Title
With what precision can the population size of Tyrannosaurus rex be estimated? A reply to Meiri

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With what precision can the population size of *Tyrannosaurus rex* be estimated? A reply to Meiri

Abstract

Interested in the absolute preservation rate of one of the best understood dinosaurs, *Tyrannosaurus rex*, Marshall et al. (2021) estimated the total number that ever lived. This required estimating its geographic range, longevity, and population density, which required estimating its body mass and physiology. Meiri (2021) questions the precision of our estimates, emphasizing the difficulties in estimating population densities and geographic ranges for living species, and in error propagation. He posits that estimating population sizes of extinct species is 'extremely unlikely'. While we agree that we did not quantify some sources of uncertainty (for example, in the physiology of *T. rex*), our calculations do not depend on short-term changes in population density and geographic range, but rather on their long-term averages, rendering many of Meiri's (2021) concerns moot. We also note that Monte Carlo Simulation propagates uncertainties robustly. That is, we feel we have, in fact, developed a general method for estimating population sizes for extinct species, regardless of any shortfalls in implementation.

Keywords: area of occupancy, extent of occupancy, geographic range, Monte Carlo simulation, population density, *Tyrannosaurus rex*.

Main Text

> '*So how do you explain fossils, then*?' said Ponder.
>
> *Ah, you see, I don't*,' said the Lecturer in Recent Runes, with a triumphant smile. '*It saves so much trouble in the long run.*' / Terry Pratchett, The Last Continent.

Meiri (2021) provides a complex critique of our attempt to estimate the standing population size of *Tyrannosaurus rex*, the absolute number that ever lived, and thus the current preservation rate (Marshall et al. 2021). While the title of Meiri's critique centers on the precision of our estimates, his Gaiman and Pratchett quote (concerning the biblical estimate of the Earth's age) suggests that he also feels that our estimates may be wildly inaccurate. In fact, he posits that "biogeographic and ecological uncertainties make it extremely unlikely to be able to estimate population sizes of long-extinct species." Fossil taxa maybe more trouble than they are worth.

Before getting to Meiri's (2021) critique we summarize the history of our approach. We began with a back-of-the-envelope calculation, surmising that the average standing population size might have been 10^4 to 10^5 individuals, or maybe as many as 10^6. With a species duration of ~2 million years and a generation time of ~20 years, the species would have persisted for about 10^5 generations. This yields a crude estimate of the total number that ever lived of between 10^9 to 10^{10} individuals, or perhaps 10^{11}, an uncertainty of about three orders of magnitude. We then asked if we could do better, including providing a more defensible estimate of the associated uncertainty.

Minimum and maximum brackets versus best estimates

Rather than try and make singular best estimates of the values for the input variables, we focused on providing brackets, that is reasonable upper and lower bounds on their values. We then used Monte Carlo Simulation to 'find' the corresponding range of output values including the median value. In some regards this is a trivial exercise, for almost any variable can be bracketed with high certainty – for example, we warrant that there were more than 2 but less than 10^{100} individuals of *T. rex* alive at any one time. Obviously, these brackets are not useful, but they illustrate the fact that any unknown can be bracketed. The central question then is not can estimates be made, but how reliably can one narrow down the size of the brackets on the relevant input variables?

The core of our framework

Recognizing the difficulty of the task (undaunted we were not), we provided a framework that would permit estimation of reasonable numbers, recognizing that the actual range of values would likely change with new data, or with refinements to the framework. Central to our calculations was the use of data from living species (Damuth 1987) to infer population densities for *T. rex*, which we then multiplied by its inferred geographic range, an approach already used by Farlow (1993) in his speculations on the rareness of big, fierce, animals.

So, now we get to the crux of Meiri's (2021) critique, the extent to which one can reasonably estimate the population size of *T. rex*, or in fact of any extinct, or for that matter, extant species. First, we note that our framework is quite flexible. Thus, for example, as Meiri (2021) suggests, we could indeed have allowed the

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mean of the normal distribution of possible intercepts for the log(population density) versus log(body mass) relationship (see Figure 1A in Marshall et al. 2021) to vary to accommodate the uncertainty in the physiology of *T. rex*. We chose not to do this, largely because we used such a large variance about the mean intercept that our range of potential mass-corrected population densities encompasses all but the three most sparse flesh-eating mammalian carnivores and about half of all the herbivores in Damuth's data set (Damuth 1987). Nonetheless, Meiri's (2021) suggestion seems like a sensible extension of our analysis, although, as he notes, it won't change the mean estimates and will only slightly increase the variance of the output variables.

Similarly, our approach can accommodate any quantified non-linearity in the relationship between these two variables, an issue Meiri (2021) raises although he provides no recommendations for how to proceed to improve our estimates.

Estimating geographic range and the value of bracketing

Meiri (2021) emphasizes that the most appropriate geographic range for our calculations is the geographic area over which the species was actually present (the area of occupancy, AOO), not the total geographic range that the species spans (the extent of occupancy, EOO), which likely includes unsuitable habitat. He seems very concerned that we did not appreciate this, but see both our text and supplementary material (Marshall et al. 2021). Nonetheless, in accord with Meiri's (2021) commentary, we felt that this was a particularly difficult part of our analysis. However, estimating minimum and maximum brackets on the input variables rather than trying to estimate the value of the variable itself (the AOO of *T. rex* in this case) helped enormously in this regard.

Let's begin with the upper bracket on the geographic area. As Meiri (2021) points out, our use of the geographic range derived from Chiarenza et al.'s (2019) ecological niche modelling is an EOO, and thus too large, even as we agree there was a degree of arbitrariness in selecting the suitability threshold (>0.45) to arrive at the value of this upper bracket. But this is exactly what we want: an estimate that is almost certainly too large, an upper bracket on the area of occupancy. Thus, what Meiri (2021) identifies as a weakness is actually valuable in bracketing the desired AOO. This is the beauty of the bracketing approach for dealing with hard-to-determine unknowns. We also note that the ecological niche modelling leads to the conclusion that *T. rex* may have lived in eastern North America even though there are no *T. rex* fossils known from that area, as Meiri (2021) similarly notes (but does not seem to appreciate that we considered).

Now turning to the minimum estimate, we recognized that the convex hull around the well-preserved specimens is also an EOO, and that it integrates that EOO over the last 1.2 million years of *T. rex*'s existence. So, the open question is whether this lower estimate, even though it is an EOO, is smaller than the true (unknown) AOO. Frankly, we don't know. But we point out two things. First, the rock record for any time period is geographically quite incomplete, let alone for the appropriate environment, so we felt that the use of this particular EOO was a reasonable lower bracket. Second, if one takes this minimum bracket at face value and combines it with the estimated range of population densities, it implies a lower limit on the average standing population size of about 10^3 individuals, which seems too low for the average population size of *T. rex* (see supplementary material in Marshall et al. [2021]). Thus, given this Bayesian-like prior, and the fact that we didn't know how to otherwise establish a lower bracket, we used the convex hull area as the minimum bracket. We welcome suggestions for how to do better.

Moment by moment variability versus long-term averages

'*They're pretty high mountains*' said Azhural, his voice now edged with doubt.

'*Slopes go up, slopes go down*' said M'bu gnomically.

'*That's true*' said Azhural. '*Like, on average, it's flat all the way*.' / Terry Pratchett, Moving Pictures.

Much of Meiri's (2021) text centers on the difficulties in estimating population densities and the geographic ranges over which those population densities are relevant. For example, he notes that population densities "vary seasonally (e.g., brown bears during the salmon run and towards hibernation), geographically, and among habitats". He goes on to note that they "fluctuate widely with predator-prey cycles, droughts, floods, changing temperatures etc." Similarly, he presents a well-informed discussion of how the geographic range of *T. rex* likely changed with time. He then concludes that our "treating [of the] ranges and densities as immutable across the existence of *T. rex* .... further ignores huge uncertainty."

Let's take this at face value to see if it is true. Formally, we agree that population density (ρ) is a complex function that varies with space and time, $\rho = f_\rho(x, y, t)$, where x is longitude, y latitude, and t is time. Similarly, we agree that the geographic area occupied (A) varies with time, $A = f_A(t)$. For ease of presentation, we will only consider population density here, but the same reasoning applies to geographic area. Logically we should integrate over this (unknown and probably unknowable) variation, given the spatial and temporal variation in climate, the changing numbers of ecologically relevant co-occurring species, etc.:

$$\iiint_{x_{min}, y_{min}, t_{min}}^{x_{max}, y_{max}, t_{max}} f_\rho(x, y, t)\,dx\,dy\,dt \qquad [1]$$

Solving this equation piecemeal is nigh impossible for extant and especially extinct species. But note that Equation [1] divided by $(x_{max} - x_{min})\,(y_{max} - y_{min})\,(t_{max} - t_{min})$ is equivalent to the mean of $f_\rho\,(x, y, t)$. Thus, what Meiri (2021) is advocating is formally equivalent to using an estimate of the average value for the density and standing population size over the duration and spatial extent of *T. rex*, as we have done. Note further that the use of these averages does not assume that the population density, or geographic range, or any other variable, was "immutable across the existence of *T. rex*" as Meiri (2021) asserts; we simply used the fact that there was an average for those variables, regardless of how much they varied with time and space.

Now this observation does not change the fact that (average) population densities are hard to estimate. Hence we would welcome an assessment of the reliability of the specific population densities we used in our analysis, that is, those compiled by Damuth (1987). Those data would be enormously useful!

Error propagation

In our analysis we provided a crude measure of the uncertainty in each of the input and output variables by providing the ratio of their 97.5% and 2.5% values (Marshall et al. 2021). We used these values to show that the bulk of the uncertainty in our analysis derives from the variation in the population densities among living mammals – to our surprise, the uncertainties associated with the paleontological data were much smaller. But these ratios are not formal measures of uncertainty, and Meiri's (2021) multiplication of these ratios to generate a measure of the overall uncertainty is inappropriate (he gives a value of >1500x) – when random variables are multiplied the uncertainties compound additively, not multiplicatively (Goodman 1960). In our analysis we used Monte Carlo Simulation for propagating the uncertainty, a robust and easy method, especially when combining distributions of different shapes (in our analysis we used normal, lognormal, and uniform distributions).

Simple errors

Finally, we note that some of Meiri's (2021) statements are simply inaccurate. For example, he states that in our computation of the ecological body mass, we did not account for uncertainties in our estimates of the growth curve, the minimum age of post-juveniles, or the sizes and masses of the age cohorts. Not so. For example, rather than simply using a 'best' survivorship curve for T. rex, we used bootstrapping to provide an estimate of the range of reasonable survivorship curves (following the procedure used by the original authors, Erickson et al. (2006) (see Figure 1D in Marshall et al. 2021). We also included uncertainty in the time of onset of sexual maturity (see Figure 1J in Marshall et al. 2021), and uncertainty in the growth curve by incorporating the uncertainty in the maximum body mass (see Figure 1C in Marshall et al. 2021). But we agree that more work needs to be done to quantify these uncertainties, for example updating the *T. rex* growth curve with better age and mass estimates (and their uncertainties) of the fossils included, and with more specimens.

Conclusion

Meiri's (2021) implication that the long-term average population density, long-term average standing population size, and the total number that ever lived cannot be estimated seems, to us, unfounded. Further, his focus on the difficulty in estimating individual population densities and AOOs, that is, on the difficulty of characterizing in detail each of the metaphorical trees in the forest, seems to miss the relative ease with which entire forests can be broadly characterized. Averages work. He also notes that many of his points will not change our median values much, or at all (for example, accommodating the unknown physiology of *T. rex*). Nonetheless, we do agree that our reported uncertainties were probably too small, but not to an egregious degree as he concludes.

Finally, we want to make a philosophical point. Knowledge advances in many ways. Following Polanyi (1958), who likens knowledge creation to the making of maps into the unknown, one of our motives for undertaking this work was to explore just how well a map could be made in terms of estimating absolute preservation rates, and all the population variables that entails, for a well-known fossil taxon such as *T. rex*. As Polanyi points out, making maps of uncharted territory is challenging, a challenge we chose to undertake. We appreciate Meiri's (2021) comments directed at how to make the map we have sketched out better, but we are not apologetic for making the attempt, despite the challenges. We also note that some of the questions raised by Meiri (2021), for example, how to quantify the geographic range of *T. rex*, might not have been raised had we not undertaken our analysis. Our results are not the final answer, but hopefully will lead to better and robust estimates than we were able to provide. We thank Meiri (2021) for providing a stimulus towards making that happen.

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