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Population sizes of *Tyrannosaurus rex* cannot be precisely estimated

Abstract

Marshall et al. recently estimated population densities, range sizes, instant and cumulative total population sizes for *Tyrannosaurus rex* with narrow ranges of uncertainly. I revisit the assumptions that led them to these conclusions and show that many of these parameters are associated with much wider margins of error than they estimated. Biogeographic estimates seem to have been especially unrealistic, seriously hampering the effort to calculate population level parameters. I posit that biogeographic and ecological uncertainties make it extremely unlikely to be able to estimate population sizes of long-extinct species.

"We demand rigidly defined areas of doubt and uncertainty" / Douglas Adams, Hitchhiker's Guide to the Galaxy.

"The earth itself is generally supposed to be about four and a half thousand million years old. These dates are incorrect. Medieval Jewish scholars put the date of the Creation at 3760 B.C. Greek Orthodox theologians put Creation as far back as 5508 B.C. These suggestions are also incorrect. Archbishop James Usher… suggested that the Heaven and the Earth were created in 4004 B.C. One of his aides took the calculation further, and was able to announce triumphantly that the Earth was created on Sunday the 21st of October, 4004 B.C., at exactly 9:00 A.M., because God liked to get work done early in the morning while he was feeling fresh. This too was incorrect. By almost a quarter of an hour."; Neil Gaiman and Terry Pratchett; Good Omens.

Estimating absolute population density is very difficult. Density estimates are affected by detectability, seasonality, weather, times of day, and the area chosen to sample it over. Estimates of the total population sizes of wide-ranging taxa are thus rare, and restricted to the best studied, easily detectible species.

Undaunted, Marshall et al. (2021) recently estimated the population density, and total population size of *Tyrannosaurus rex* across their entire range, and not only at a single point in time but across the duration of the existence of this most charismatic of dinosaurs, thus calculating the total number of *T. rex* that have ever lived. This bold and ambitious attempt earned them a place in the pages of *Science*. Unfortunately, I think that their estimates for densities and population sizes of *Tyrannosaurus rex* are more precise than the data they used allow and are stated with too narrow intervals. Biogeographic considerations are, in my view, among the most important sources of unaccounted variation in Marshall et al.'s (2021) results.

To estimate *T. rex* population size, Marshall et al. (2021) estimated its body size, diet, and metabolic rate.

They used a 1980's cross-taxon allometry of population density on body size to ascribe a density value for *T. rex* (Damuth 1987). Next, they estimated geographic range using a convex hull, and an ecological niche model. To obtain instantaneous total population size they multiplied density by area. To obtain the number of *T. rex* individuals that ever lived, they multiplied population size by the number of generations it persisted.

All these estimates are associated with substantial uncertainties, some were considered, others neglected. Thus, for example, Marshall et al. (2021) "assumed a physiology midway between… mammalian carnivores and… large varanid lizards". The metabolic rate of *T. rex* is unknown. It may have been similar to that of extant reptiles, or extant birds and mammals (had there been anything in these clades approaching its size), and it is likely to have occupied a position somewhere between these extremes (e.g., Benton 2021, Legendre and Davesne 2020), and a midpoint position (Marshall et al. 2021) is as likely as any. But "midway" is a point estimate that has no direct support and using a range of values would have been appropriate. While this will probably not introduce a great source of error into the resulting figures (less than an order of magnitude separates the metabolic rate of carnivores of varanids and similar sized carnivorans, and the using the midpoint halves even this) it will not be negligible. One should also bear in mind that the mass/metabolic rate relationship is non-linear even on a logarithmic scale (Clarke et al. 2010, Kolokotrones et al. 2010) – and is further influenced by body and environmental temperatures, even in mammals (Clarke et al. 2010). Such non-linearity most strongly affects estimates at the extreme ends of the mass distribution – and *T. rex* was larger than all extant land mammals, let alone varanids. The extrapolation beyond the range of data used to calculate the model, and uncertainties about the environmental and body temperatures of *T. rex*, both mean that such variation should not simply be waved.

Densities of wide-ranging living animals are difficult to precisely estimate. They vary seasonally (e.g., brown bears during the salmon run and towards hibernation), geographically, and among habitats. They fluctuate widely with predator-prey cycles, droughts, floods, changing temperatures etc. Density estimates vary greatly with detectability, which is influenced by e.g., habitat, weather, time of day, and survey methods. Marshall et al. (2021) acknowledged some of this variability, used the confidence interval around density estimates at a single body size (from Damuth 1987, neglecting the uncertainty in body size, see below) to estimate a 241-fold 95% confidence interval for population densities (0.00058 to 0.14 individuals/km^2). In a recent comprehensive dataset or tetrapod densities (TetraDENSITY; Santini et al. 2018) 12 large (>10kg) mammalian carnivore species (*T. rex* analogs; Marshall et al. 2021)*,* have > 10 density estimates each. These vary from 17-fold in *Panthera onca,* to 2309-fold in *P. leo,* and 5220-fold in *Crocuta crocuta* (mean across the 12 species: 826-fold). It is unlikely that we can pinpoint the variation in *T. rex* density, across its age and size spectra, across the varied environments it inhabited (Sampson and Loewen 2005), and taking metabolic uncertainty into account, to greater precision.

Different methods yield different estimates of *T. rex* size, something Marshall et al. (2021) discuss at length. Yet they use one equation "despite the range of values in the literature" – ignoring this uncertainty. For adults even a 2-fold variation in mass estimates (see e.g., Therrien and Henderson 2007, Brassey 2017 [Figure 8], Campione and Evans 2020), is unlikely to influence density estimates by much. But they then average the mass of "all postjuvenile age cohorts". This requires knowing several specific parameters: one needs to define the minimum age of postjuveniles and reconstruct the body sizes of each cohort. Because shape changed markedly during the ontogeny of *T. rex* individuals (Hutchinson et al. 2011, Carr 2020, Persons et al. 2020), however, both assigning fossils to age groups and the mass reconstructions at each age cohort contain further uncertainty – since few individuals are known from each such cohort. Furthermore, such averaging of masses across all age cohorts requires the sex and age-specific survival rates to be known. The ecological shift that occurred during *T. rex* ontogeny (e.g., Holtz 2021) would further complicate our ability to assess sizes and survival rates and potentially also metabolic rates for different cohorts. Survival rates of different age cohorts of long-lived organisms in the wild are yet another parameter that we only know for the best studied living organisms. Calculating them for animals that went extinct 66 million ago, and known from few specimens of each age cohort, is bound to include an error rate the magnitude of which is very difficult to assess – but is likely to be substantial. Thus, all the factors involved in calculating masses across *T. rex* ontogeny encapsulate much uncertainty – especially in an animal known only from fossils.

All these factors, however, remain unaccounted for in the calculations of Marshall et al. (2021).

Biogeographic issues in my view, may encapsulate the greatest weakness in the estimation of *T. rex* numbers. Marshall et al. (2021) claimed their minimum range size estimate is area of occupancy. But they calculated it using a convex hull ("For our minimum estimate of the geographic range occupied by *T. rex* we used the area encompassed by the convex hull around the 32 post-juvenile *T. rex* specimens"). It is thus an extent of occurrence (EOO; Gaston 1991). Multiplying local density by EOO overlooks the strong relationship between density and the size of the area it is sampled across (Novosolov et al. 2016). Sampling larger and larger areas, more and more unsuitable habitats are included, thus density estimates decline with increasing sampling area. Using the data in TetraDENSITY (Santini et al. 2018), across 11,085 populations with reported sampling area, I obtained a log-log relationship with sampling area explaining 68% of the variation in density. Across 19,494 amniote populations a model with log-mass (from Meiri et al., 2021, slope = -0.56, not -0.75) explained only 43% of the variation in log-density. Using only density data for which I had both sampling area and body mass (10,031 populations representing 1,516 species; Supplementary Material - Appendix S1), a multiple regression model had both (log) mass and (log) sampling area as significant predictors of density. Sampling area, however, has a much steeper slope: -0.531±0.007 (1 se) vs. -0.043±0.008 for mass. This model explained 64.8% of the variation in (log) density whereas a model with the same data with log sampling area alone explained 64.7% of the variation in density. Thus, the addition of mass has a very small added explanatory power, and a very weak effect (near zero slope). Moreover, the slope of the sampling area alone was very similar to the one in the full model: -0.562±0.004, while a model with (log) mass alone explains only 46.2% of the variance in log density, and the slope for mass changes drastically: -0.548±0.006. Furthermore, the mass/density relationship varies by ~6 orders of magnitude across all body sizes, and is non-linear, undermining the utility of "Damuth's law". Extrapolating beyond the range of observed mass data undermines it further.

The geographic ranges calculated by Marshall et al. (2021) varied from 1.42 to 3.18 million km^2. The upper value assumes 1. an arbitrary suitability threshold (>0.45); 2. that *T. rex* had the same habitat requirements of all the Tyrannosauridae (akin to assuming sloth bears have similar habitat suitability to all ursids, from giant pandas to sun bears to Asiatic black and brown bears); 3. range size (and habitat) stationarity across the geological duration of *T. rex* (which they give as 1.2-3.6 MA).

Tyrannosaurus rex is known from Laramidia, a large island (or small continent) comprising what is today the Western part of North America. Laramidia was characterized by a dynamic and complex geography, with large scale orogeny, sediment depositions, and sea level fluctuations (Gates et al. 2012, Loewen et al. 2013,

Holtz 2017, Brownstein 2018). It was connected to Asia on the one hand, and increasingly as the Cretaceous neared its end, to the eastern part of North America: Appalachia (e.g., Sampson et al. 2010 who mention this "reconnection of Laramidia and Appalachia" is "complicating biogeographic interpretations"). This complex geological history of Laramidia means the area available for *T. rex* to inhabit has likely changed much and often (e.g., Loewen et al. 2013, see e.g., their Figure 4). Furthermore, while some claim *T. rex* potentially spread across Laramidia arriving from elsewhere (Brusatte & Carr 2016), others claim it evolved there (e.g., Loewen et al. 2013). Appalachia drew nearer and nearer to Laramidia, finally connecting near the K-Pg mass extinction (Gates et al. 2012, Brownstein 2018). The poor preservation of dinosaurs in Appalachia (Brownstein 2018), make it possible to postulate *T. rex* might have inhabited it at some point. Finally, there is even a hypothesis that Laramidia had two distinct biogeographic provinces (north and south) each serving as a center of endemism for dinosaurs (Sampson et al. 2010) – but this is strongly debated (e.g., Sampson 2012, Maidment et al. 2021). Even whether all Laramidia (or North Laramidia) was potentially suitable for *T. rex*, or whether latitudinal band or the Laramidian mountains served as a barrier to dispersal, is unknown. Thus, we are unsure whether *T. rex* inhabited Asia, Appalachia or South Laramidia or not – and this might have changed over time. The area available to it inside Laramidia has undoubtedly changed during its existence (e.g., Loewen et al. 2013). Such range lability is probably the rule in organisms generally rather than an exception. Ranges vary drastically with climate (Lyons 2003) and with the biotic environment, over very short (e.g., global warming), intermediate (e.g., glacial periods; Lyons 2003), and long timescales (Foote et al. 2007, Liow & Stenseth, 2007, Carotenuto et al. 2010). Under a peripatric model of speciation the range of *T. rex* would have started small, then increased. Such range size variability is well documented for fossil species (Foote et al. 2007, Liow and Stenseth 2007, Carotenuto et al., 2010). All these factors make the assumption of 2.4 million years of range stationarity highly suspect. Treating ranges and densities as immutable across the existence of *T. rex* (R0 = 1), and drawing convex hulls across non-contemporary specimens, further ignores huge uncertainty.

With measures that are all associated with uncertainties, one expects the error rates to increase when one is multiplied by the other (Graur and Martin 2004). Marshal et al. (2021) calculated the number of individuals to have ever lived by multiplying density by area, by the number of generations (i.e., in geological longevity divided by generation time). They calculated 95% confidence intervals as encapsulating a 241-fold density range, and a 2.2-fold in range size, a 1.1 range in generation time (because they allowed only age at sexual maturity to vary, and estimates were based only on two individuals as 15.5±1.5 years; Marshall et al. 2021), a 2.7-fold variation in geological longevity. As these four measures (density, range size, geological

longevity, and generation time) are independent their error propagation should reflect a multiplication. Yet Marshal et al. (2021) give the 95% interval for multiplying density by area (to obtain population size) as 252-fold difference (1,300-328,000). They then calculate the interval for all individuals that ever lived as encapsulating a mere 300-fold range whereas even their too-narrow estimates of 241, 2.2, 2.7 and 1.1 yields a range higher than 1500.

Estimates of population densities, range sizes, and population sizes – are associated with much uncertainty, even for well-studied living organisms. Range size dynamics and the relationship between range size and population density are extremely difficult to estimate in the best of cases (except maybe in easy to count small-range endemics). We can set parameters for many factors but unless we use reasonable measures of uncertainty and propagate them when one uncertain parameter is multiplied by another, such endeavors will only give an illusion of accuracy and precision.

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Supplementary Material

The following materials are available as part of the online article from https://escholarship.org/uc/fb
Appendix S1. population densities, sampling areas & body sizes

References

Benton, M. J. (2021) The origin of endothermy in synapsids and archosaurs and arms races in the Triassic. Gondwana Research, https://doi.org/10.1016/j.gr.2020.08.003.

Brassey, C. A. (2016) Body-mass estimation in paleontology: a review of volumetric techniques. The Paleontological Society Papers, 22, 133-156. https://doi.org/10.1017/scs.2017.12

Brownstein, C. D. (2018) The biogeography and ecology of the Cretaceous non-avian dinosaurs

of Appalachia. Palaeontologia Electronica, 21, 1-56. https://doi.org/10.26879/801

Brusatte, S.L. and Carr, T.D., (2016) The phylogeny and evolutionary history of tyrannosauroid dinosaurs. Scientific Reports, 6, 20252. https://doi.org/10.1038/srep20252

Carotenuto, F., Barbera, C. & Raia, P. (2010) Occupancy, range size, and phylogeny in Eurasian Pliocene to recent large mammals. Paleobiology, 36, 399-414. https://doi.org/10.1666/09059.1

Carr, T. D. (2020) A high-resolution growth series of *Tyrannosaurus rex* obtained from multiple lines of evidence. PeerJ, 8, e9192. https://doi.org/10.7717/peerj.9192

Campione, N. E. & Evans, D. C. (2020) The accuracy and precision of body mass estimation in non-avian dinosaurs. Biological Reviews, 95, 1759-1797. https://doi.org/10.1017/scs.2017.12

Clarke, A., Rothery, P. R. & Isaac, N. J. B. (2010). Scaling of basal metabolic rate with body mass and temperature in mammals. Journal of Animal Ecology, 79, 610-619. https://doi.org/10.1111/j.1365-2656.2010.01672.x

Damuth, J. (1987) Interspecific allometry of population density in mammals and other animals: the independence of body mass and population energy-use. Biological Journal of the Linnean Society, 31, 193-246. https://doi.org/10.1111/j.1095-8312.1987.tb01990.x

Foote, M., Crampton, J. S., Beu, A. G., Marshall, B. A., Cooper, R. A., Maxwell, P. A. & Matcham, I. (2007) Rise and fall of species occupancy in Cenozoic fossil mollusks. Science, 318, 1131-1134. https://doi.org/10.1126/science.1146303

Gaston, K. J. (1991) How large is a species' geographic range? Oikos, 61, 434-438.

Graur, D. & Martin, W. (2004) Reading the entrails of chickens: molecular timescales of evolution and the illusion of precision. Trends in Genetics, 20, 80-86. https://doi.org/10.1016/j.tig.2003.12.003

Holtz, T.R., (2014) Laramidia: engine of dinosaur diversity or perfect storm for collecting? (Or both?). The Paleontological Society Special Publications, 13, 169.

Holtz, T. R. (2021) Theropod guild structure and the tyrannosaurid niche assimilation hypothesis: implications for predatory dinosaur macroecology and ontogeny in later Late Cretaceous Asiamerica. Canadian Journal of Earth Sciences. https://doi.org/10.1139/cjes-2020-0174

Hutchinson, J. R., Bates, K. T., Molnar, J., Allen, V. & Makovicky, P. J. (2011) A computational analysis of limb and body dimensions in *Tyrannosaurus rex* with implications for locomotion, ontogeny, and growth. PLoS ONE, 6, e26037. https://doi.org/10.1371/journal.pone.0026037

Kolokotrones, T., Savage, V., Deeds, E. J. & Fontana, W. (2010) Curvature in metabolic scaling. Nature, 464, 753-756. https://doi.org/10.1038/nature08920

Legendre, L.J. & Davesne, D., (2020) The evolution of mechanisms involved in vertebrate endothermy. Philosophical Transactions of the Royal Society B, 375, 20190136. https://doi.org/10.1098/rstb.2019.0136

Liow, L. H. & Stenseth, N. C. (2007) The rise and fall of species: implications for macroevolutionary and macroecological studies. Proceedings of the Royal Society B, 274, 2745-2752. https://doi.org/10.1098/rspb.2007.1006

Loewen, M. A., Irmis, R. B., Sertich, J. J. W., Currie, P. J. & Sampson, S. D. (2013) Tyrant dinosaur evolution tracks the rise and fall of late Cretaceous oceans. PLoS ONE, 8, e79420. https://doi.org/10.1371/journal.pone.0079420

Lyons, S. K. (2003) A quantitative assessment of the range shifts of Pleistocene mammals. Journal of Mammalogy, 84, 385-402. https://doi.org/10.1644/1545-1542(2003)084<0385:AQAOTR>2.0.CO;2

Maidment, S. C. R., Dean, C. D., Mansergh, R. I. & Butler, R. J. (2021) Deep-time biodiversity patterns and the dinosaurian fossil record of the Late Cretaceous western interior, North America. Proceedings of the Royal Society B, 288, 20210692. https://doi.org/10.1098/rspb.2021.0692

Marshall, C. R., Latorre, D. V., Wilson, C. J., Frank, T. M., Magoulick, K. M., Zimmt, J. B. & Poust, A. W. (2021) Absolute abundance and preservation rate of *Tyrannosaurus rex*. Science, 372, 284-287. https://doi.org/10.1126/science.abc8300

Meiri, S., Murali, G., Zimin, A., Shak, L., Itescu, Y., Caetano, G. & Roll, U. (2021) Different solutions lead to similar life history traits

across the great divides of the amniote tree of life. Journal of Biological Research-Thessaloniki, 28. https://doi.org/10.1186/s40709-021-00134-9

Novosolov, M., Rodda, G. H., Feldman, A., Kadison, A. E., Dor, R. & Meiri, S. (2016) Power in numbers. The evolutionary drivers of high population density in insular lizards. Global Ecology and Biogeography, 26, 87-95. https://doi.org/10.1111/geb.12390

Persons, W. S., Currie, P. J. & Erickson, G. M. (2020) An older and exceptionally large adult specimen of *Tyrannosaurus rex*. The Anatomical Record, 303, 656-672. https://doi.org/10.1002/ar.24118

Sampson, S. D. & Loewen, M. A. (2005) Tyrannosaurus rex from the Upper Cretaceous (Maastrichtian) North Horn Formation of Utah: biogeographic and paleoecologic implications. Journal of Vertebrate Paleontology, 25, 469-472. https://www.jstor.org/stable/4524461

Sampson, S. D., Loewen, M. A., Farke, A. A., Roberts, E. M., Forster, C. A., Smith, J. A. & Titus, A. L. (2010) New horned dinosaurs from Utah provide evidence for intracontinental dinosaur endemism. PLoS ONE, 5, e12292. https://doi.org/10.1371/journal.pone.0012292

Santini, L., Isaac, N. J. & Ficetola, G. F. (2018) TetraDENSITY: a database of population density estimates in terrestrial vertebrates. Global Ecology and Biogeography, 27, 787-791. https://doi.org/10.1111/geb.12756

Therrien, F. & Henderson, D. M. (2007) My theropod is bigger than yours… or not: estimating body size from skull length in theropods. Journal of Vertebrate Paleontology, 27, 108-115. https://doi.org/10.1671/0272-4634(2007)27[108:MTIBTY]2.0.CO;2

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