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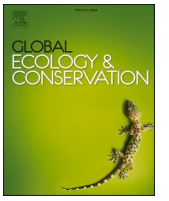

# Inflated predictions from a flawed model influenced the decision to deny federal protection for the gopher tortoise

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To the editors,

The United States Fish and Wildlife Service (USFWS) recently withdrew the Gopher Tortoise (*Gopherus polyphemus)* as a candidate for federal protection under the Endangered Species Act (ESA) across the vast majority of the species range (U.S. Fish and Wildlife Service, 2022). The scientific grounds for this decision, documented in a Species Status Assessment (SSA) commissioned by U.S. Fish and Wildlife Service (2021), were derived in part from a rangewide demographic simulation model which was published in *Global Ecology and Conservation* (Folt et al., 2022). We have identified serious flaws in this analysis that call into question the results and conclusions derived from the gopher tortoise SSA model, including the recent USFWS listing decision. While the published version of the SSA model (Folt et al., 2022) differed in some minor aspects from the model used in the SSA document (U.S. Fish and Wildlife Service, 2021; for example, the SSA model included some very small populations that were excluded from the published version), they are otherwise identical and we hereafter refer to both versions as the 'SSA model'. The SSA model predicted considerable population declines and local extinctions over an 80-year time horizon across many scenario tests (sea level rise, climate warming, habitat management intensity, etc.). However, the model also predicted that a substantial subset of populations across the species range would remain large and self-sustaining over this time frame, leading USFWS to conclude "…the future condition of the species with relatively large numbers of individuals and populations suggests resiliency to withstand stochastic environmental and demographic change, and redundancy to buffer from future catastrophic events." (U.S. Fish and Wildlife Service, 2022 p 61859). In this note, we argue that this conclusion is wrong because it is a direct result of two critical errors in the model.

The most consequential error in the SSA model concerns the modeling of immigration from metapopulations into focal populations (the term 'metapopulation' is used in Folt et al., 2022 while the SSA and listing decision use the term 'landscape population'). In the SSA model, population growth and local extinction risk were extremely sensitive to the 'immigration rate' parameter (rate of movement among subpopulations within a metapopulation) (Folt et al., 2022): when immigration was high (4 %), total rangewide population size *grew* by a median of 11 % (across 50 replicates); when immigration was zero, rangewide population size *decreased* by a median of 98 %, falling to virtual extinction in 80 years (Table 3 in Folt et al., 2022). Here, we demonstrate that this surprising result – and, ultimately, the projected resiliency and redundancy of gopher tortoises across their range – is an artifact of an incorrect specification of metapopulation processes that introduces a strong positive feedback between focal populations and their associated metapopulations.

Rather than following standard metapopulation modeling practices (e.g., Akçakaya, 2000) – in which immigrants to a focal population are necessarily drawn from a different source population (Fig. 1) – each local population in the SSA model is paired with a "dummy" metapopulation that functions as a source of immigrants (Fig. 1). The SSA model initially assigns local populations to a distinct metapopulation (cluster of local populations) based on geographic proximity. Each local population is then assigned a dummy

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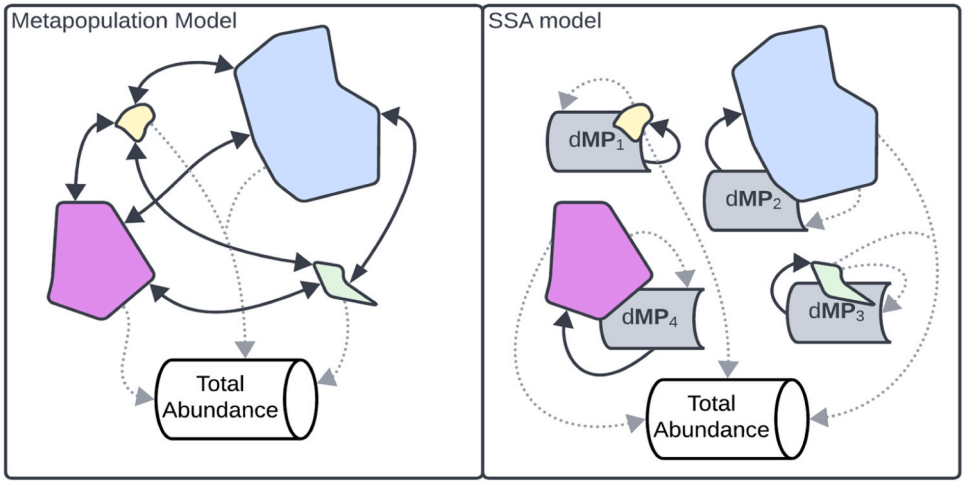


**Fig. 1.** Schematic illustration of the SSA model approach (right) versus a standard metapopulation model (left). Each panel represents the same metapopulation (cluster of populations; the SSA model comprises many such metapopulation units). Irregular polygons represent local populations within a single metapopulation, solid arrows depict movement of individuals (immigration and emigration), dotted arrows depict information flows. In the standard model (left), individuals (here, tortoises) are allowed to move among populations within the metapopulation, such that immigrants to one population are necessarily drawn from a different population; although dispersal mortality may occur, the immigration process cannot spontaneously generate new individuals. However, in the SSA model, immigrants to each population are derived not from other populations but from abstract structures we refer to as "dummy" metapopulations (gray shaded objects labeled $dMP_1$ through $dMP_4$). Although each dummy metapopulation in this diagram conceptually represents the same metapopulation (identical set of constituent populations), dummy metapopulations are decoupled from the metapopulation units they are intended to represent. Instead, after initialization, dummy metapopulations are assumed to follow identical dynamics to their paired local populations (each of which is modeled independently). Thus, dummy metapopulations from the same metapopulation unit can diverge substantially from one another over time. In both models, regional or rangewide abundance (white cylinders labeled "Total Abundance") is derived as the sum of local populations (dummy metapopulations are not factored directly in abundance estimates). However, the dummy metapopulations enable the immigration process to spontaneously produce new immigrants seemingly out of nowhere, and introduces a strong feedback loop that can lead to unrealistic, hyper-inflated immigration rates and accelerated growth of local populations (see text).

metapopulation, which is initialized as the sum of initial abundances across all populations belonging to the same metapopulation unit (i.e., all dummy metapopulations belonging to the same metapopulation are initialized identically). After initialization, each dummy metapopulation is assumed to grow or decline in lockstep with the local population to which it is paired; specifically, dummy metapopulation growth is assumed to reflect the proportional change in the number of adults in the paired local population from one year to the next. Each dummy metapopulation and its paired local population are modeled independently and are effectively decoupled from other populations nested within the same metapopulation (Fig. 1); this results in the logically impossible property that dummy metapopulations ostensibly representing the same metapopulation can be both growing and declining at the same time. Examining model outputs using the original code and data from Folt et al. (2022), we found that dummy metapopulations that represented the same metapopulation unit often varied in final size by orders of magnitude (Fig. S1).

Although local population growth is constrained by a density ceiling (which is often many times larger than the density at initial abundance, especially for smaller populations), there are no further limits imposed on the growth of each dummy metapopulation in the SSA model. In fact, the way dummy metapopulations are modeled unintentionally introduces a strong feedback loop that can drastically inflate population growth of local populations and their paired dummy metapopulations: increases in local adult abundance (often driven by immigration from a large dummy metapopulation) are assumed to induce an equivalent proportional increase in the paired dummy metapopulation, leading to an even larger influx of immigrants to the focal population in subsequent years. Although tortoises that "belong" to a dummy metapopulation do not factor directly in regional or rangewide abundance computations (only local populations are considered when computing aggregated regional or range-wide estimates of abundance; Fig. 1), rapid growth of the dummy metapopulations can lead to sustained, hyper-inflated immigration rates into local populations (Fig. 1).

While rapid local population fluctuations can and do occur in nature, there is no ecological or even logical mechanism by which these local population fluctuations could imply equivalent proportional jumps in a much larger metapopulation; many of the mechanisms responsible for local fluctuations (immigration, demographic stochasticity, etc.) simply do not scale to the metapopulation level. Notably, the metapopulation units described in the SSA model (and which the dummy metapopulations are supposed to represent) are by definition closed to immigration, which is one of the primary drivers of population dynamics for local populations in this model. Among the many consequences of this feedback loop is that individual dummy metapopulations often greatly exceed the combined abundance of all their constituent populations. Indeed, some dummy metapopulations occasionally exceed the total rangewide abundance at model initializations by an order of magnitude or more. In our examination of model outputs, some dummy metapopulations (for which population dynamics are presumed to be driven solely by endogenous births and deaths) grew from

thousands to millions within a single tortoise generation – a biologically impossible growth rate for this species.

Consider the dynamics of a small local population starting with ~ 20 adults paired with a large dummy metapopulation of ~ 5000 individuals (such as population 66; Fig. 2). In the example replicate, the local population contains 22 adults in year 4 and receives 37 immigrants (all adults, stochastically sampled from the dummy metapopulation), more than doubling the number of adults in the local population (~ 150 % increase). In turn, the dummy metapopulation undergoes a proportional increase from 5609 to 14,277 tortoises – an increase of over 8000 new adult tortoises in a single year. Although this spontaneous increase in the dummy metapopulation does not directly contribute to local or regional abundance estimates (Fig. 1), it causes a large increase in the number of effective immigrants entering the local population in subsequent years. This sets the stage for runaway growth that only stops when the local population hits its density limit.

Because immigration into a local population is computed as a proportion of its dummy metapopulation, this runaway feedback is most consequential in very small populations that occur within large metapopulations (i.e., where the initial abundance of the dummy metapopulation far exceeds the initial abundance in the focal population), where the addition of a small number of individuals to a local population can produce an equivalent proportional change in the dummy metapopulation that is extremely large in absolute terms. In the SSA model, these populations tend to experience an initial exponential growth phase followed by stable persistence at their local carrying capacity until the end of the simulation (Fig. 2). For such populations, (spurious) stability in the final stages of the simulation is virtually guaranteed, as the dummy metapopulation will remain large and will continue to feed large numbers of

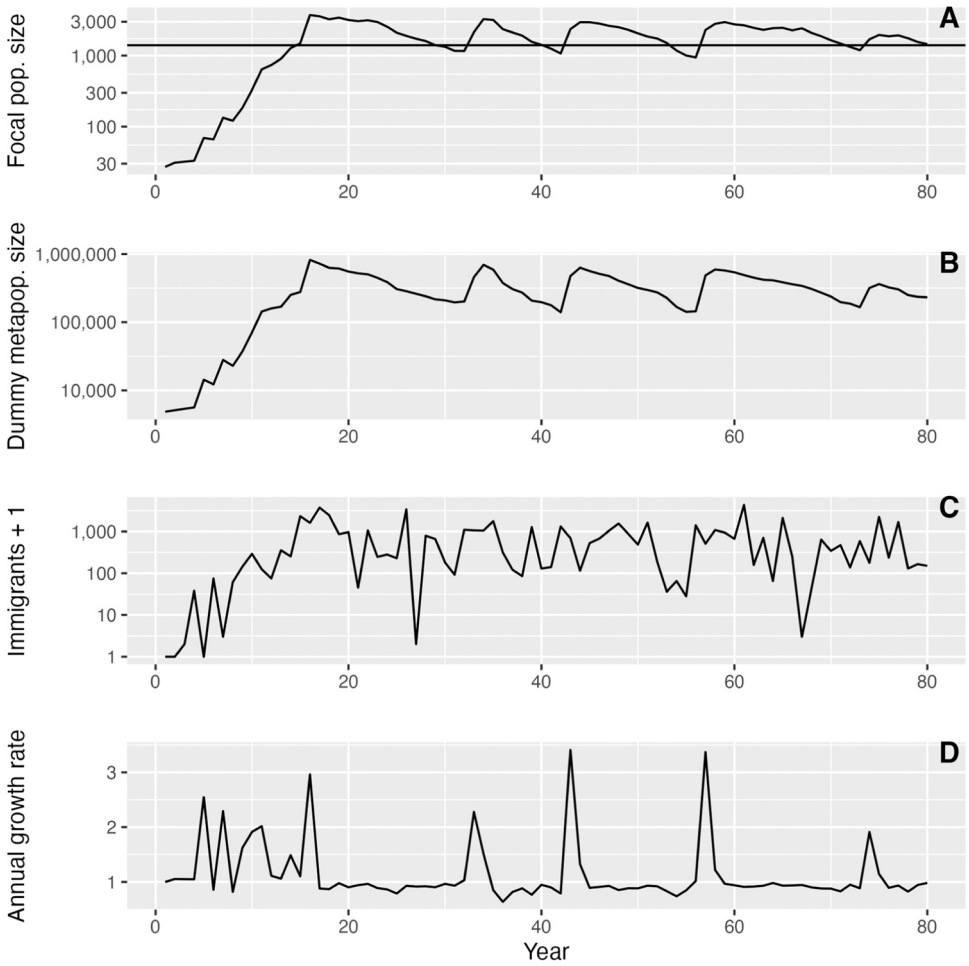


**Fig. 2.** An example replicate from population 66 of the SSA model in the "maximum density high" scenario (4 females/ha maximum density) showing exponential growth (note log scale on y-axis) and positive feedback between growth in the focal population and its paired 'dummy' metapopulation. The focal population (A) and dummy metapopulation (B) grew rapidly until the focal population reached carrying capacity (horizontal line in A) after 16 years; in this time, the dummy metapopulation grew from ~ 5000 to ~ 1,000,000 individuals (B). Extreme (stochastically drawn) annual immigration from the dummy metapopulation (C) maintained the focal population at carrying capacity (potential immigrants only join the population if the population size is below carrying capacity). The annual fractional population growth rate of the focal population, and by extension the dummy metapopulation, was often exceptionally high (D), driving the positive feedback in growth (a value of 2 indicates doubling of population size in one year). This figure depicts the outcome after correcting a typo that occasionally caused density dependence to fail (see Supplementary methods; Fig. S2).

'phantom' individuals to the focal population indefinitely. In some cases, the problem is exacerbated by a coding error that occasionally enables local populations to far exceed their imposed density limits (Fig. S2; see Supplementary methods for details). However, this typo is largely inconsequential in that it rarely manifests, and only after populations have already experienced extreme runaway growth; correcting this typo yields results that are qualitatively similar to the original SSA model (see below; Figs. S3–4).

The impact of this positive feedback on the results and conclusions derived from the SSA model is severe and consequential. Of the 32 populations predicted to have > 100 tortoises at the end of the simulation, all but two have dummy metapopulations that experience > 10-fold growth over 80 years on average (Fig. 3A,C). In extreme cases, dummy metapopulations experience > 100-fold growth in 80 years – 15 of them individually contain > 70,000 tortoises on average across replicates, more than the total number range-wide at the start of the simulation; Fig. 3A). As expected, all of these problematic populations start small and occur within large metapopulations at the start of the simulation (Fig. 3B). Thus, virtually all of the populations that the SSA model predicts to be large and stable (or growing) by the end of the century are in fact propped up by hyper-inflated immigration from unrealistically large dummy metapopulations, while all other populations are projected to experience moderate or severe declines (Fig. 3C).

The SSA model contains a second consequential error: the mis-specification of the maturation rate between juvenile and adult stages (Kendall et al., 2019). In order to estimate the percentage of juveniles that are eligible to transition to the adult stage in each year, the SSA model uses the flat age-within-stage structure (FAS; per Kendall et al., 2019) approach, assuming that $1/d$ juveniles are eligible to mature to adulthood each year, where $d$ is the duration of the juvenile stage. This approach is attractively simple but rarely correct: Kendall et al. (2019) identified it as one of three major, common errors in matrix population modeling. The problem lies in the fact that the FAS approach assumes an even age distribution within the juvenile stage, which is rarely the case in real populations. In most real-world cases (including gopher tortoises) a multi-year juvenile stage class is expected to contain fewer old juveniles than young juveniles simply because older juveniles have had to survive for more years (Fig. 4; Fig. S5). In such cases, the FAS approach will overestimate the number of individuals that are old enough to mature into adults, resulting in an erroneously high population growth estimate (Kendall et al., 2019). A simple and intuitive solution is to use an age-structured matrix population model that explicitly tracks the abundance of each juvenile cohort (the 'unrolling' solution discussed by Kendall et al., 2019; for details, see Supplementary methods). Although age-structured matrix models have more age classes than their stage-structured counterparts (seemingly adding complexity), they are simpler than stage-structured models in they do not require specification of a maturation rate parameter, relying instead simply on age-specific survival terms, which are more easily conceptualized and estimated. Indeed, maturation rate is an emergent property of age-structured models; only those individuals that have survived the requisite number of years are allowed to transition to adulthood.

To assess the effects of the positive feedback and maturation rate errors on model outcomes, we made modifications to the SSA model and compared the results to the original model outputs (see Supplementary methods for details). To mitigate the effects of the positive feedback and improve the biological plausibility of the existing SSA model, we imposed a (generous) 3 % cap on annual growth (maximum lambda [multiplicative annual growth rate] of 1.03 per year) on all dummy metapopulations. This modification was extremely consequential: after 80 years, total rangewide abundance declined from ~ 70,000 to ~ 2000 individuals versus a final abundance of ~ 20,000 predicted in Folt et al. (2022) (Fig. 5). Additionally correcting the maturation rate error by modeling juvenile age classes explicitly further reduced the number of persisting individuals and populations to near extinction (Fig. 5; Figs. S3–4). Thus, virtually all of the original conclusions derived from the SSA model regarding the projected resiliency, redundancy and representation of gopher tortoises across their range are artifacts of modeling errors and are primarily driven by the unintended feedback process and the maturation rate error described above. This finding demonstrates that the original SSA model does not represent the best available science and calls into question several of the key results that were used to justify the decision to deny federal protection under the ESA

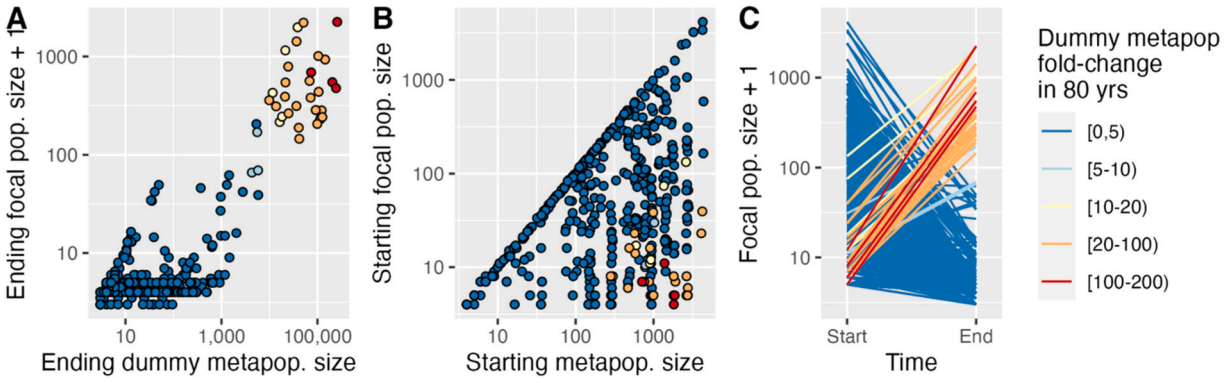


**Fig. 3.** Output from the original SSA model demonstrates that (A) virtually all populations projected to be large and self-sustaining at the end of the simulation are those that exhibit extreme metapopulation growth (> 10-fold increase in 80 years) and end with unrealistically large 'dummy' metapopulations. (B) The populations that exhibit extreme metapopulation growth all begin the simulation as small populations within much larger metapopulations, setting the stage for a strong positive feedback that results in runaway exponential growth. (C) Populations with extreme metapopulation growth due to this positive feedback are virtually the only populations that grow in the simulation. Each point (panels A and B) and line (panel C) represents the median value across 50 replicates for focal populations or their paired dummy metapopulations in the "low management + medium threat" scenario.

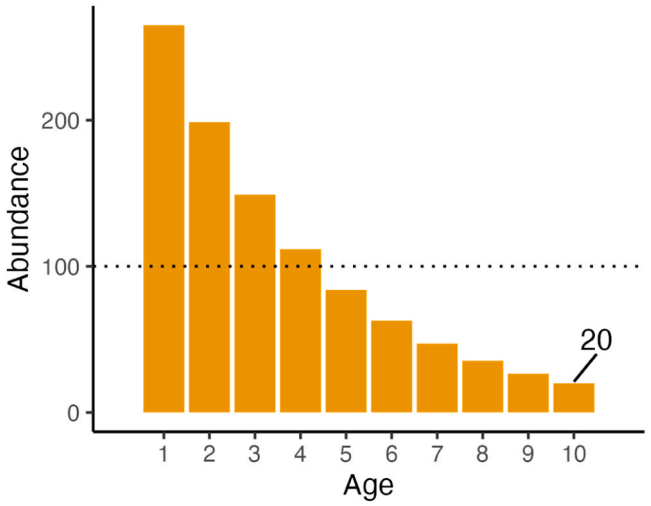


**Fig. 4.** Example theoretical age structure illustrating the overestimation of maturation rate caused by the FAS approach. The histogram depicts the age structure of 1000 juveniles when juvenile annual survival is 0.75 (as in the SSA model) and age at maturity is 11. The relative abundance of age class i was calculated as $\varphi_j^{i-1}$ where $\varphi_j$ is juvenile survival, then abundances were normalized to total 1000. Yearly mortality in the juvenile stage skews the distribution towards the younger age classes within the stage (this example assumes stable population growth; results are similar for declining populations; see Fig. S5). The FAS approach assumes an equal number of individuals in each age class (dotted line), such that the fraction of individuals in the maturing age class (here age 10) is 1/d where d is the duration of the stage. In this example, the FAS approach estimates that an average of 100 juveniles are eligible to transition to adulthood each year. The correct number accounting for juvenile mortality is ~ 20.

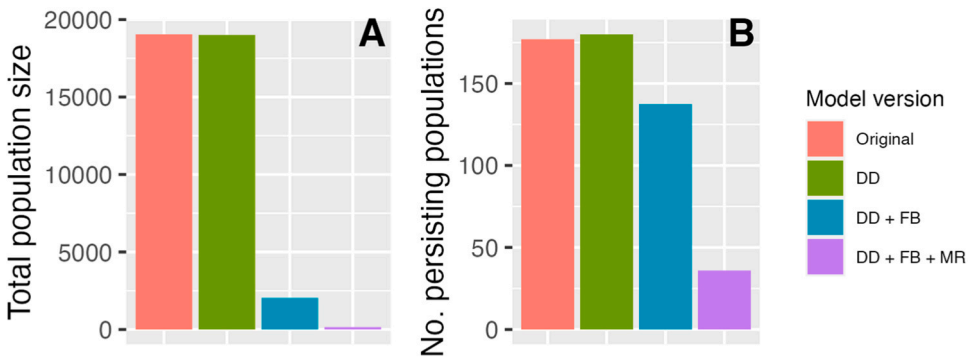


**Fig. 5.** Median total population size (A) and number of persisting populations (B) at the end of the 80 year simulation for the original model and three modified versions correcting or mitigating three errors: "DD" corrects just the density dependence typo; "DD + FB" corrects both the density dependence typo and limits positive feedback by imposing a 3% cap on annual growth for all dummy metapopulations, and "DD + FB + MR" addresses both of the above errors and also corrects the maturation rate error by implementing a modified matrix model that explicitly tracks the dynamics of each age class in the juvenile stage. Depicted are medians across 50 replicates from the "low management + medium threat" scenario referenced frequently in the SSA discussion; for results from all 32 scenarios examined in Folt et al. (2022), see Figs. S3 and S4.

for the eastern portions of the species range (U.S. Fish and Wildlife Service, 2022).

There are good reasons to suspect that the feedback error described above is even more consequential under the version of the model used in the SSA (U.S. Fish and Wildlife Service, 2021). The presence of ~ 169 additional very small populations (with initial abundance of 2–8 individuals) that were omitted from the published version of the model (Folt et al., 2022) but included in U.S. Fish and Wildlife Service (2021) would be expected to result in numerous additional populations prone to the erroneous positive feedback (small population paired with large dummy metapopulations). This likely explains why the final abundances reported in U.S. Fish and Wildlife Service (USFWS) (2021) are over two times larger than Folt et al. (2022) (e.g., 47,202 for U.S. Fish and Wildlife Service, 2021 [scenario "Medium threats, low management"] versus 19,463 for the same scenario in Folt et al., 2022), despite only minor differences in initial abundance (~ 70,600 in the U.S. Fish and Wildlife Service, 2021 [p. 159] versus ~ 70,500 in Folt et al., 2022 [p. 8]).

The adjustments we made to the SSA model serve to illustrate the magnitude of the effects of the spurious positive feedback and inflated maturation rate on the model's predictions, but do not correct the fundamental flaws in the approach to metapopulation modeling used in the SSA model. Thus, although our model adjustments predict concerningly steep declines, results from our modified model runs should not be interpreted as valid predictions for use in decision-making. While the comprehensive data compilation and

threat assessments performed as part of the recent SSA process represent valuable steps towards a rangewide population viability assessment for gopher tortoises, conservation decisions regarding this species should be informed by a correctly specified metapopulation model. We strongly urge re-evaluation of all conservation and management decisions that were informed by the original SSA model. More broadly, this case study underscores the need for rigorous code review (Ivimey-Cook et al., 2023) and model assessment in addition to standard peer-review, especially where complex simulation models are used to support important conservation decisions.

## 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

All data and code are available at a link provided in the main text, except for the tortoise population dataset, which is available from the USFWS Jacksonville Office.

## Acknowledgements

We thank Carola Haas, Elizabeth Hunter, and Houston Chandler for comments on an earlier version of this letter to the editor, editor Kim McConkey for assistance in publishing this letter, and Brian Folt for discussion of these issues and sharing data and code used in Folt et al. (2022).

### *Code Availability*

All code used to generate the results presented here is available online: https://github.com/kevintshoemaker/GT_modified_SSA_model with comments to indicate changes from the original code of Folt et al. (2022) (available as a software release: https://code.usgs.gov/cooperativeresearchunits/modeling-gopher-tortoises-population-viability). As stated in the software release, the data on tortoise populations is available by request from the USFWS Jacksonville Office. For details, see README on the code repository.

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e03089.

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