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Strengths and opportunities in gopher tortoise population modeling: Reply to Loope et al.

To the editors,

We read the letter written by [Loope et al. \(2024\)](#) that evaluated the predictive population model for gopher tortoises from our previous paper ([Folt et al., 2022](#)), and, despite criticism raised, we contend that our effort remains a valuable contribution. In our previous paper, we performed an unprecedented and exhaustive review of gopher tortoise population demography, which synthesized a large volume of literature about the current state of knowledge on gopher tortoise population dynamics and factors that influence demographic rates, including anthropogenic threats ([Folt et al., 2022](#)). We then built a predictive population model that examined the relative influence of multiple anthropogenic stressors on tortoise populations into the future, while accounting for important geographic variation ([Folt et al., 2022](#)).

First, we agree with [Loope et al. \(2024\)](#) that the density dependence limit from our analysis included an error in the code that intermittently but infrequently led to unexpected behavior in density-dependent ceilings. However, correcting that error had little effect on the model predictions for gopher tortoise populations ([Loope et al., 2024](#)). Second, the immigration functions in our model were hypothetical and could have been formulated differently. We created this immigration structure in an attempt to model the possibility of movement between sub-populations within metapopulation networks that have been anecdotally reported. Our comprehensive review found that little was quantified about gopher tortoise immigration, and the approach we devised, with expert input and review, was intuitively and computationally simple within the population projection structure we had created. Because of the lack of quantifiable data, we note that any immigration function developed for this system would be hypothetical and thus we tested the model output for sensitivity to the immigration rate. [Loope et al. \(2024\)](#) applied an arbitrary limit to immigration in our model to demonstrate that our immigration structure could potentially lead to runaway population growth in some circumstances. We note that the imposed immigration limitation was not a proposed improvement or alternative modeling suggestion, but rather an exploration of model behavior. Because of the hypothetical nature and the exhibited high sensitivity, immigration might be an area for improvement in future modeling efforts. Last, [Loope et al. \(2024\)](#) argued that the stage-based population model we used may have been an inadequate approach to model gopher tortoise populations, due in large part to lessons learned from a recent review of matrix population models ([Kendall et al., 2019](#)). The noted [Kendall et al. \(2019\)](#) paper was published around the same time as when we initiated our work. We chose, at that time, to use a flat age-within-stage approach in our stage-based model, despite the issues raised by [Kendall et al. \(2019\)](#), because at that time the approach was a common and accepted way to model populations when empirical information on stage-based transition rates or age-based survival rates were not available. We acknowledge that since that time, a flat-age-within-stage approach is increasingly viewed as sub-optimal in favor of age-based models or other approaches. Changing the model structure from a flat age-within-stage to an age-based model should be further evaluated for interactions with other model parameters and model inputs.

Revisions to metapopulation and matrix population model structures may be opportunities for improvement in future gopher tortoise modeling efforts. If undertaken, we suggest that revisions are carefully evaluated to determine if revised metapopulation immigration structure or age-based population models are appropriate with model structure, assumptions, and model inputs. In the meantime, we contend that the many contributions of our paper ([Folt et al., 2022](#)) – including the comprehensive review of tortoise demography and threats, evaluation of the relative effects of climate change, sea level rise, urbanization, and fire management, and sensitivity analysis to uncertainty in those effects – remain useful as decision-support science. Thus, our original paper continues to offer useful insights on gopher tortoise population demography and the potential future effects of multiple anthropogenic stressors to populations.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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