Reply

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Joint estimation of growth and survival from mark–recapture data to improve estimates of senescence in wild populations: Reply

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We are grateful for Keevil's (2020) identification of a mistakenly limited prior in the code we supplied as a supplement to Reinke et al. (2020), describing a new model. Within our paper, we demonstrated use of a hierarchical model using mark–recapture datasets that were also published as supplementary material. The introduction of the model was the focus of our paper and the code was included as a courtesy to those who would like to use the model, with parameters adjusted to suit their needs. This transparency allowed Keevil (2020) to run our model with the provided example datasets, identify the limited prior, and set values of their choosing. We are therefore pleased to see firsthand the benefits of open access in science.

The second goal of Keevil (2020) was to cast doubt on the validity of an earlier paper that a subset of us published, with additional authors, in a different journal, using a different statistical approach, and different data (i.e., Warner et al. 2016). We address these criticisms of our earlier work here with three points.

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1) To quote Keevil (2020), "An initial comparison of the rates of mortality senescence estimated by Reinke et al. (2020) and Warner et al. (2016) reveals substantial empirical differences." Long-term studies with databases that are updated annually are dynamic; and it is not surprising that with the accumulation of additional years of data, updated analyses provide updated parameter estimates. For an example from an author's other peer-reviewed work, see Bronikowski et al. (2011) versus Bronikowski et al. (2016). Particularly if age-specific mortality is low, species are longevous, and recapture probabilities are not perfect, the sample sizes required to measure low mortality acceleration or deceleration are quite large. Therefore, it is wholly expected that additional years of observations will result in changes in parameter estimates. The hope, of course, is that additional data help to move the parameter estimate closer to the true parameter value.
2) Intraspecific variation in mortality senescence is rampant both among populations and between the sexes. Examples of variation in aging rates among wild populations of the same species include non-human primates (Bronikowski et al. 2002), garter snakes (Miller et al. 2014, Schwartz et al. 2015), and vipers (Tully et al. 2020). Our results from Warner et al. (2016) – that a population of painted turtles in the Mississippi River exhibit both mortality and reproductive senescence – is not meant to suggest that all populations of painted turtles everywhere must have measurable mortality and reproductive senescence. Rather, these data show that at least one population does senesce along reproductive and survival axes, which negates a broad conclusion that painted turtles – or any turtles – do not ever senesce.
3) Given the specific questioning of the mortality results from Warner et al. (2016), we have run the BASTA survival package (Colchero and Clark 2012, Colchero et al. 2012) – the modeling approach used in Warner et al. (2016) – on the painted turtle data collected through 2019 from the same population (i.e., adding four years of data to the data used in Warner et al. (2016), which represents our most recent fieldwork, more than doubling our sample size from N = 1,031 females to N = 2,681 females, and adding N = 1,328 males). Using that same well established and peer-reviewed statistical approach for estimating mortality, we find significant and slow mortality aging in both sexes (Bronikowski et al., *unpublished data*) (see Table 1).

TABLE 1. Estimates from Program BASTA (Colchero and Clark 2012, Colchero et al. 2012) for the two-parameter Gompertz model ($U_x = Ae^{bx}$), where A is the initial adult mortality rate, and b is the rate of increasing mortality with advancing adult age, and MRDT is the mortality rate doubling time.

Gompertz model $U_x = Ae^{bx}$	Gompertz slope (b) (95% credible interval)	MRDT yr	Initial mortality rate (A)/year (95% credible interval)
Data through 2015 – Female (N = 1,031) (Warner et al. 2016)	0.05 (0.034–0.067)	14 yr	0.102 (0.090–0.116)
Data through 2019 – Female (N = 2,681)	0.021 (0.006–0.038)	35 yr	0.114 (0.098–0.132)
Data through 2019 – Male (N = 1,328)	0.071 (0.036–0.142)	10 yr	1.03×10^{-4} (1.30×10^{-5}–2.33×10^{-4})

To summarize our three points in opposition to the critique of Warner et al. (2016): growing databases will result in parameter estimate variation – one hopes in the direction of the true parameter value – but changes nonetheless; intraspecific variation in rates of aging are common with results from one population not necessarily dictating a value representative of all populations of a species; and, using the same Bayesian framework as used in our earlier publication, we reaffirm that mortality senescence can be measured in this population of painted turtles. We end by recommending that a more productive consideration is the interpretation of aging rates. Whether turtles age very slowly, not at all, or slowly increase survival with age, what are the biological ramifications of such findings? As was argued in Warner et al. (2016), turtle aging is much slower than seen in mammals of similar body size. The point at which extremely slow positive or negative aging can be considered to be negligible is an interesting and open question. When considered in a broad comparative context, future studies that contrast turtles as a monophyletic group versus other such groups will help to resolve this question.

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OPEN RESEARCH

Code and data examples were published with the original Statistical Report as Supplemental Information (Reinke et al. 2020): https://doi.org/10.1002/ecy.2877