processes. In line with this, and following the reviewer's suggestion, we have incorporated the suggested citation in the Discussion: “This challenges the centrality of life-history trade-offs in shaping sex differences in longevity and highlights the need for targeted empirical studies – such as manipulations of reproductive investment or survival costs, which can directly reveal such trade-offs (e.g., Garratt *et al.*, 2026) – as well as further theoretical work incorporating different assumptions.”

Reviewer #3 (Remarks to the Author):

Good responses to my critiques and the others, thoughtful and clear. The revision is better and acceptable, in my view.

We thank the reviewer again for their constructive feedback which has helped to improve the manuscript.

Reviewer #3 (Remarks on code availability):

NA