

Round #1

Author's Reply:

by Gabriel Ramos-Fernández, 2021-07-18 22:13

Manuscript: <https://ecoevorxiv.org/bg94n>

Minor revisions

Two reviewers have written a positive opinion of your preprint. Reviewer [1] is asking for several clarifications which I think could increase the readability of the manuscript, as well as suggesting some restructuring which you might want to consider.

Thank you very much for your work and the positive comments. Please find below our answers. We hope you will find them satisfactory.

Both reviewers point at the possible negative or deleterious effect of social capital on aging, which you might want to address and cite some evidence with respect to these effects.

We have further developed this part.

We have added the following sentence with new references: "Of course, social capital can have a negative impact on fitness [1–3], but this is relative to other group members, and this negative impact of social capital on fitness is still lower than the cost associated to solitary living[4]. Yet, perception of ambivalent relationships in humans is related to shorter telomere length[5] which suggest that social capital could also negatively impact biological ageing."

We have also added the sentence: "Costs of sociality are important. For instance, high social status males experience accelerated epigenetic aging in wild baboons [3] and higher oxidative damage but only during the mating season in mandrills [6]."

In my own reading, I have the following comments:

Line 18 and throughout the manuscript: what do you mean by individuals "adjusting" their social capital? Is there an implication of some kind of optimality? How can the optimal social capital at each life stage be determined, by organisms and by researchers? This point, mentioned in the abstract, is not followed up thoroughly in the body of the paper, and one is left wondering if there is really a strategy to adjust social capital throughout an individual's lifetime, and if so, how can it be determined to be the "optimal" strategy.

We have added the following sentence to clarify this point: "By adjusting, we mean that changes in social capital are not random but made in a way to increase fitness (survival and/or reproduction) and/or healthy ageing. This adjustment is the result of behavioural strategies (e.g., favouring, selecting or avoiding social interactions). Although these strategies may or may not be ruled by intermediary mechanisms (e.g., stress, genetics, mating system), the latter being most likely evolutionary selected[7]."

We prefer to not talk about optimality because behavioural strategies are a matter of trade-off between pressures.

In general, I am left wondering how to measure social capital. You acknowledge that its defined broadly and depending on the discipline, and provide a very nice table summarizing the concept. But perhaps it would be useful if, at least for a certain taxonomic category (primates and other social mammals?), you could suggest a few quantitative metrics of social capital at the individual and group levels. This would certainly promote research and rethinking of the many ways in which social relationships are related to senescence and healthy aging. For example, you could review the existing literature on how the structure of social networks (and quantitative metrics of this structure) determine information flow and thus the social resources related to information (about resources, mates, environmental variables, etc.).

We have added details about metrics that could be used in Box 2 and in table S1. We also added a table S2 detailing these emtrics

Figure 2: What the graph shows is the change in social capital with respect to chronological age. If biological age is not an axis, how can it be represented in a two-dimensional graph?

The graph represents the relation between social capital and chronological age (whatever x or y), which is biological age. For instance, if biological age would be not influenced by social capital, it should only be a line parallel to chronological age.

Table S1 is a bit saturated—it could use a synthesis, grouping similar components of social capital into broader categories. Also, each component should have a reference.

We understand the table may look busy, but we preferred keeping this level of details. To improve its readability, we have changed its layout. We have also added references.

Reviews

Reviewed by anonymous reviewer, 2021-06-15 12:12

The preprint of a review entitled “Social capital: an independent dimension of healthy ageing” focuses on very interesting connection between healthy aging and social relationships. The review is clearly written and although sometimes very information dense I really enjoyed reading it.

Thank you very much for your positive comments.

The authors define and describe all the variables and phenomena and illustrate the complex relationships between health, aging and social relationships on a range of studies focused on wide range of species. The review represents very interesting introduction to the topic for a reader not completely familiar with the topic but also provides deeper insights for an informed reader. The boxes and figures are useful and provide additional relevant information.

Thank you again for these nice comments.

While reading the paper several questions pop in my head, e.g. like “Are there any costs to social relationships? What kind of measures can be applied to social capital?” Most of them answered or at least mentioned by the authors in subsequent text.

To address your questions and those from the editor, we have added the following sentence with new references: “Of course, social capital can have a negative impact on fitness [1–3], but this is relative to other group members, and this negative impact of social capital on fitness is still lower than the cost associated to solitary living[4]. Yet, perception of ambivalent relationships in humans is related to shorter telomere length[5] which suggest that social capital could also negatively impact biological ageing.”

We have also added the sentence: “Costs of sociality are important. For instance, high social status males experience accelerated epigenetic aging in wild baboons [3] and higher oxidative damage but only during the mating season in mandrills [6].”

Remained unanswered questions are related to more details of the relationship between aging and social capital, e.g., “Do we see differences related to sex of the individuals? or How would individual variation in personality play into the mentioned relationships?”. It is clear, that given the space constrains not everything can be mentioned and the text actually benefits from authors’ ability to stay focused on the main topic. The authors also mention some of the connections that are less known as the relationship with microbiome.

We have added details about the sex and the personality differences:

“In line with these observations, one can hypothesize that variations in social capital in different life stages influence variability in post-reproductive longevity (Figure 2b) and indirectly modulate sex-differences in senescence [8]. This means that sex-related differences in social capital could lead to sex-related differences in longevity because of health or because of fitness benefits of social capital. However, such sex-related differences in longevity can be buffered when males associate with females. For instance, male baboons who are more strongly bonded to females have longer lifespans [2].”

“For instance, personality, which is heritable, has an impact on longevity and pace of life[9], and one of its basis is sociality. Social capital could be encoded in this personality variable, a hypothesis that need to be tested *via* the demonstration of a covariation at the individual level among social capital, personality and longevity.”

Some of the many phenomena related to the relationship between health, aging, mortality and social relationships mentioned by authors comes from studies that experimentally housed some individuals solitary (e.g. *Drosophila*). This is rather drastic and rare condition in natural populations of social animals. Although the authors also cite studies with more natural settings it is obvious that more research is needed to demonstrate similar effects under natural variation of social relationships.

We fully agree with the reviewer that natural settings are important to consider, especially in complement of the more extreme experimental studies. To address this point, we have added some details in the following sentences:

“Social isolation itself, i.e. independent of the usually associated increased risk of predation and lower feeding efficiency, causes death in carpenter ants (*Camponotus fellah* [10]) by disrupting energy homeostasis. In reproductive fruit flies (*Drosophila melanogaster*), social isolation induces stress, significantly accelerates the progression of tumour growth, and triggers rapid death [11]. Of course, usually social isolation increases predation risks or decreases feeding efficiency, but the latter results were done in absence of predation and with ad libitum food. In primates, males often disperse and this social isolation period is the most dangerous for them[2].”

“Future research should further explore the potential components of social capital and their independent or additive/synergistic effects on ageing outcomes, in laboratory but more importantly in natural settings to demonstrate similar effects under natural variation of social relationships.”

I can only applaud the authors for gathering such diverse literature in terms of topics and studied species and compile it to such a clear, well-structured and readable review. I should probably add some weak points too but I could not identify any. I think it is really well written and inspiring paper.

We thank you again for your comments which enhance the quality of the manuscript.

Reviewed by anonymous reviewer, 2021-07-03 05:14

The authors provide interesting discussion on interplay between the availability of social resources, or social capital, and aging of an animal. They argue that social capital could be one of the key factors explaining the fitness and the life trajectory of individuals, and even decide inter-specific variation in longevity.

Thank you very much for your positive comments.

I have a series of questions and comments I feel that the authors should address prior to the publication. Overall, the discussion seems clear to me, but still, I have some difficulty in understanding it (probably because I am not that familiar with the topic of aging).

We have made edits hoping to clarify it.

The key role of social relationships in ageing

L27-36: I thought that you should also mention that social capital could have a negative impact on animals' fitness sometime, as it is one of the main topics in “Future perspective” section (please also see my comments on it).

To address your questions and those from the editor, we have added the following sentence with new references: “Of course, social capital can have a negative impact on fitness [1–3], but this is relative to other group members, and this negative impact of social capital on fitness is still lower than the cost associated to solitary living[4]. Yet, perception of ambivalent relationships in humans is

related to shorter telomere length[5] which suggest that social capital could also negatively impact biological ageing.”

We have also added the sentence: “Costs of sociality are important. For instance, high social status males experience accelerated epigenetic aging in wild baboons [3] and higher oxidative damage but only during the mating season in mandrills [6].”

Social capital changes with chronological age

L55-56: It may be better to include a summary of the following three examples, like “...with chronological age, where older individuals play an important role for mediating social resources (or social capitals) to group members,”

Done

Biological age changes with social capital

Longevity is not necessarily related to senescence, because it is also possible that socially isolated individuals have the higher mortality simply because of the larger predation risks or lower feeding efficiency, not because of the accelerated aging. How have these confounding effects been considered in the previous studies (for example study in L89)?

This is a good point. We have added the sentence: Social isolation itself, i.e. independent of the usually associated increased risk of predation and lower feeding efficiency, causes death in carpenter ants (*Camponotus fellah* [10]) by disrupting energy homeostasis.”

Future perspectives

L106-108: I don't understand why the fact that social capital reverses the biological age connects to the discussion that social capital is modifiable. I thought it was a matter of course that social capital is flexible, because social relationships is usually dynamic and fluid at some extent. Would you please give an explanation

You are correct. We have now replaced “social capital can reverse biological age” by “social capital is flexible”.

L110: “biological age” instead of “age”?

done

L142–165: Although (2) is more focused on genetics, I felt (1) and (2) are basically discussing on the same topic, i.e., the evolutionary relationships between sociality and longevity. Please consider combining these two into one section, otherwise please try to avoid redundancy.

We have chosen to keep the sections 1) and 2), but tried to better specify in what regard they are different, and made sure to avoid any redundancy.

L166 - 194: (3) should be mentioned prior to (1) and (2) (or even in the “The key role of social relationships in ageing” section), because the knowledge and definition on the social capital

is quite fundamental, while the discussion on evolution and genetics is rather practical. For example, you cannot conduct inter-specific comparison on the relationships between longevity and social capital, if you don't have enough information on the social capital itself, no?

Done

L176-178: "positive to negative social capital": change to "positive to negative consequences".

Done

Box1

L223-224: Does "pervasive effect" mean positive impact? Sorry, I am not familiar with this term.

We have replaced it by "negative".

L224-225: I don't really understand what "inflammation" refers to, and how it relates to the social capital. Please add explanations.

We have added a sentence to explain this point: "Indeed, various forms of social adversity are associated with elevated expression of proinflammatory genes and decreased expression of genes related to innate immune responses in humans [12] and rhesus macaques [13]."

L231: Perhaps "feedback" instead of "retroaction"

done

L232-236: I am not sure the examples shown in the first two sentences could be used as an evidence of social capital-fitness autoregulation. "Autoregulation" implies that the fitness (or maybe stress level in this context) maintains a stable state through controlling the level of social capital, but I felt that these examples do not say that. Would you please give more detailed explanation?

We have added some details: "For instance, some authors suggest possible causal effects of short telomeres on unhealthy behaviours as smoking in humans [14]. It means that some physiological traits (short telomeres) can conduct to some bad aspects of sociality (here being conformist with risky behaviours for health) enhancing the physiological traits (decreasing telomeres). Another example is the accelerated death of ill flies (*Drosophila melanogaster*) who are isolated from their conspecifics, likely because of reluctant physiological traits as cancer [11]. Because individuals have cancer, they are isolated from others but this in turn accelerates cancer progression."

References

- 1 Snyder-Mackler, N. *et al.* (2020) Social determinants of health and survival in humans and other animals. *Science* 368,
- 2 Campos, F.A. *et al.* (2020) Social bonds, social status and survival in wild baboons: a tale of two sexes. *Philosophical Transactions of the Royal Society B* 375, 20190621
- 3 Anderson, J.A. *et al.* (2021) High social status males experience accelerated epigenetic aging in wild baboons. *eLife* 10, e66128
- 4 Krause, J. and Ruxton, G.D. (2002) *Living in groups*, Oxford University Press.
- 5 Uchino, B.N. *et al.* (2012) Social relationships and health: Is feeling positive, negative, or both (ambivalent) about your social ties related to telomeres? *Health Psychology* 31, 789
- 6 Beaulieu, M. *et al.* (2014) The oxidative cost of unstable social dominance. *J Exp Biol* DOI: 10.1242/jeb.104851
- 7 Sueur, C. *et al.* (2019) Mechanisms of network evolution: a focus on socioecological factors, intermediary mechanisms, and selection pressures. *Primates*
- 8 Lemaître, J.-F. *et al.* (2020) Sex differences in adult lifespan and aging rates of mortality across wild mammals. *PNAS* 117, 8546–8553
- 9 Réale, D. *et al.* (2010) Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions: Biological Sciences* 365, 4051–4063
- 10 Koto, A. *et al.* (2015) Social isolation causes mortality by disrupting energy homeostasis in ants. *Behav Ecol Sociobiol* 69, 583–591
- 11 Dawson, E.H. *et al.* (2018) Social environment mediates cancer progression in *Drosophila*. *Nature Communications* 9,
- 12 Cole, S.W. (2014) Human social genomics. *PLoS genetics* 10, e1004601
- 13 Simons, N.D. and Tung, J. (2019) Social status and gene regulation: conservation and context dependence in primates. *Trends in cognitive sciences* 23, 722–725
- 14 Bateson, M. and Nettle, D. (2018) Why are there associations between telomere length and behaviour? *Philosophical Transactions of the Royal Society B: Biological Sciences* 373, 20160438