

## PALEONTOLOGY

# Absolute abundance and preservation rate of *Tyrannosaurus rex*

Charles R. Marshall<sup>1,2\*</sup>, Daniel V. Latorre<sup>1,2</sup>, Connor J. Wilson<sup>1,2</sup>, Tanner M. Frank<sup>1,2</sup>, Katherine M. Magoulick<sup>1,2</sup>, Joshua B. Zimmit<sup>1,2</sup>, Ashley W. Poust<sup>1,2,3</sup>

Although much can be deduced from fossils alone, estimating abundance and preservation rates of extinct species requires data from living species. Here, we use the relationship between population density and body mass among living species combined with our substantial knowledge of *Tyrannosaurus rex* to calculate population variables and preservation rates for postjuvenile *T. rex*. We estimate that its abundance at any one time was ~20,000 individuals, that it persisted for ~127,000 generations, and that the total number of *T. rex* that ever lived was ~2.5 billion individuals, with a fossil recovery rate of 1 per ~80 million individuals or 1 per 16,000 individuals where its fossils are most abundant. The uncertainties in these values span more than two orders of magnitude, largely because of the variance in the density–body mass relationship rather than variance in the paleobiological input variables.

Despite the famed incompleteness of the fossil record, much can be inferred from fossil material, including cell sizes and thus genome sizes (1); individual longevities (2, 3); and growth and cohort survivorship curves (2, 4, 5). However, quantifying population-level variables such as population density and abundance is made difficult by the incompleteness of the fossil record (6, 7), largely because fossilization rates are unknown, which means that the number of fossils cannot be used to calculate these variables.

Nonetheless, data from living species indicate a strong relationship between population density and body mass (8), which makes it possible to estimate population-level variables. Here, for one of the best understood dinosaurs, *Tyrannosaurus rex* (Fig. 1) (9, 10), we use this relationship to estimate its population density, which we combine (Fig. 2) (11) with our rich knowledge of the species to estimate several population-level variables, including the total number of *T. rex* that ever lived and the species' preservation rate. We assessed the impact of uncertainties in the data used with Monte Carlo simulations (11), but these simulations do not accommodate uncertainties that might stem from the choices made in the design of our approach (11).

Our calculations depend on the ability to estimate the population density ( $\rho$ ) of *T. rex* (Fig. 2). Here, we use Damuth's Law (8, 12, 13) to constrain that density. Derived from living species, Damuth found that  $\rho$  is negatively correlated with a species' body mass ( $M$ ) through a power law (8)

$$\log_{10}(\rho) = \log_{10}(a) - b \times \log_{10}(M) \quad (1)$$

<sup>1</sup>Department of Integrative Biology, University of California, Berkeley, CA, USA. <sup>2</sup>University of California Museum of Paleontology, University of California, Berkeley, CA, USA. <sup>3</sup>San Diego Natural History Museum, San Diego, CA, USA. \*Corresponding author. Email: crmarshall@berkeley.edu

In applying Eq. 1, we used the broadly accepted value of  $b = -3/4$  for the slope (8, 11, 12, 14) [see (11) for  $b = -2/3$ ], which leaves two unknowns: the intercept [ $\log_{10}(a)$ ] and the body mass ( $M$ ).

The intercept [ $\log_{10}(a)$ ] depends on trophic level and physiology. Trophically, *T. rex* was clearly a carnivore, but establishing its physiology has proven challenging (7, 15). Among living species, a slower metabolism is reflected in larger population densities, hence larger values of the intercept. However, ecological differences between species within the same trophic level, regardless of physiology, translate into a large scatter in population densities, independent of the intercept (Fig. 2A). For example, flesh-eating mammals have a 150-fold variation ( $\pm 1.96\sigma$ ) in population density for species of the same body mass (11) (Fig. 2A).

This ecological scatter swamps the uncertainty introduced by the unknown physiology of *T. rex*. Nonetheless, we need an estimate of *T. rex*'s physiology to assign an intercept. There is general agreement that dinosaurs were broadly endothermic (7, 16–21) but that different species had different physiologies

(19–21) with metabolisms equal to or lower than those of living mammals (20, 21). Energetic considerations suggest that dinosaurs were more mesothermic than living mammals (7, 17, 18). For example, the extreme size of saurischian dinosaurs (which include *T. rex*) would be best explained if they had a metabolism similar to that of large varanid lizards such as the Komodo dragon, which uses ~22% as much energy per unit mass as that used by flesh-eating mammals (17). However, dinosaur paleobiologists tend to favor a more energetic physiology (22), so we assumed a physiology midway between that of mammalian carnivores and that of large varanid lizards (11) (Fig. 2A). This translates into population densities 2.1 times as large as the population densities of the average mammalian carnivore and population densities 1/2.1 times the size of population densities of large varanids for the same body mass. By contrast, mammalian herbivores average ~35-fold higher population densities than those of flesh-eating mammals (11), and reptiles have, on average, ~30-fold higher population densities than those of mammals for the same body mass (8). The scatter about the line of best fit noted above (Fig. 2A) means that our analysis encompasses the full range of physiologies proposed for *T. rex*, including physiologies even more energetic than those of the average mammalian carnivore.

For the body mass estimate of *T. rex*, we took into account the fact that Damuth's data included individuals that had not reached maximum size (11). Thus, rather than using the maximum body mass of *T. rex*, we computed the average body mass of postjuvenile individuals (Fig. 1B and Table 1) [see (11) for why we used this cutoff], which we call the ecological body mass. This was estimated by summing, over all postjuvenile age cohorts, the product of the average mass of individuals in each cohort, using a *T. rex* growth curve (2) (Fig. 2C), and the proportion of individuals in that cohort, using available *T. rex* survivorship data (4) (Fig. 2D) (11). This yielded a

**Table 1. Input variable values for calculating *T. rex* population variables and absolute individual preservation rate.** The uncertainty values (bottom row) are the ratios of the 97.5% and 2.5% values, derived from the Monte Carlo simulations.

Values	Intercept, population density $\log_{10}(a)$	Ecological body mass (kg) $M$	Area (million km <sup>2</sup> ) $A$	Temporal range (million years) $T$
2.5% tail	1.80	3700	1.42	1.3
Mean	2.99	5200	2.30	2.4
97.5% tail	4.18	6900	3.18	3.5
Approximate uncertainty	240×*	1.6×†	2.2×	2.7×

\*The uncertainty of the intercept,  $a$ , is equal to  $10^{(97.5\% \text{ tail cutoff} - 2.5\% \text{ tail cutoff})} = 240$ . †Populations density =  $M^b$ . For  $b = -0.75$ , the ratio of the 97.5% tail and 2.5% tail is  $6900/3700 = 1.86$ , which, when raised to the exponent  $b$ , is  $(1.86)^{-0.75} = 1.6$ .



**Fig. 1. Skeletal outline of *T. rex*.** Illustration credit: Danielle Dufault, Royal Ontario Museum.

mean of 5200 kg, ranging from 3700 to 6900 kg ( $\pm 1.96\sigma$ ) (Fig. 2B and Table 1).

Given these values, we estimate that *T. rex*'s population density (Eq. 1) was between 0.00058 and 0.14 postjuvenile individuals/km<sup>2</sup> (with 95% confidence), with a median of 0.0091 individuals/km<sup>2</sup> (Fig. 2E and Table 2). This agrees well with Farlow's (7) estimate of 0.01 individuals/km<sup>2</sup> and is ~0.16 times the population density of tigers and ~0.07 times the population density of lions (8). The median estimate translates into a population size of 3800 *T. rex* in an area the size of California and just two individuals in an area the size of Washington, DC.

To calculate the standing population size of *T. rex* (Fig. 2G), we multiplied the population density by the estimated geographic area (Fig. 2F) occupied by *T. rex* (eq. S2). For a minimum constraint on the geographic area, we used the convex hull around *T. rex* fossil localities that have yielded published postjuvenile individuals held in public repositories (11). We used this as a minimum constraint given the geographic incompleteness of the fossil and rock records (23). For a maximum constraint, we used the size of the inferred ecological niche for tyrannosaurs in the Late Maastrichtian (11, 24). This is a maximum estimate because it is an extent of occurrence (EOO), whereas Damuth's Law is based on the smaller areas

of occupancy (AOOs) (8, 11). Given these constraints, the estimated geographic area for *T. rex* is  $2.3 \pm 0.88$  million km<sup>2</sup> ( $\pm 1.96\sigma$ ) (Fig. 2F and Table 1).

Multiplying the plausible population densities by the plausible geographic areas yielded an average population size of 20,000 individuals, with a 95% interval from 1300 to 328,000 individuals (Fig. 2G and Table 2). The lower limit seems too low, given the loose consensus that at least thousands of individuals are needed for long-term persistence (11). Our median estimate of postjuvenile *T. rex* biomass alive at any one time—the population size multiplied by the ecological body mass—is  $1.1 \times 10^5$  tonnes with a 95% interval from  $6.6 \times 10^3$  to  $1.7 \times 10^6$  tonnes.

To estimate the total number of *T. rex* that ever lived, we multiplied the standing population size by the total number of generations that *T. rex* persisted. To estimate the latter, we divided the estimated temporal range of *T. rex* (Fig. 2H) by its generation time (Fig. 2K).

The temporal range of *T. rex* is uncertain because of the poor temporal control on most *T. rex* fossil localities (25) and because there is a substantial dinosaur preservational gap below the oldest *T. rex* fossils (11, 25, 26). Thus, we established minimum and maximum age brackets on its temporal duration (11) from 1.2 to 3.6 million years, which led to a mean

estimate of 2.4 million years (Fig. 2H and Table 1).

The generation time was calculated using the proportion of individuals living to age  $x$  years ( $l_x$ ), derived from its cohort survivorship curve (4), and the average number of progeny produced at each age ( $b_x$ ), which requires an estimate of the onset of sexual maturity and its maximum lifetime (eq. S25) (11). This yielded an estimate of  $19.0 \pm 1.2$  years ( $\pm 1.96\sigma$ ) (Table 2 and Fig. 2K) (11). Dividing the longevity by the generation time yielded an estimated persistence for *T. rex* of 127,000 generations, with a 95% interval from 66,000 to 188,000 generations (Fig. 2L and Table 2).

The total number of *T. rex* that ever lived ( $N$ ) (Fig. 2M) was then estimated by multiplying the number of generations that *T. rex* persisted (Fig. 2L) by its standing population size (Fig. 2G). This gave a median of  $2.5 \times 10^9$  individuals, with a 95% interval from  $1.4 \times 10^8$  to  $4.2 \times 10^{10}$  individuals (Fig. 2M and Table 2). The median estimate, although large, is about half of the total number of adult humans currently alive. This translates into a median total postjuvenile biomass for all *T. rex* of  $1.3 \times 10^{10}$  tonnes, with a 95% interval from  $7.5 \times 10^8$  to  $2.2 \times 10^{11}$  tonnes.

With an estimate of the total number of *T. rex* that ever existed and the minimum number of described postjuvenile fossil individuals curated in public repositories (10, 11), which consists of 32 individuals, the minimum median per-individual fossil recovery rate is 1 fossil individual for every 80 million individuals (Fig. 2N and Table 2), with a 95% interval ranging from 1 in every 4.5 million to 1 in every 1.3 billion individuals (Fig. 2N and Table 2). The number of *T. rex* individuals represented in museums and in the hands of private collectors—excluding nondiagnostic elements such as teeth, vertebrae, or phalanges, whether formally described or not—is on the order of 100 individuals, so the current overall fossil recovery rate is approximately three times these values.

However, *T. rex* fossils can only be recovered from places where we have rock of appropriate

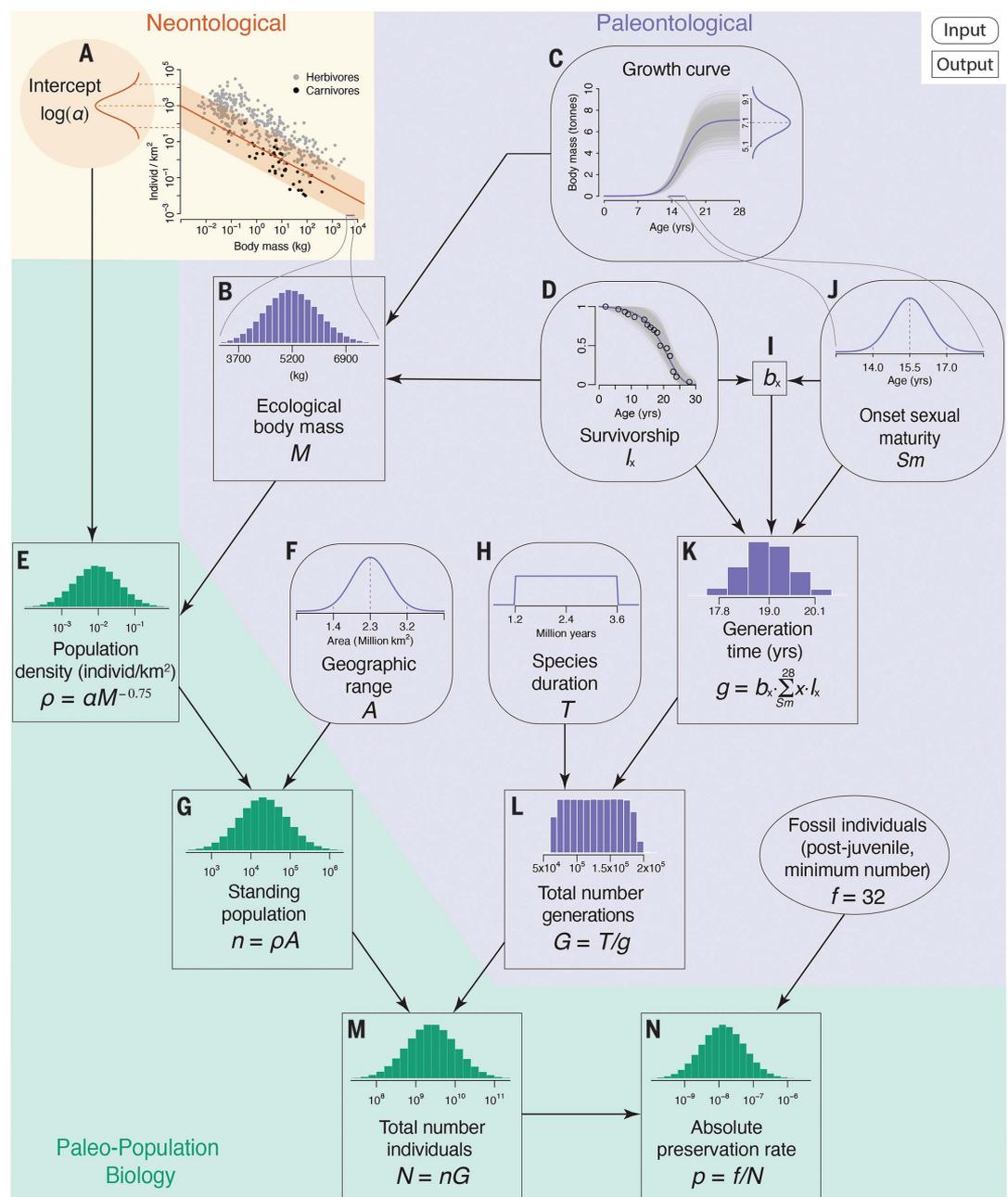
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**Table 2. Output variable estimates for *T. rex* population variables and absolute individual preservation rate.** The uncertainty values (bottom row) are the ratios of the 97.5% and 2.5% values, derived from the Monte Carlo simulations. These values are approximate because of rounding errors in the numbers presented in the table.

Values	Population density (individuals/km <sup>2</sup> ) $\rho$	Standing population size $n$	Generation time (years) $g$	Number of generations $G$	Total number of <i>T. rex</i> $N$	Absolute preservation rate $p$	Number of individuals per fossil $1/p$
2.5% tail	0.00058	1300	17.8	66,000	$1.4 \times 10^8$	$2.2 \times 10^{-7}$	4.5 million
Middle value	0.0091	20,000	19.0	127,000	$2.5 \times 10^9$	$1.3 \times 10^{-8}$	80 million
97.5% tail	0.14	328,000	20.1	188,000	$4.2 \times 10^{10}$	$7.6 \times 10^{-10}$	1.3 billion
Approximate uncertainty	240×	250×	1.1×	2.8×	295×	295×	295×

**Fig. 2. Schematic showing the use of paleontological and neontological data to estimate population variables and the absolute preservation rate for *T. rex*.** The quantitative relationships between the variables (11) are indicated in the insets.

(A) Distribution of intercepts used for the  $\log(\text{population density})$  versus  $\log(\text{body mass})$  plot. (B) *T. rex* ecological body mass distribution. (C) Range of growth curves for *T. rex*, given the uncertainty in the maximum body size. (D) Cohort survivorship curves for *T. rex* (5). (E) Inferred *T. rex* population density. (F) Possible geographic ranges for *T. rex*. (G) Inferred *T. rex* population size at any given time. (H) Range of plausible geologic longevities of *T. rex*. (I) Age-specific rates of reproduction,  $b_x$ . (J) Time of onset of sexual maturity ( $S_m$ ). (K) Estimated *T. rex* generation time. (L) Estimated longevity of *T. rex* in generation times. (M) Estimate of total number of *T. rex* that ever lived. (N) Minimum absolute individual preservation rate. Continuous probability distributions were used for the input variables, where the limits shown on the normal distributions represent  $\pm 1.96$  standard deviations. The limits shown for the ecological body mass (B) and generation time (K) also represent  $\pm 1.96$  standard deviations. The output variables are shown as histograms derived from 1 million Monte Carlo simulations (11).



age deposited in the appropriate environments. Thus, we computed the per-individual fossil recovery rate for just the geographic range ( $\sim 1000 \text{ km}^2$ ) (27) and duration ( $\sim 1.2$  million years) of the portion of the Hell Creek Formation that has yielded the most *T. rex* fossils. The estimated total number of postjuvenile individuals of *T. rex* that occupied this region during that 1.2 million years is  $\sim 610,000$  (table S6), or about nine at any given time. A decade-long survey (27) yielded fossils from 37 presumed postjuvenile individuals (11), which translates into a median per-individual preservation rate of 1 in 16,000, with a 95% interval ranging from 1 in 1100 to 1 in 260,000 (table

S6), ignoring the possibility that fossils might have been washed in from a larger area.

The largest source of uncertainty in our analysis stems from the scatter in the body mass–population density relationship from living species, which is about two orders of magnitude larger than the paleobiological uncertainties (Table 2). Nonetheless, our capacity for inferring population sizes of extinct taxa greatly exceeds what Simpson (6) thought possible more than 75 years ago and Farlow's (7) pioneering work on the population size of *T. rex* from almost 30 years ago. This capacity has been enabled by the discovery of many more fossils and the ability to estab-

lish growth and survivorship curves from age and body mass estimates. Further insights into the ecology of *T. rex* should reduce the uncertainty in its population density, for example, through the use of paleontological methods for determining whether predator guilds are under- or overrepresented (28). The framework developed here can be applied to any taxon with the appropriate data, or where the data can be developed through the collection of more fossils. It also opens the door for other types of analysis—for example, determining how rare, geographically restricted, or short-lived a species had to be to escape discovery in the fossil record or combining

population size estimates with measured rates of morphological evolution to infer selection coefficients. The range and quantity of data now available for well-sampled and well-studied fossil taxa have the potential to greatly enhance our ecological understanding of extinct species.

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#### SUPPLEMENTARY MATERIALS

[science.sciencemag.org/content/372/6539/284/suppl/DC1](https://science.sciencemag.org/content/372/6539/284/suppl/DC1)  
Materials and Methods  
Tables S1 to S6  
References (30–60)

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### Estimating dinosaur abundance

Estimating the abundance of a species is a common practice for extant species and can reveal many aspects of its ecology, evolution, and threat level. Estimating abundance for species that are extinct, especially those long extinct, is a much trickier endeavor. Marshall *et al.* used a relationship established between body size and population density in extant species to estimate traits such as density, distribution, total biomass, and species persistence for one of the best-known dinosaurs, *Tyrannosaurus rex*, revealing previously hidden aspects of its population ecology.

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