Vital statistics, absolute abundance and preservation rate of *Tyrannosaurus rex*

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Abstract: I present a simulation model on vital statistics, absolute abundance (N, total number of individuals that ever lived) and preservation rate (p, minimum number of fossils known divided by N) of *Tyrannosaurus rex*. It is based on a published age-structured population model that assumes a reptile or bird-like reproduction for *T. rex* to estimate its age-specific survival rates. My model applies input variables and equations from a recently published model on N and p. This model yielded 2.5 billion *T. rex* individuals (N) and one fossil per 80 million individuals (p). The average N values calculated by my model were at minimum 27.6% and p values at maximum 361.5% that of a previous model and uncertainties in all output variables were always larger in my model. The equation on output variable 'population density' introduced the largest uncertainty to N and p. The output variable 'generation time' differed the most between models, but for N and p, the huge size of the input area modelled and geological longevity minimized this difference. Unlike my model, the generation time as well as life expectancies, gross reproduction rates, and reproductive values of individuals calculated from the previous model all strongly contradicted our current understanding of the biology of *T. rex* and of other theropods. Their values also disagreed with those of large extant reptiles, birds and mammals. All of these shortcomings of the previous model favour the assessment of individual and population characteristics of *T. rex* and of other extinct species using my model.
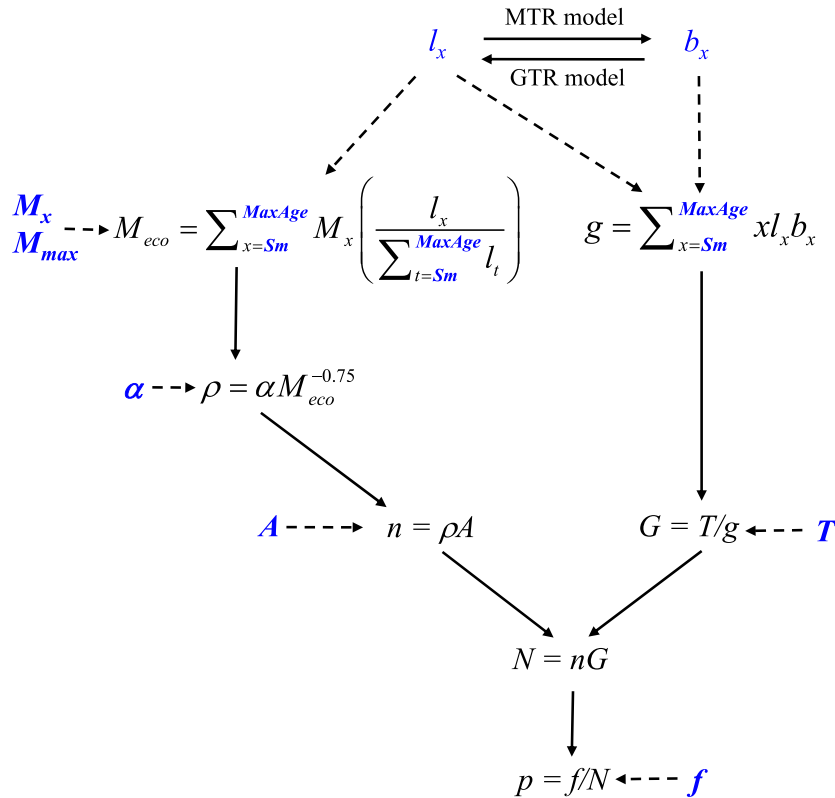
Key words: survival, fecundity, life expectancy, gross reproduction rate, reproductive value, generation time.

BONE histology is central to our understanding of the life histories and population biology of extinct vertebrate species. Specifically, skeletochronology, a field of bone histology studying cyclical growth marks preserved in bones, provides information on the age and size of onset of sexual maturity, the age at which maximum individual size was achieved, and the length of an individual's life (Castanet *et al.* 1993; Woodward *et al.* 2013; but see Heck & Woodward 2021; Schucht *et al.* 2021). Growth trajectories erected from histological growth records not only allow an objective estimation of all these traits, but also of traits being undocumented in the fossil record (e.g. hatchling size, asymptotic size, maximum growth rate; Lehmann & Woodward 2008; Erickson *et al.* 2009; Griebeler *et al.* 2013; Klein *et al.* 2015).

Compared to the individual level, there has been less progress in the understanding of populations of extinct dinosaurs. Researchers have been able to establish age distributions of populations from bone assemblages and survivorship curves for only a small number of dinosaur species (Erickson *et al.* 2006, 2009, 2010; Woodward *et al.* 2015). For four tyrannosaurs including *Tyrannosaurus rex*, Erickson *et al.* (2006) published convex survivorship curves, indicating that these species had a high survival throughout most of their life with mortalities considerably increasing towards its end. Convex shaped curves are observed in extant captive animals and in humans living in highly industrialized countries (Pianka 1999; Smith & Smith 2006).

Marshall *et al.* (2021) made use of the exceptionally good information on aging, maturation and growth in *T. rex* to model its absolute abundance (the total number of individuals that ever lived) and preservation rate (the minimum number of *T. rex* fossils known divided by its absolute abundance). The authors input a growth trajectory (Erickson *et al.* 2004) and survivorship curve (Erickson *et al.* 2006) on *T. rex* to their model as well as estimates on its maximum age (Erickson *et al.* 2006) and age of onset of sexual maturity (Erickson *et al.* 2004; Myhrvold 2013). The first calculation step in their model is the estimation of a constant fecundity value from the survivorship curve, thereby assuming that fecundities of all mature individuals were equal and that the population size was constant throughout its persistence time. The authors failed to check whether the fecundity and survivorship curve yielded vital statistics (e.g. life expectancy at birth, gross reproduction rate, reproductive value at maturation, generation time) consistent with our current knowledge on the biology of *T. rex* and of other theropod populations. Such a check is essential as populations are

$$ l_x \underset{\text{GTR model}}{\overset{\text{MTR model}}{\rightleftarrows}} b_x $$

$$ \begin{matrix} \boldsymbol{M_x} \\ \boldsymbol{M_{max}} \end{matrix} \dashrightarrow M_{eco} = \sum_{x=\boldsymbol{Sm}}^{MaxAge} M_x \left(\frac{l_x}{\sum_{t=\boldsymbol{Sm}}^{MaxAge} l_t} \right) \qquad g = \sum_{x=\boldsymbol{Sm}}^{MaxAge} x l_x b_x $$

$$ \boldsymbol{\alpha} \dashrightarrow \rho = \alpha M_{eco}^{-0.75} $$

$$ \boldsymbol{A} \dashrightarrow n = \rho A \qquad\qquad G = T/g \dashleftarrow \boldsymbol{T} $$

$$ N = nG $$

$$ p = f/N \dashleftarrow \boldsymbol{f} $$

FIG. 1. Schematic representation of the MTR and GTR models. Input variables are shown in blue (Table 1A) and those shared between the MTR and GTR models are in bold. Arrows indicate which variables determine an output variable (Table 1B). The MTR model estimates age-specific fecundities b_x from given age-specific survival rates l_x (Erickson *et al.* 2006), whereas the GTR model takes the complementary approach (Griebeler 2021). For more information on input and output variables, refer to Table 1.

made up of individuals and characteristics of individuals determine those of populations (Pianka 1999).

In a recent study, Griebeler (2021) strongly questioned the convex survivorship curve of *T. rex* (Erickson *et al.* 2006) that Marshall *et al.* (2021) input to their model. She suggested a linear (a rather constant mortality throughout life; seen in extant small birds, mammals and lizards; Pianka 1999; Smith & Smith 2006) to concave curve (high mortalities at the beginning of life are followed by low mortalities towards its end; seen in extant long-lived reptiles; Pianka 1999; Smith & Smith 2006). In her study on six dinosaurs (Erickson *et al.* 2004; Erickson *et al.* 2009; Woodward *et al.* 2015), she applied an age-structured population model with age-dependent fecundities and survival rates. Inputs to her model are maximum age, age of onset of sexual maturity and annual egg number of fully-grown individuals. While estimates on maximum age (Erickson *et al.* 2006) and age of onset of maturation (Erickson *et al.* 2004; Myhrvold 2013) exist from bone histological studies on *T. rex*, annual egg numbers cannot be preserved in the fossil record. Given empirical evidence for a reptile or bird like reproduction in theropods (Schweitzer *et al.* 2005; Lee & Werning 2008;

Werner & Griebeler 2013), Griebeler (2021) evaluated her model for annual egg numbers as seen in scaled-up extant reptiles and birds (Werner & Griebeler 2013) and applied different functions relating fecundity to age (Frazer 1984; Martin 1995; Pianka 1999).

Thus, while Marshall *et al.* (2021) assumed that the convex survivorship curve on *T. rex* is correct (note, even bootstrapping of age samples always revealed convex curves, Erickson *et al.* 2006, Marshall *et al.* 2021) and used it to predict age-specific fecundities, Griebeler (2021) started from realistic age-specific fecundities and used them to predict age-specific survival rates. The complementary approaches taken by the two studies invited an investigation of whether the absolute abundance and preservation rate as well as other population characteristics of *T. rex* that Marshall *et al.* (2021) calculated with their model change under the approach of Griebeler (2021). There is also a need to establish potential differences arising in the vital statistics of *T. rex* populations.

Here, I present a model on *T. rex* (hereafter GTR model; Appendix S1) that only differs from that in Marshall *et al.* (2021) (hereafter MTR model) by inferring age-specific survival rates from age-specific fecundities and not

vice versa (Fig. 1). As in the study of Griebeler (2021), I evaluated my model for a reptile and bird model on annual egg number (Werner & Griebeler 2013) and considered different functions on age-specific fecundities in order to estimate the absolute abundance and preservation rate of *T. rex*. I further investigated differences in values of several standard variables of the vital statistics of *T. rex*. With this analysis, I checked whether the vital statistics generated by both models are consistent with our current knowledge of the biology of this theropod and that of large extant amniotes. I thus verified, whether both models are sound from the individual to the population level.

MATERIAL AND METHOD

The model of Marshall et al. (2021) and its evaluation

The MTR model developed by Marshall *et al.* (2021) (Table 1; Fig. 1) estimates several population-level variables of *T. rex* to infer its absolute abundance (N, total number of individuals that ever lived), absolute preservation rate (p = f/N, where f is the minimum number of post-juvenile individuals curated in public repositories) and the fossil recovery rate (the inverse of absolute preservation rate, 1/p). Inputs to the MTR model are age-specific survival rates (l_x, hereafter survivorship schedule; Erickson *et al.* 2006), maximum age (MaxAge; Erickson *et al.* 2006), age of onset of sexual maturity (Sm; Erickson *et al.* 2004; Myhrvold 2013) and a growth trajectory (M_x; Erickson *et al.* 2004). These individual-level variables for *T. rex* are complemented by its geographical range (A, size of its distribution area), the intercept of a power law ($\log_{10}(\alpha)$, log–log-transformed data) relating population density to body mass (it assumes a physiology intermediary between that of varanid lizards and carnivorous mammals) as well as its geological longevity (T, species duration). From all these input variables (Table 1A), the MTR model estimates six output variables (Table 1B, Fig. 1) needed to calculate N, p and 1/p. These are: (1) the constant fecundity of mature individuals (b_{mature}, note that the MTR model uses the symbol *x*, which would be confusing as fecundities of mature individuals depend on age *x* in my model); (2) the generation time (g); (3) the total number of generations (G); (4) the ecological body mass (M_{eco}); (5) the population density (ρ); and (6) the standing population (n). For the calculation of b_{mature}, the MTR model evaluates the Lotka–Euler equation (LEE; Eqn 1) formulated for an age-structured population (Pianka 1999). The LEE relates age-specific survivorship schedule (l_x) and fecundities (b_x) to the net reproductive rate (R_0). R_0 is the average number of class zero offspring that an average newborn individual of a population gives during its entire lifetime.

$$R_0 = \sum_{x=0}^{MaxAge} l_x b_x \qquad (1)$$

with age *x* being a natural number (years), l_x the probability that an individual survives from birth (*x* = 0) to a given age *x* (>0), and b_x the number of births given by an individual of age *x* (within 1 year). Under the three assumptions that the population size of *T. rex* was approximately constant over its geological longevity T (i.e. R_0 = 1), its age-specific survivor rates (l_x) are known and the annual fecundities (b_x) of mature individuals do not differ between ages, the b_{mature} value calculated from l_x and LEE (Eqn 1) is:

$$b_{mature} = \frac{1}{\sum_{x=Sm}^{MaxAge} l_x} \qquad (2)$$

For modelling survival rates l_x, the MTR model used the age sample in Erickson *et al.* (2006) on *T. rex* and a Gompertz equation:

$$l_x = \exp\left(\frac{a}{g}(1 - \exp(gx))\right) \qquad (3)$$

with a = 0.002 and g = 0.2214 derived for this sample (Fig. 2).

As the fecundities of mature individuals (b_{mature}) do not differ between ages and fecundities of non-mature individuals must be zero, Marshall *et al.* (2021) implemented a step function on age-specific fecundities (hereafter fecundity schedule b_x) that, among others, Griebeler (2021) applied in her age-structured population model. Because the MTR model uses b_{mature} for calculating generation time g, b_{mature} must affect values of all output variables directly or indirectly derived from g (Table 1B, Fig. 1). These are G, N, p and 1/p. Besides, for calculating b_{mature} and g, the survivorship schedule l_x is also used for calculating M_{eco}. Specifically, M_{eco} is obtained by summing up the products of the mass of each age cohort (M_x; Erickson *et al.* 2001; Table 1B) and the proportion of mature individuals alive in that cohort (l_x). To predict ρ, M_{eco} is passed to a power law (Table 1A). Thus, by setting the values of M_{eco} and ρ, the survivorship schedule (l_x) also affects the values inferred for n, N, p and 1/p (Fig. 1).

To assess the impact of uncertainties in input variables on each of the output variables, Marshall *et al.* (2021) conducted one million Monte Carlo simulations and used uncertainty distributions on the survivorship schedule l_x and on each of the five input variables Sm, M_{max}, T, $\log_{10}(\alpha)$ and A (Table 1A). In particular, by applying uncertainties in M_{max} and Sm, these authors have taken into consideration plasticity in growth and variability in ages coinciding with a trajectory's inflection point (Sm; Erickson *et al.* 2001; Myhrvold 2013). To capture

TABLE 1. Input variables (A), output variables (B) and other variables and abbreviations (C) for the MTR and GTR models.

A Input variables

Variable	Meaning	Value	Uncertainty distribution
A	Area modelled	$23\,000\,000 \pm 880\,000$ km^2 (mean, 95% CI)	Normal
$\log_{10}(\alpha)$	Intercept power law on population density	2.991 ± 1.188 (mean, 95% CI)	Normal
f	Minimum number of *T. rex* fossils known	32	None
MaxAge	Oldest *T. rex* individual known	28 years	None
M_{max}	Maximum adult body mass	7090 ± 1985 kg (mean, 95% CI)	Normal
M_x	Growth model for *T. rex*	$M_x = \frac{M_{max}}{1+\exp(-0.55(x-16.2))} + 5$ (kg)	Via M_{max}
Sm	Age of onset of sexual maturity	15.5 ± 1.5 years (mean, 95% CI)	Normal
T	Geological longevity	1.2–3.6 million years	Uniform

B Output variables

Variable	Meaning	Formula
g	Generation time (years)	$g = \sum\limits_{x=Sm}^{MaxAge} x l_x b_x$ (see also Eqn 9)
G	Number of generations	$G = T/g$
M_{eco}	Ecological body mass (kg)	$M_{eco} = \sum\limits_{x=Sm}^{MaxAge} M_x \left(\frac{l_x}{\sum_{t=Sm}^{MaxAge} l_t} \right)$
n	Standing population	$n = \rho A$
N	Absolute abundance (total number of individuals)	$N = nG$
p	Absolute preservation rate	$p = f/N$
ρ	Population density (individuals/km^2)	$\rho = \alpha M_{eco}^{-0.75}$, M_{eco} (g)

C Other variables and abbreviations

Variable	Meaning	Formula
AEN	Annual egg number	Only for GTR model, see Fig. 2B, equations in Griebeler (2021)
b_{mature}	Constant fecundity value of mature individuals	Only for MTR model, Eqn 2
b_x	Age-specific fecundities, fecundity schedule	Equations in Griebeler (2021); only for GTR model
E_0	Life expectancy of a newborn individual	Eqn 5
E_{Sm}	Life expectancy of an individual that has just reached maturity	Eqn 6
GRR	Gross reproduction rate	Eqn 7
g_t	Generation time	Eqn 9
λ	Controls the shape of the survivorship curve	Only GTR model, Eqn 4
LEE	Lotka–Euler equation	Eqn 1
l_x	Age-specific survival rates, survivorship schedule	Eqn 3 for the MTR, Eqn 4 for the GTR model
R_0	Net reproductive rate of the population	Eqn 1
v_{Sm}	Reproductive value of an individual of age Sm	Eqn 8

One million Monte Carlo simulation runs were carried out for both models. At the beginning of each run a value on Sm, M_{max}, T, $\log_{10}(\alpha)$ and A was randomly chosen from the respective uncertainty distribution. Both models use a power law with an exponent of -0.75 on the relation between M_{eco} and ρ. For more details of the MTR and GTR models, refer to the main text and Fig. 1.

uncertainties in l_x, they generated bootstrapped age samples of the specimens in Erickson *et al.* (2006) and fitted a Gompertz curve (Eqn 3) to each sample. For generation time T, Marshall *et al.* (2021) chose a uniform distribution, whereas they applied a normal distribution to Sm, M_{max}, $\log_{10}(\alpha)$ and A (Table 1A). For each of the input variables with an uncertainty distribution, a value was

randomly chosen at the beginning of each simulation run. Then the model was evaluated with this combination of input parameter values.

Marshall *et al.* (2021) assessed uncertainties in all output variables of their model by middle values (median) as well as by 2.5% and 97.5% tail values. All were calculated for each variable from the distribution of values generated

by the one million Monte Carlo simulation runs. The authors further calculated an approximate uncertainty for each output variable, which is the ratio of the distribution's 97.5% and 2.5% tail value.

GTR model

The evaluation of the LEE (Eqn 1) under $R_0 = 1$ is central to the MTR and GTR models. The only difference between the two models is that the MTR model derives the fecundity schedule b_x from a given survivorship schedule l_x (Eqn 2), whereas the GTR model assumes a fecundity schedule b_x for *T. rex* and then estimates its survivorship schedule l_x (Fig. 1). I chose this approach because the modelling study of Griebeler (2021) strongly questioned the convex shape of the survivorship curve on *T. rex* (Erickson *et al.* 2006) and favoured a concave to linear shaped curve (Fig. 2A). Griebeler (2021) further demonstrated that survivorship curves derived from the LEE are shaped by the assumed values of fecundity schedules b_x and R_0. Thus, in order to address uncertainties in values of output variables arising from different fecundity schedules b_x assumed for *T. rex*, the GTR model considers the b_x step function from the MTR model and also three others from Griebeler (2021) (Fig. 2B). For the b_x step function and for all others, evidence exists in extant reptiles and birds (Frazer 1984; Martin 1995; Pianka 1999). The hyperbolic function (b_x hyperbolic), also considered here, implements an increase and the linear function (b_x linear) a decrease in b_x with an increasing individual's age x. The Weibull function (b_x Weibull) further applied simulates an increase in b_x that is followed by a senescence driven die-off. All of the four fecundity functions of my GTR model are parametrized by the dinosaur's Sm (the fecundity of non-mature individuals is zero), MaxAge and annual egg number (AEN). AEN is derived from a reptile or bird allometric model (Werner & Griebeler 2013; Griebeler 2021) that is evaluated for the maximum adult body mass M_{max} used in the respective simulation run. For establishing age-specific survival rates l_x, the GTR model adopted the function from Griebeler (2021). It is parametrized by a single parameter (λ) directly controlling the survivorship curve's shape within the concave to convex spectrum (Fig. 2A; Pearl 1928; Pearl & Minor 1935):

$$l_x = 1 + \frac{\exp(\lambda \tilde{x}) - 1}{1 - \exp(\lambda)}(1 - 0.001) \qquad (4)$$

It is formulated for an initial cohort of 1000 individuals (Pearl 1928; Pearl & Minor 1935) and $\tilde{x}$ is the standardized age of an individual ($0 \leq \tilde{x} \leq 1$; $\tilde{x} = 1$ for MaxAge). Details on the root-finding-algorithm used for

inferring λ from the LEE (Eqn 1) under $R_0 = 1$ and a given fecundity schedule b_x are provided in Griebeler (2021).

Simulation scenarios studied with the GTR model and evaluation of simulation results

I implemented my GTR model in the software R (v3.5.2; R Core Team 2013) and studied five scenarios on the fecundity schedule b_x of *T. rex*. In the first two scenarios, I used the b_x step function for which b_x was either parametrized from the reptile ('reptile with b_x step' scenario) or bird model ('bird with b_x step' scenario) for AEN (Griebeler 2021). Two further scenarios assumed either a reptile ('reptile with b_x vertebrate' scenario) or bird model ('bird with b_x vertebrate' scenario) for AEN. In both scenarios, at the beginning of each simulation run, one of the four fecundity functions (Fig. 2B) was randomly chosen and parametrized by the AEN value from the reptile or bird model, respectively. In the last, so-called 'reptile or bird with b_x vertebrate' scenario one of the four fecundity functions was randomly assigned as well as whether a reptile or bird model provided the AEN value for the run. The last scenario thus recognizes that we have no clear evidence for either a reptile or bird-like AEN in *T. rex* and that we do not know how its fecundities changed throughout its life. Compared to the four other scenarios, the last scenario therefore establishes the largest palaeobiological uncertainty in the fecundity schedule b_x for *T. rex*.

I evaluated the one million simulation runs conducted for each of the five fecundity scenarios as in Marshall *et al.* (2021), but calculated two further measures quantifying absolute and relative differences between the MTR and GTR models for each output variable. The absolute change in an output variable is the difference between the median of the GTR and the respective of the MTR model. The relative change in an output variable is the ratio of the median of the GTR model and that of the MTR model.

Calculation of variables on vital statistics of T. rex populations with both models

I calculated five standard variables on the vital statistics of a population (Pianka 1999) using the approaches of the MTR and of the GTR models on the relationship between the survivorship schedule l_x and the fecundity schedule b_x. With this analysis I investigated whether population-level characteristics that are calculated from the survivorship and fecundity schedule by the MTR and GTR model are consistent with our current knowledge of the vital statistics of *T. rex* and of other theropods. I

further investigated whether their values are consistent with those seen in large extant amniotes. The first was the life expectancy of a newborn individual, which is the expected number of years that it will live before it dies:

$$E_0 = \sum_{x=0}^{MaxAge} \frac{l_x}{l_0} \qquad (5)$$

The second characteristic is the life expectancy of an individual of age Sm (E_{Sm}). This is the expected number of years that an individual that has just reached maturity will live before it dies:

$$E_{Sm} = \sum_{x=Sm}^{MaxAge} \frac{l_x}{l_{Sm}} \qquad (6)$$

The third characteristic is the gross reproduction rate (GRR), which is the total number of births that in the absence of mortality a mature individual would give before it dies at age MaxAge:

$$GRR = \sum_{x=Sm}^{MaxAge} b_x \qquad (7)$$

The fourth characteristic is the reproductive value of an individual of age Sm (v_{Sm}). It is the expected number of future births given by an individual that has just reached maturity:

$$v_{Sm} = \sum_{x=Sm}^{MaxAge} b_x \frac{l_x}{l_{Sm}} \qquad (8)$$

The last characteristic is the generation time g_t, which is the average age of parenthood in individuals reproducing repeatedly. It is also an output variable of the MTR model (g; Table 1B):

$$g_t = \sum_{x=0}^{MaxAge} x l_x b_x \qquad (9)$$

Following Marshall et al. (2021), I repeated the calculation of each of these five characteristics for four different Sm values (14, 15, 16 and 17 years). They cover the full range of uncertainty arising from such in the growth trajectory of T. rex from which Sm was inferred (Erickson et al. 2001; Myhrvold 2013). For the MTR model, I calculated b_{mature} from Equations 2 and 3. For the GTR model, I used either the step, hyperbolic, linear or Weibull function on the fecundity schedule b_x. Each function was parametrized by an AEN value that either was derived from the reptile or bird model evaluated for M_{max}. This resulted in eight different fecundity schedules b_x, which were considered for each of the four Sm values. For each combination of Sm, AEN and b_x function, I applied the root-finding-algorithm from Griebeler (2021) to estimate the shape parameter value λ of the survivorship schedule (l_x; Eqn 4) that, together with the given fecundity schedule, yielded a net reproductive rate R_0 of unity (Eqn 1). Then, for the GTR model, Equations 5–9 were evaluated for the survivorship schedule l_x erected from λ (Eqn 4) and for the fecundity schedule b_x set by both AEN and the b_x function (Fig. 2B). For the MTR model, Equations 5–9 were evaluated applying Equation 2 to fecundities and Equation 4 to survival rates. In this case, I obtained the λ value parametrizing Equation 4 by fitting the survival rates calculated from the age sample for T. rex (Erickson et al. 2006, fig. 1A) to this equation. Curve fitting was done with the nls function in R (v3.5.2).

RESULTS

Comparison of simulation results between models

Table 2 summarizes the simulation results of the GTR model and those from Marshall et al. (2021). Under all five fecundity scenarios, middle values of output variables M_{eco}, g and p were larger for the GTR than for the MTR model, and they were smaller for variables ρ, G, N and 1/p (Table 2). The middle values of output variable n were smaller for the GTR than for the MTR model under all scenarios, except for the 'bird with b_x vertebrate' scenario yielding a slightly larger middle value than that of the MTR model.

The largest absolute and relative changes in middle values of N, p and 1/p were for the 'reptile with b_x step' scenario and the smallest for the 'bird with b_x vertebrate' scenario. The 'bird with b_x step' scenario had the second smallest changes, in the 'reptile or bird with b_x vertebrate' scenario changes were intermediary, and in the 'reptile with b_x vertebrate' scenario changes were the second largest. In the 'reptile with b_x step' scenario the middle value of N was 27.6%, the middle value of p was 361.5% and the middle value of 1/p was 26.9% of that of the MTR model. For the 'bird with b_x vertebrate' scenario, the N value was 91.0% of that of the MTR model, that of p was very close (c. 100%) to that of the MTR model and that of 1/p was 93.8% of that of the MTR model. In the 'reptile or bird with b_x vertebrate' scenario, the middle value of N was 68.0%, that of p was 146.2% and that of 1/p was 68.5% of that of the MTR model. Thus, for the 'reptile or bird with b_x vertebrate' scenario that implements the largest uncertainty in the reproductive mode of T. rex, the absolute abundance of this tyrannosaur was 1.7 billion individuals (instead of 2.5 billion individuals calculate by the MTR model). Its fossil recovery rate was 1 per 52.5 million individuals (instead of 1 per 80 million individuals calculated by the MTR model).
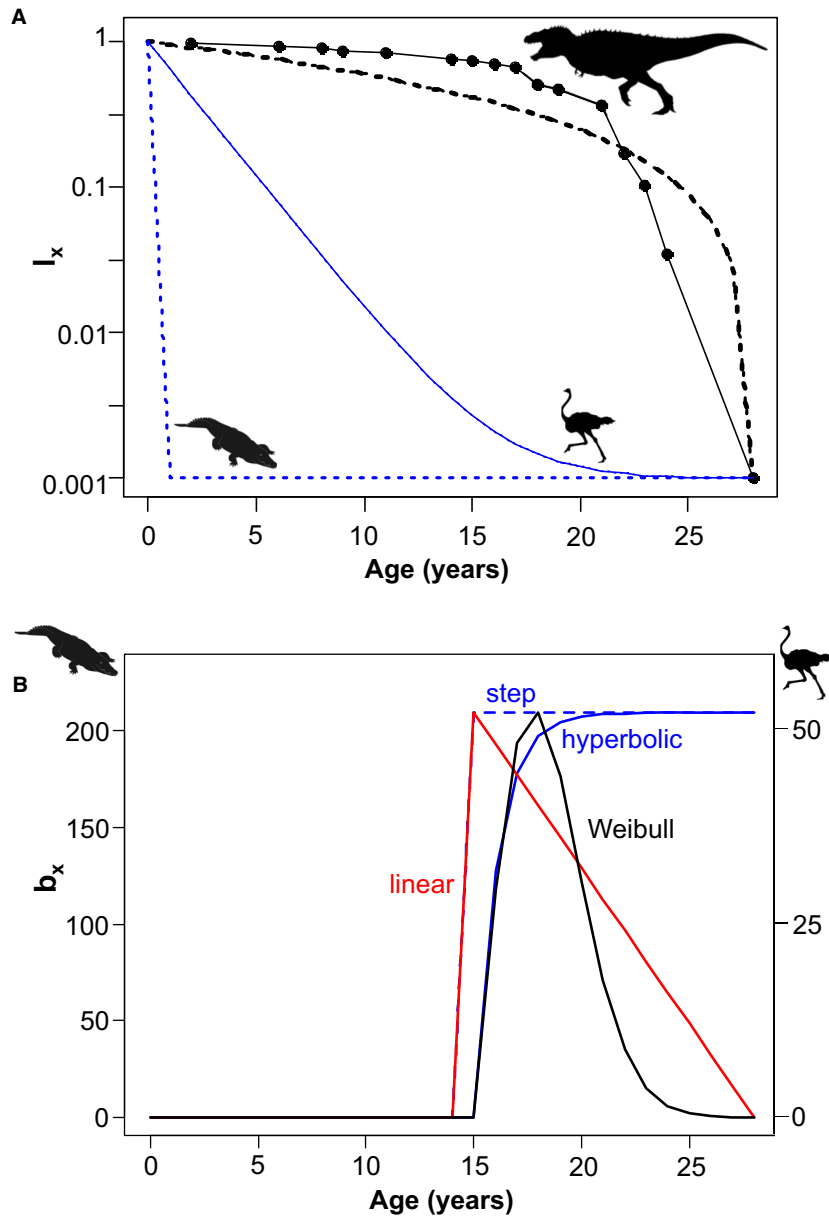
FIG. 2. Survivorship schedules l_x (A) and fecundity schedules b_x (B); Sm = 15 years (Table 1). A, solid black line with dots: curve erected by Erickson *et al.* (2006) from the age sample on *T. rex*, empirical survivorship curve (SC); dotted black line: uses the non-linear least squares *nls* R function for fitting Eqn 3 to the empirical SC; dashed black line: result of fitting Eqn 4 to the empirical SC ($\lambda = -0.395$); note that the latter two curves are virtually identical; blue dotted line: curve yielding $R_0 = 1$ for the AEN reptile model with the b_x step fecundity function (GTR model, $\lambda = -998.969$); blue solid line: the respective curve for the AEN bird model (GTR model, $\lambda = -11.914$). B, fecundity schedules b_x (Griebeler 2021) used by the GTR model and shown for the reptile (left axis) and bird (right axis) models for AEN; the AEN value of a *T. rex* individual with a mass of 7090 kg (Marshall *et al.* 2021) is 209.4 eggs under the reptile and 53.5 eggs under the bird model (i.e. the maximum annual fecundity in each fecundity function). Silhouette images from PhyloPic (http://phylopic.org: *Tyrannosaurus*, Maija Karala (CC BY-SA 3.0); *Struthio camelus*, Ferran Sayol; *Crocodylia*, Becky Barnes (both CC0 1.0)).

The approximate uncertainties in middle values from the MTR and GTR model were about two magnitudes larger for output variables ρ, n, N, p and 1/p than for M_{eco}, g and G (Table 2). The GTR model produced larger uncertainties than the MTR model under all five fecundity scenarios, except for M_{eco}. For M_{eco}, the 'reptile with b_x step' scenario and the 'reptile with b_x vertebrate' scenario gave rather similar uncertainties that were slightly smaller than in the MTR model, but the uncertainties in M_{eco} were again larger for the other three

TABLE 2. Population and preservation characteristics calculated by the MTR and GTR models for *T. rex*.

Model	b_x scenario	Values	Ecological body mass M_{eco} (kg)	Population density ρ (ind./km²)	Standing population size n	Generation time g (years)	Number of generations G	Absolute abundance N	Absolute preservation rate p	Number of individuals per fossil 1/p
MTR	b_x step	Middle value	**5200**	**0.0091**	**20 000**	**19.0**	**127 000**	**2.5×10^9**	**1.3×10^{-8}**	**80.0×10^6**
		2.5% tail	3700	0.0006	1300	17.8	66 000	1.4×10^8	2.2×10^{-7}	4.5×10^6
		97.5% tail	6900	0.1400	328 000	20.1	188 000	4.2×10^{10}	7.6×10^{-10}	1300×10^6
		Approximate uncertainty	1.86×	240×	250×	1.1×	2.8×	295×	295×	295×
GTR	Reptile (b_x step)	Middle value	**6057**	**0.0081**	**18 279**	**61.3**	**39 181**	**6.9×10^8**	**4.7×10^{-8}**	**21.5×10^6**
		2.5% tail	4331	0.0005	1131	53.0	20 312	3.9×10^8	2.7×10^{-9}	1.2×10^6
		97.5% tail	7835	0.1260	292 318	69.2	60 282	1.2×10^{10}	8.1×10^{-7}	268.6×10^6
		Approximate uncertainty	1.81×	243×	259×	1.3×	3.0×	300×	300×	300×
		abs. change	+857	−0.0010	−1721	+42.3	−87 819	-1.8×10^9	$+3.4 \times 10^{-8}$	-58.5×10^6
		rel. change	116.5%	89.0%	91.4%	322.6%	30.9%	27.6%	361.5%	26.9%
GTR	Bird (b_x step)	Middle value	**5583**	**0.0086**	**19 371**	**20.6**	**116 915**	**2.2×10^9**	**1.5×10^{-8}**	**67.6×10^6**
		2.5% tail	3777	0.0006	1206	19.6	61 320	1.3×10^8	8.6×10^{-10}	3.9×10^6
		97.5% tail	7.520	0.1347	311 773	21.4	173 095	3.7×10^{10}	2.6×10^{-7}	1166.0×10^6
		Approximate uncertainty	1.99×	244×	259×	1.1×	2.8×	298×	298×	298×
		abs. change	+383	−0.0005	−629	+1.6	−10 085	-0.3×10^9	$+0.2 \times 10^{-8}$	-12.4×10^6
		rel. change	107.4%	94.5%	96.9%	108.4%	92.1%	88.0%	115.4%	84.5%
GTR	Reptile (b_x vertebr.)	Middle value	**6030**	**0.0081**	**18 242**	**38.5**	**58 936**	**1.2×10^9**	**2.8×10^{-8}**	**36.0×10^6**
		2.5% tail	4283	0.0005	1143	18.4	22 414	5.8×10^7	1.4×10^{-9}	1.8×10^6
		97.5% tail	7820	0.1261	292 644	66.6	178 103	2.3×10^{10}	5.6×10^{-7}	726.9×10^6
		Approximate uncertainty	1.83×	241×	256×	3.6×	7.9×	404×	404×	404×
		abs. change	+830	−0.0010	−1758	+19.5	−68 064	-1.3×10^9	$+1.5 \times 10^{-8}$	-44.0×10^6
		rel. change	116.0%	89.0%	91.2%	202.6%	46.4%	48.0%	215.4%	45.0%
GTR	Bird (b_x vertebr.)	Middle value	**5262**	**0.0090**	**20 276**	**19.6**	**123 368**	**2.4×10^9**	**1.3×10^{-8}**	**75.0×10^6**
		2.5% tail	3531	0.0006	1260	16.8	63 167	1.4×10^8	7.7×10^{-10}	4.3×10^6
		97.5% tail	7.190	0.1407	325 220	21.8	193 561	4.1×10^{10}	2.3×10^{-7}	129.2×10^6
		Approximate uncertainty	2.04×	244×	258×	1.3×	3.1×	300×	300×	300×
		abs. change	+62	−0.0001	+276	+0.6	−3632	-0.1×10^9	0.0×10^{-8}	-5.0×10^6
		rel. change	101.2%	98.9%	101.4%	103.2%	97.1%	91.0%	100.0%	93.8%

(continued)

TABLE 2. (Continued)

Model	b_x scenario	Values	Ecological body mass M_{eco} (kg)	Population density ρ (ind./km²)	Standing population size n	Generation time g (years)	Number of generations G	Absolute abundance N	Absolute preservation rate p	Number of individuals per fossil 1/p
GTR	**Reptile or bird** (b_x **vertebr.**)	**Middle value**	**5655**	**0.0085**	**19 223**	**20.9**	**96 801**	$\mathbf{1.7 \times 10^9}$	$\mathbf{1.9 \times 10^{-8}}$	$\mathbf{52.5 \times 10^6}$
		2.5% tail	3752	0.0005	1199	17.2	24 576	7.9×10^7	9.7×10^{-10}	2.5×10^6
		97.5% tail	7613	0.1336	310 528	64.9	188 109	3.3×10^{10}	4.0×10^{-7}	1028.1×10^6
		Approximate uncertainty	$2.03 \times$	$244 \times$	$259 \times$	$3.8 \times$	$7.7 \times$	$416 \times$	$416 \times$	$416 \times$
		abs. change	$+455$	-0.0006	-777	$+1.9$	$-30\ 199$	-0.8×10^9	$+0.6 \times 10^{-8}$	-27.5×10^6
		rel. change	108.8%	93.4%	96.1%	110.0%	76.2%	68.0%	146.2%	68.5%

MTR model values are from Marshall *et al.* (2021). GTR model considered five scenarios for fecundity schedule (b_x) of *T. rex*. (1) Reptile (b_x step): b_x step function with reptile model AEN ('reptile with b_x step' scenario, Fig. 2B). (2) Bird (b_x step): b_x step function with bird model AEN ('bird with b_x step' scenario, Fig. 2B). (3) Reptile (b_x vertebr.): reptile model AEN and one of the four the fecundity functions (Fig. 2B; 'reptile with b_x vertebrate' scenario) randomly chosen for the simulation run. (4) Bird (b_x vertebr.): bird model AEN with a randomly chosen fecundity function ('bird with b_x vertebrate' scenario). (5) Reptile or bird (b_x vertebr.): fecundity function with reptile or bird AEN model randomly chosen ('reptile or bird with b_x vertebrate' scenario). Middle values are medians of distributions from one million Monte Carlo simulations. Approximate uncertainties of output variables are the ratios of the distributions' 97.5% and 2.5% tail values (Marshall *et al.* 2021). Absolute changes give differences between the middle value of the GTR and the MTR model. Signs indicate whether the GTR model's values are larger (+) or smaller (−) than the respective of the MTR model. Relative changes are the ratio of the middle value from the GTR and the MTR model and are in percentages. Percentages larger (smaller) than 100% indicate larger (smaller) values in the GTR than in the MTR model.

scenarios than for the MTR model. The 'reptile with b_x step', the 'bird with b_x step' and the 'bird with b_x vertebrate' scenario yielded rather similar uncertainties for output variables N, p and 1/p when compared to the MTR model (c. 300×; Table 2). Conversely, under both the 'reptile with b_x vertebrate' scenario and the 'reptile or bird with b_x vertebrate' scenario the uncertainties in these three output variables were clearly the largest (c. 400×, Table 2).

Comparison of variables on vital statistics of T. rex *populations between models*

Values of variables on the vital statistics of *T. rex* populations substantially differed between the MTR and the GTR models (Table 3). Changes in these variables caused by differences in Sm values were comparatively small as well as changes resulting from applying different functions on age-specific fecundities for the reptile and bird AEN model, respectively (Table 3). When compared to those of the allometric reptile and bird AEN models used by the GTR model, the b_{mature} value of the MTR model was three and two orders of magnitude smaller, respectively. Likewise, the different survivorship schedules (l_x) applied by the MTR and GTR models resulted in l_{Sm} values being at least one (bird AEN model) and up to two orders of magnitude (reptile AEN model) smaller in the GTR model than in the MTR model. Life expectancies of newborns (E_0) were up to one order of magnitude higher under the MTR than under the GTR model, irrespective of which AEN model or b_x function were used. The reptile AEN model always yielded smaller E_0 values than the bird AEN model for a given b_x function. For both AEN models, E_0 was smallest for the b_x step function, somewhat larger for the b_x hyperbolic function, again somewhat larger for the b_x linear function and largest for the b_x Weibull function. Life expectancies of mature individuals (E_{Sm}) were highest for the GTR model with the reptile AEN model, lowest for the GTR model with the bird AEN model and intermediate for the MTR model. However, differences among all E_{Sm} values did not cover one order of magnitude. Conversely, both the GRR and v_{Sm} values were larger for the GTR than for the MTR model. Under the reptile AEN model, the GRR and v_{Sm} values were three orders of magnitude larger and under the bird AEN model, they were two orders of magnitude larger for the GTR than for the MTR model. When using the reptile AEN model with the b_x step or the b_x hyperbolic function, the GTR model yielded about three times larger g_t values than for the b_x linear or b_x Weibull function and also when compared to the g_t values of the MTR model. The g_t values of the GTR model with the b_x linear function and the b_x Weibull function were rather similar to those of the MTR model, irrespective of whether the reptile or bird AEN model was used.

# DISCUSSION

Comparison of simulation results between models

Compared to the MTR model, middle values of M_{eco}, g and p were larger for all five fecundity scenarios of the GTR model, whereas values of ρ, G, N and 1/p were all smaller. The middle value of n showed no clear pattern across fecundity scenarios (Table 2). Specifically, the 'reptile with b_x step' scenario had the smallest middle values on N (0.7 billion individuals, 27.6% of the value of the MTR model) and 1/p (1 per 21.5 million individuals, 26.9% of the value of the MTR model). The 'reptile or bird with b_x vertebrate' scenario implementing the largest uncertainty in the fecundity schedule of *T. rex* estimated an average N of 1.7 billion individuals, which is 68.5% of that of the MTR model. Thus, in this scenario 1/p is 1 per 52.5 million individuals instead of 1 per 80 million individuals (MTR model).

Only the formulas used on output variables M_{eco} and g make a direct use of b_x and l_x values (Table 1B; Fig. 1). While the MTR model is based on a convex survivorship curve yielding very small b_{mature} values (−0.395 for the non-bootstrapped age sample from Erickson *et al.* 2006, for all Sm values; Table 3; Fig. 2A), the GTR model applies a linear (bird model for AEN, 53.453; Fig. 2A) to concave shaped curve (reptile model for AEN, 209.379, Fig. 2A). Generally, small b_{mature}/AEN values imply more convex survivorship curves than large ones because in a population, the overall number of births must be compensated for by deaths in order to yield a given R_0 value (Eqn 1; Pianka 1999; Griebeler 2021). In the MTR and GTR models, M_{eco} is calculated from mass at age x (M_x) and survival rate l_x of mature individuals (Table 1B, Fig. 1). Figure 3A shows for three different growth trajectories for *T. rex* that differ in maximum adult body mass (M_{max}; mean, upper and lower limits of the 95% confidence interval, Table 1B), how the shape of the survivorship curve (λ) alters M_{eco}. There is only a small range around zero, in which λ substantially affects M_{eco}. This range is rather similar for the three growth trajectories. Table 3 lists λ values for four different Sm values (14, 15, 16 and 17 years) and eight different fecundity functions b_x (Fig. 2B). While all λ values from the GTR model are smaller than −7 (linear curve; Griebeler 2021), the MTR model's λ value is larger (−0.395, convex curve; Griebeler 2021). For the three M_{max} values considered, λ values around −7 yield the minimal M_{eco} value, and M_{eco} increases with decreasing λ smaller than −7 (Fig. 3A).

TABLE 3. Values of different variables of the vital statistics of *T. rex* populations for the MTR and GTR models.

Model	b_x Scenario	Sm (years)	b_{mature}/AEN	λ	E_0 (years)	l_{Sm}	E_{Sm} (years)	GRR	v_{Sm}	g_t (years)
MTR	**b_x step**	**14**	**0.167**	**−0.395**	**19.346**	**0.826**	**7.221**	**2.510**	**1.097**	**17.963**
GTR	Reptile (b_x step)	14	209.379	−998.969	1.027	0.001	14.000	3140.685	2931.306	65.954
GTR	Reptile (b_x hyperbolic)	14	209.379	−998.969	1.027	0.001	14.000	2781.665	2868.935	60.671
GTR	Reptile (b_x linear)	14	209.379	−998.969	1.027	0.001	14.000	1570.343	1166.540	28.790
GTR	Reptile (b_x Weibull)	14	209.379	−998.969	1.027	0.001	14.000	1015.570	905.733	18.034
GTR	Bird (b_x step)	14	53.453	−13.135	3.330	0.002	4.670	801.795	464.788	19.940
GTR	Bird (b_x hyperbolic)	14	53.453	−11.274	3.684	0.005	4.348	702.900	315.357	20.360
GTR	Bird (b_x linear)	14	53.453	−10.877	3.727	0.005	4.332	400.898	162.631	16.755
GTR	Bird (b_x Weibull)	14	53.453	−9.474	4.141	0.010	4.315	259.268	145.082	17.055
MTR	**b_x step**	**15**	**0.194**	**−0.395**	**19.346**	**0.786**	**6.538**	**2.719**	**1.147**	**18.598**
GTR	Reptile (b_x step)	15	209.379	−998.969	1.027	0.001	13.000	2931.306	2721.927	63.023
GTR	Reptile (b_x hyperbolic)	15	209.379	−998.969	1.027	0.001	13.000	2588.248	2669.836	57.658
GTR	Reptile (b_x linear)	15	209.379	−998.969	1.027	0.001	13.000	1465.653	1063.654	27.847
GTR	Reptile (b_x Weibull)	15	209.379	−998.969	1.027	0.001	13.000	948.572	830.480	17.544
GTR	Bird (b_x step)	15	53.453	−11.914	3.330	0.003	4.982	748.342	410.000	20.360
GTR	Bird (b_x hyperbolic)	15	53.453	−10.389	3.684	0.005	4.487	654.099	296.602	20.904
GTR	Bird (b_x linear)	15	53.453	−10.145	3.727	0.005	4.456	374.171	155.202	17.344
GTR	Bird (b_x Weibull)	15	53.453	−8.864	4.141	0.010	4.337	242.164	141.673	17.933
MTR	**b_x step**	**16**	**0.229**	**−0.395**	**19.346**	**0.739**	**5.892**	**2.979**	**1.215**	**19.246**
GTR	Reptile (b_x step)	16	209.379	−998.969	1.027	0.001	12.000	2721.927	2512.169	59.882
GTR	Reptile (b_x hyperbolic)	16	209.379	−998.969	1.027	0.001	12.000	2394.651	2470.007	54.462
GTR	Reptile (b_x linear)	16	209.379	−998.969	1.027	0.001	12.000	1360.964	959.654	26.765
GTR	Reptile (b_x Weibull)	16	209.379	−998.969	1.027	0.001	12.000	893.948	764.564	17.193
GTR	Bird (b_x step)	16	53.453	−10.938	3.330	0.003	5.305	694.889	368.945	20.720
GTR	Bird (b_x hyperbolic)	16	53.453	−9.657	3.684	0.005	4.633	605.256	281.853	21.267
GTR	Bird (b_x linear)	16	53.453	−9.413	3.727	0.006	4.586	347.445	145.951	18.390
GTR	Bird (b_x Weibull)	16	53.453	−8.315	4.141	0.010	4.353	228.219	138.056	18.880
MTR	**b_x step**	**17**	**0.276**	**−0.395**	**19.346**	**0.684**	**5.286**	**3.310**	**1.307**	**19.908**
GTR	Reptile (b_x step)	17	209.379	−998.969	1.027	0.001	11.000	2512.548	2303.169	56.532
GTR	Reptile (b_x hyperbolic)	17	209.379	−998.969	1.027	0.001	11.000	2200.831	2269.571	51.081
GTR	Reptile (b_x linear)	17	209.379	−998.969	1.027	0.001	11.000	1256.274	856.550	25.544
GTR	Reptile (b_x Weibull)	17	209.379	−998.969	1.027	0.001	11.000	810.323	672.433	16.182
GTR	Bird (b_x step)	17	53.453	−10.084	3.330	0.003	5.604	641.436	333.158	21.146
GTR	Bird (b_x hyperbolic)	17	53.453	−8.925	3.684	0.005	4.773	556.362	263.938	22.038
GTR	Bird (b_x linear)	17	53.453	−8.803	3.727	0.006	4.711	320.718	136.330	18.973
GTR	Bird (b_x Weibull)	17	53.453	−7.766	4.141	0.010	4.361	206.870	128.137	19.458

For the MTR model, b_x step fecundity function applied as in Marshall *et al.* (2021), parametrized by b_{mature} (Eqn 2). For the GTR model, each of the four fecundity functions was used (Fig. 2B) and each evaluated for both the reptile and bird AEN models. Ages of 14–17 years on onset of sexual maturity cover the full range of uncertainty in the growth trajectory of *T. rex* (Myhrvold 2013; Marshall *et al.* 2021). To estimate λ for the MTR model, Eqn 4 was fitted to the age sample in Erickson *et al.* (2006) using the non-linear least squares *nls* function in R. For the GTR model, λ is the value for which Eqn 4 yields $R_0 = 1$ for the given fecundity schedule b_x. For abbreviations, see Table 1.
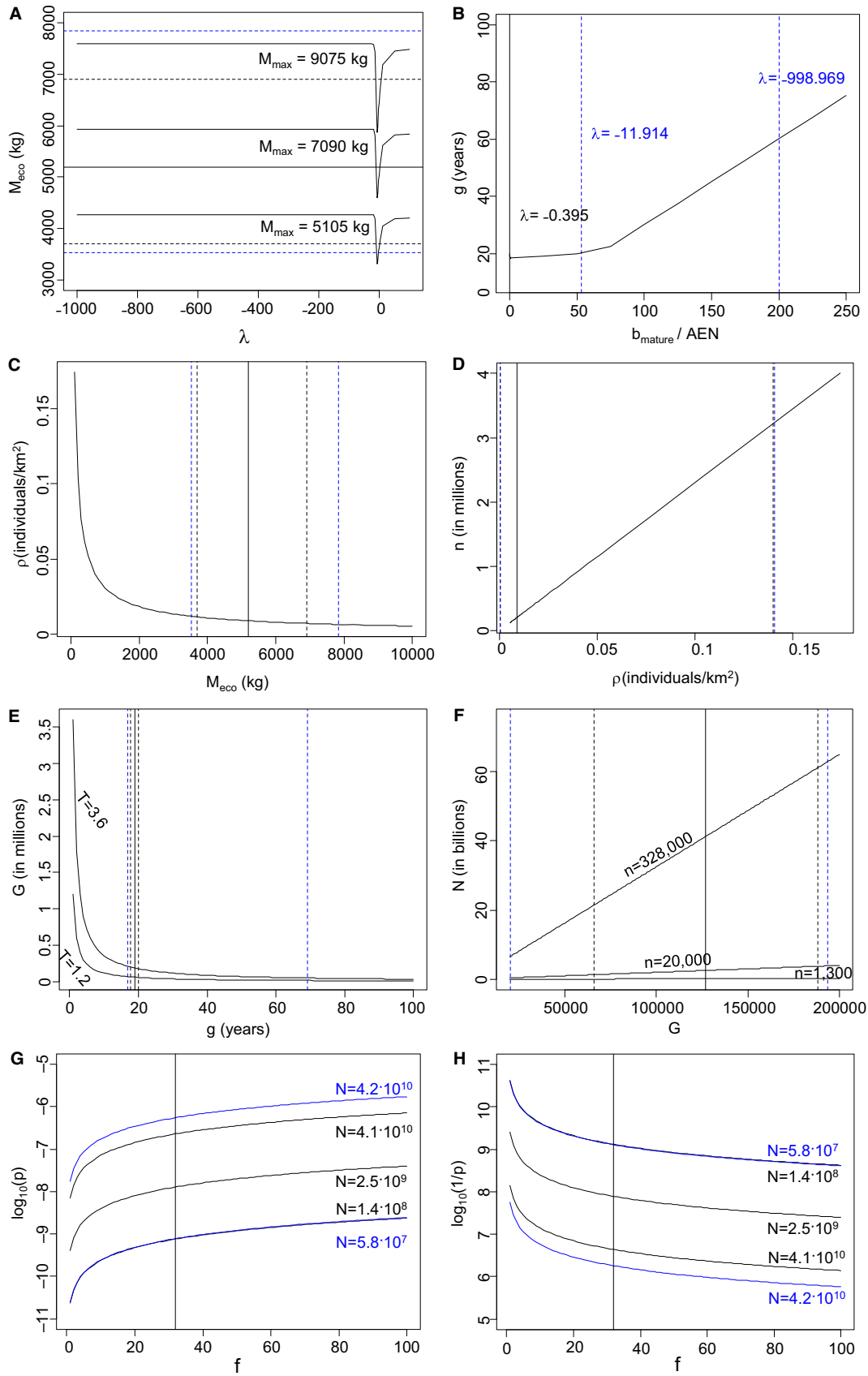
FIG. 3. Relationships of input and output variables of the MTR and GTR models. A, M_{eco} shown for different λ values (Eqn 4; GTR model) and three growth trajectories (M_x) differing in M_{max} (mean = 7090 kg; lower 95% confidence interval limit = 5105 kg; upper 95% confidence interval limit = 9075 kg; Table 1). B, relationship between g, b_{mature}/AEN and λ: first, λ was estimated from the LEE (Eqn 1) and a given b_{mature}/AEN value; then g was calculated from l_x (using the λ estimate) and b_x/AEN (Eqn 9); the black solid line marks the average b_{mature} value (MTR model, $\lambda = -0.395$), the blue dotted lines the AEN value for the bird ($\lambda = -11.914$) and reptile AEN model ($\lambda = -998.969$) (GTR model; Fig. 2B; Table 3). Sm = 15 years in A and B; λ values are for the b_x step function (Fig. 2B). C, the power law on ρ evaluated for different M_{eco} values. D, relationship between ρ and n. E, relationship between g and G for the lower and upper limits of T. F, relationship between G and N for three n values: the middle value, the 2.5% tail and 97.5% tail value of the MTR model (Table 2). G–H, relationship between f and p, 1/p, respectively; vertical black line marks f = 32; N values used are: 2.5×10^9 (MTR model; Table 2), 1.4×10^8 (MTR model, 2.5% tail; Table 2), 4.2×10^{10} (MTR model, 97.5% tail; Table 2), 5.8×10^7 (GTR model, smallest 2.5% tail across fecundity scenarios; Table 2) and 4.1×10^{10} (GTR model, largest 97.5% tail across fecundity scenarios; Table 2). For A, C–F: solid black line/curve = middle value of the MTR model; dotted black line = 2.5% and 97.5% tail of the MTR model; dotted blue line = smallest and largest 2.5% and 97.5% tail of the GTR model. See Table 1 for variable definitions.

Thus, differences in the value of λ used and the relation between M_{eco} and λ (Fig. 3A) explain why the MTR model's middle value of M_{eco} is always smaller than any M_{eco} from the GTR model.

The middle value of g was smaller for the MTR model than any g value derived from the GTR model (Table 2). Output variable g is calculated from both the fecundity schedule b_x and the survivorship schedule l_x. For the b_x step fecundity function used by the MTR model and applied in the 'reptile with b_x step' scenario by the GTR model, Figure 3B shows how g relates to both b_{mature} (AEN for the GTR model) and λ. Small b_{mature} values as used by the MTR model imply convex survivorship curves (with large λ values; Table 3) and small g values, whereas large b_{mature} values as used by the GTR model ($AEN_{bird} = 53.453$; $AEN_{reptile} = 209.379$; Table 3) move the survivorship curve towards the concave end of the spectrum (small λ values, Table 3) and yield large g values. Whether this holds for all fecundity functions and thus for the five fecundity scenarios of the GTR model can be assessed from Table 3. It lists g_t (= g) values for four different Sm values and eight fecundity schedules (Fig. 2B). Not all of these g_t values corroborate the observation that the middle value of g of the MTR model is always smaller than any middle value of the GTR model, as for all four Sm values some fecundity functions used by the GTR model reveal somewhat smaller g_t values than the MTR model. Specifically, when assuming a reptile-like reproductive mode for *T. rex*, g_t values of the GTR model are indeed substantially larger than the MTR model's, except for the b_x Weibull function that revealed somewhat smaller g_t values for Sm = 15, 16 and 17 (Table 3). When assuming a bird-like reproductive mode for *T. rex*, however, differences in g_t values obtained for all fecundity functions were very small and g_t values of the GTR model did only slightly vary around the MTR model's value (Table 3). The observation that some middle values (medians) of g derived from one million Monte Carlo simulations show deviations from the pattern found for the deterministically calculated generation time g_t could

indicate that the number of Monte Carlo simulation runs was not always sufficient to estimate the true mean value of g.

Large λ yields small M_{eco} and large g, whereas small λ implies a large M_{eco} and small g values. The λ values obtained under the reptile AEN model were smaller than those from the bird AEN model (Table 3) for all fecundity scenarios, but all λ values were smaller than -7. As for λ values smaller than -7, the output variable M_{eco} increases with decreasing λ values; Figure 3A also explains why middle values of M_{eco} are larger in the 'reptile with b_x step' than in the 'bird with b_x step' scenario (and Fig. 3B shows why the middle values of g have the opposite relationship with the same two scenarios). They also explain why middle values of M_{eco} (g) are larger (smaller) in the 'reptile with b_x vertebrates' than in the 'bird with b_x vertebrates' scenario (Table 2).

Differences in λ further explain the differences seen in other output variables of the MTR and GTR models that make direct (ρ, G; Figs 1, 3C) or indirect (n, N, p, 1/p, Figs 1, 3D, F–H) use of M_{eco} or g, because all model equations used for calculating these output variables are monotonous functions (Fig. 3). Thus, consistent with the observation that the GTR model always yielded larger middle values on M_{eco} than the MTR model, the middle values of ρ were always larger for the GTR than for the MTR model. In both models, ρ is calculated from a power law with an exponent of -0.75 to which M_{eco} is passed (Fig. 3C). As n is the product of A (constant, >1) and ρ, the GTR model's middle values of n must be larger than those of the MTR model (Fig. 3D). This was true for all scenarios, except for the 'bird with b_x vertebrate' scenario. As the middle value of n from the 'bird with b_x vertebrate' scenario was only slightly larger than that from the MTR model, this could indicate that the number of Monte Carlo simulation runs was again insufficient.

The value of G is calculated as T divided by g (Table 1). Thus, for a given T value, G decreases hyperbolically with increasing g values (Fig. 3E); larger g values result in smaller G values. In both models, G is used to calculate

N for the area modelled. Output variable N is n times G. Figure 3F shows the relation between G and N for three different n values. Given that, the middle value of G is larger for the MTR model than for GTR model and that middle values of n are indeed larger for the MTR than the GTR model, N must increase with increasing G and N values (Fig. 3F). Finally in both models, input variable f is divided by N in order to calculate output variables p and 1/p. Figure 3G and 3H show p and 1/p for different f and N values, respectively. As all middle values of N are smaller for the GTR than for the MTR model, Figure 3G and 3H corroborate that this is also true for p and the opposite for 1/p.

The MTR model reveals small approximate uncertainties for M_{eco} (1.9×), g (1.1×) and G (2.8×), and more than two orders of magnitude larger for ρ (240×), n (250×), N (295×), p (295×) and 1/p (295×). Although uncertainties were always larger for the GTR than for the MTR model, the large differences seen between these groups of output variables was also apparent in the GTR model, irrespective of which fecundity scenario was studied. The value of output variable N determines that of p and 1/p, and N is the product of n and G. The small uncertainty in M_{eco} stemming from the survivorship schedule (that substantially differs between the MTR and GTR models, Fig. 2A) and the growth trajectory assumed for T. rex translates via a power law into an uncertainty of more than two orders of magnitude larger in ρ, which is basically maintained in n (Fig. 3A, C, D). Conversely, the hyperbolic relationship between g and G maintains the comparative small uncertainty in g originating from the survivorship and fecundity schedule (Fig. 3E). The overall large uncertainties in ρ indicate that the model equation used for ρ is very sensitive to changes in M_{eco} (Fig. 3C).

Only for the 'reptile with b_x step' scenario and the 'reptile with b_x vertebrate' scenario, both showing the largest differences in N, p, and 1/p between the MTR and GTR models, the relative changes in middle values were substantially larger for g than for M_{eco} (322.6% vs 116.5%; Table 2). For all other scenarios, relative changes in M_{eco} and g were smaller than ±20% (Table 2). The maximum difference seen in the middle values of M_{eco} even decreased to ±10% for the output variable n that is calculated from the power law on ρ and M_{eco}, whereas that in G is maintained (Table 2). Thus, differences in middle values of N, p and 1/p basically stem from G and difference in G values seen between fecundity scenarios explain the variance in N, p and 1/p. However, all changes in middle values of n and G observed between models are small when compared to values of input variables A and T. Although an effect of the approach taken on the relation between age-specific survival rates and fecundities is clearly apparent for output variables M_{eco}, n

and g, the huge A ($c.$ 10^7; Table 1A) and T values ($c.$ 10^6; Table 1A) minimize these comparatively small changes observed at the level of output variables N (n, $c.$ 10^5; G, $c.$ 10^3 up to 10^4; N = nG, $c.$ 10^8 up to 10^9), p and 1/p. A quick calculation exemplifies this strong effect of A and T on N. When setting M_{eco} to M_{max} and G to T and then evaluating the MTR model's equations for N (Fig. 1; Table 1), N is 3.9×10^{11}. This rough estimate of N is barely an order of magnitude larger than the 97.5% tail values of the MTR and GTR models, and two orders larger than their middle values (MTR, 2.5×10^9; GTR, 6.9×10^8–2.4×10^9; Table 2). As middle values of g show the largest difference between the MTR and GTR models, and g is a standard variable of the vital statistics of populations, this justifies a closer look at differences between models at the individual and population level.

Comparison of variables on vital statistics of T. rex populations for models

The life history generated by the MTR model strongly contradicts our current understanding of the biology of theropods and of the vital statistics of extant amniotes. The convex survivorship curve that Marshall *et al.* (2021) used for T. rex yields an E_0 value of 19.346 years (Eqn 5) and E_{Sm} values (Eqn 6; Table 3) ranging from 3.310 to 7.221 years (mean = 6.234 years; for Sm 17 down to 14 years; Myhrvold 2013; Marshall *et al.* 2021). The convex shaped survivorship schedule implies a high survival of premature individuals. Thus, l_{Sm} values range between 0.684 and 0.826 (mean = 0.759, across four Sm values, Table 3). As each individual must on average recruit only a single offspring to the next generation ($R_0 = 1$), the values derived for output parameter b_{mature} must be small given the high survival rates of premature individuals. Thus, b_{mature} values range between 0.167 and 0.276 eggs per year (mean = 0.216 eggs per year) and v_{Sm} values are close to one (1.097–1.307; mean = 1.192). Hence, a modelled T. rex female that has just reached maturity (x = Sm) had on average about six further years (E_{Sm}) for recruiting one female offspring to the next generation and it had an AEN of around 0.216. The GRR (Eqn 7), which is the total reproductive output of a mature female that dies at age MaxAge is between 2.510 and 3.310 (mean = 2.880) for Sm values ranging between 14 and 17 years and is thus around three eggs.

That a mature female lays one (v_{Sm}) to three (GRR) eggs within about six years of life strongly contradicts what we currently know about theropod reproduction. For T. rex, there is evidence for medullary bone, a calcium source for creating egg shell (Schweitzer *et al.* 2005). This bone type would be advantageous if this large tyrannosaur laid large clutches. The fossil record

indeed documents clutches with multiple eggs for several theropod taxa. It is the most abundant and informative on reproduction in oviraptorsaurs. Adult-associated clutches of *Oviraptor philoceratops* indicate a clutch size of 15 eggs (Osborn 1924). For *Citipati osmolskae*, Norell *et al.* (1995) reported a clutch with 15 visible eggs and estimated a clutch size of 22 eggs for the specimen IGM 100/979, whereas the clutch size of the specimen IGM 100/1004 was only 12 eggs (Clark *et al.* 1999; Norell *et al.* 2018). The clutch size of a specimen of *Nemegtomaia barsboldi* is 18 eggs (Fanti *et al.* 2012). In a recent study, Yang *et al.* (2019) reported non-adult-associated oviraptorid clutches with more than 30 eggs that are substantially larger than clutch sizes observed in all above-mentioned adult-associated species. The clutch size of *Troodon* ranges from 12 to 24 eggs (Horner 1987; Varricchio *et al.* 1997, 1999, 2002) and has a range similar to that of *Citipati osmolskae*. A clutch assigned to the carnivorous theropod *Lourinhanosaurus antunesi* even consists of 100 eggs (Mateus *et al.* 1998). Araújo *et al.* (2013) reported a clutch attributed to a large basal megalosaurid theropod *Torvosaurus* from Portugal of at least three eggs based what is clearly three mounds of crushed eggs. The taxon *Torvosaurus* includes the largest predatory theropod from Europe with an estimated body mass in the range of *T. rex*. In total, the clutch sizes of the substantially smaller oviraptorosaurs and troodontids (12–22 eggs, >30 eggs) and of the larger *Lourinhanosaurus antunesi* (100 eggs) clearly contradict a small annual egg number ($b_{mature} = 0.216$) in *T. rex*. Only the not well-constrained smaller clutches of *Torvosaurus* (>3 eggs) might fit better to the small AEN ($b_{mature} = 0.216$), the small residual reproductive value of a mature individual ($v_{Sm} = 1.192$) and the small gross reproduction rate (GRR = 2.880) used by the MTR model. However, given the very small values of b_{mature}, v_{Sm} and GRR, three eggs would suggest that a mature *T. rex* female laid only laid a single clutch within her lifetime, or had up to three clutches with one egg. This contradicts the finding that reproductive maturity occurs while growth continues, which points to a reptile-like reproductive strategy in *T. rex* (Lee & Werning 2008). Extant reptiles have multiple clutches within their life. Moreover, consistent with a reptilian reproductive mode, Sato *et al.* (2005) reported a gravid oviraptosaur with two eggs preserved within its body cavity. This observation shows that even these maniraptoran dinosaurs, phylogenetically closer to extant birds than to tyrannosaurs, retained two functional oviducts as in other reptiles and thus had clutches of at least two eggs, whereas extant birds have only one oviduct and can have clutches with a single egg. However, allometric modelling of annual egg number favours a bird-like over a reptile-like strategy for theropods (Werner & Griebeler 2013). While a reptile-like strategy in *T. rex* implies three orders of magnitude larger v_{Sm} and GRR than those derived from the MTR model, a bird-like strategy yields two orders of magnitude larger v_{Sm} and GRR for this theropod than the MTR model (Table 3). Thus, allometric modelling also questions whether a *T. rex* laid a single clutch of up to three eggs or had up to three clutches of one egg within its life.

The MTR model's convex survivorship curve displays a high probability (around 0.8) of being alive at age Sm (l_{Sm}). This l_{Sm} value is about twice as large as the values found in extant large mammals (Table 4). The mean l_{Sm} of the MTR model calculated for four different Sm values (14, 15, 16, 17 years) is one to two orders of magnitude higher than any l_{Sm} from the GTR model (Table 3). Likewise, in large extant birds (Table 4) one order of magnitude smaller l_{Sm} values than those from the MTR model are observed, and in large extant reptiles even two orders of magnitude smaller (Table 4). The high l_{Sm} of the MTR model is even exceptional when compared to today's largest mammals that have convex survivorship curves (Table 4). These mammals achieve their high survival rates throughout most of their life, which are substantially smaller than that used by the MTR model for *T. rex*, by effectively sheltering their young from predation. Table 4 lists l_{Sm} of large solitary and gregarious extant mammals. In contrast to what the MTR model predicts for *T. rex*, the life of extant large species is long enough to shelter their premature young until they are mature, in other words, the life expectancy of an individual of age Sm (E_{Sm}) exceeds Sm (Table 4). In the MTR model, E_{Sm} is only about 6 years and thus clearly smaller than Sm (14–17 years). This observation strongly questions whether solitary mothers raising young could achieve a high survival rate for their own premature offspring and could imply a gregarious lifestyle for *T. rex* for which evidence is lacking so far. However, as a 6-year-old *T. rex* individual already had a mass of about 2.6 tons (M_6; Table 1A) their shear body mass could have made such and also older juveniles nearly safe from predation; they had high l_x values in the absence of shelter from mature individuals.

To summarize, in extant mammals, convex survivorship curves as used by the MTR model are associated with small annual fecundities, GRR, v_{Sm} and g and with high E_0 and E_{Sm} (compared to maximum life span; Table 4). They contradict what we currently know about reproduction in *T. rex*. Concave curves of extant reptiles are associated with large annual fecundities, GRR, v_{Sm}, g and E_{Sm} (compared to maximum life span) and with small E_0 (compared to maximum life span; Table 4). The linear curve seen in extant birds yields an intermediary

TABLE 4. Vital statistics of large extant mammals, birds and reptiles.

Species	BM (kg)	Sm (years)	AEN	MaxAge (years)	λ	E_0 (years)	l_{Sm}	E_{Sm} (years)	GRR	v_{Sm}	g_t (years)
Loxodonta africana	4500.0	12	0.21	80	−6.546	12.680	0.374	12.615	14.49	2.648	23.149
Hippopotamus amphibius	2640.0	5	0.61	61	−13.867	4.974	0.322	5.077	34.77	3.121	9.722
Rhinoceros unicornis	1600.0	6	0.30	49	−6.790	7.714	0.435	7.698	13.20	2.309	12.676
Giraffa camelopardalis	800.0	4	0.60	40	−10.084	4.522	0.365	4.570	22.20	2.756	7.812
Syncerus caffer	646.3	4	0.43	30	−6.180	5.334	0.438	5.296	11.61	2.272	8.142
Ursus maritimus	371.7	5	0.66	45	−10.572	4.815	0.310	4.887	27.06	3.244	9.194
Ursus arctos	240.5	4	0.91	50	−15.697	3.758	0.286	3.859	42.77	3.562	7.605
Panthera leo	149.0	3	2.83	30	−18.869	2.170	0.152	2.305	79.24	6.923	5.109
Panthera tigris	128.8	3	1.03	26	−10.206	3.102	0.309	3.142	24.72	3.267	5.302
Struthio camelus	109.3	3	10.88	50	−58.278	1.502	0.031	2.910	522.24	63.294	15.492
Casuaris casuaris	44.0	4	14.18	12	−10.023	1.776	0.036	1.928	127.62	30.197	5.190
Aptenodytes forsteri	29.8	5	1.00	40	−11.426	4.060	0.240	4.152	36.00	4.194	8.534
Vultur gryphus	10.5	7	1.00	75	−12.769	6.456	0.304	6.590	34.50	3.313	13.413
Cygnus cygnus	9.4	4	4.92	27	−16.795	2.184	0.084	2.407	118.08	12.874	6.378
Harpia harpyia	4.8	5	1.00	17	−4.472	4.140	0.261	3.821	13.00	3.721	7.434
Aquila chrysaetos	4.4	4	2.00	48	−21.614	2.803	0.166	3.007	90.00	6.293	7.579
Dermochelys coriacea	420.0	13	411.50	80	−998.969	1.079	0.001	67.000	30 022.00	29 580.500	396.023
Crocodylus porosus	200.0	10	47.80	42	−998.969	1.041	0.001	32.000	1577.40	1529.600	41.012
Aldabrachelys gigantea	117.2	25	27.00	176	−998.969	1.178	0.001	151.000	4104.00	4077.000	412.452
Caretta caretta	109.2	10	147.78	76	−998.969	1.075	0.001	66.000	9901.26	9753.480	425.754
Crocodylus niloticus	76.7	10	40.00	33	−24.908	1.918	0.002	15.716	960.00	752.393	21.073
Alligator mississipiensis	62.0	13	39.70	85	−998.969	1.084	0.001	72.000	2898.10	2858.400	142.007
Iguana iguana	15.3	5	35.00	20	−19.418	1.628	0.009	3.134	560.00	175.026	9.460

BM, body mass; l_{Sm}, Sm, AEN, MaxAge, E_0, E_{Sm}, GRR, g_t: see Table 1. Species' BM, Sm, AEN and MaxAge values were retrieved from the Amniote database (Myhrvold *et al.* 2015). λ values of their survivorship curves (Eqn 4) were inferred by setting R_0 to 1, using a b_x step function with the respective AEN value on age-specific fecundities and then evaluating the LEE for the survivorship curve given by λ (Eqn 1, Griebeler 2021).

vital statistic to that of mammals and reptiles (Table 4). Only the linear to concave survivorship curves generated by the GTR model reveal a vital statistic for *T. rex* consistent with our current knowledge on reproduction in theropods.

Application of the GTR model to other dinosaurs

In addition to *T. rex*, there are three other tyrannosaurs (*Albertosaurus sarcophagus*, *Dasplatosaurus torosus*, *Gorgosaurus libratus*; Erickson *et al.* 2004, 2006), a ceratopsian (*Psittacosaurus lujiatuensis*; Erickson *et al.* 2009) and a hadrosaur (*Maiasaura peeblesorum*; Woodward *et al.* 2015) for which growth trajectories and even survivorship curves exist in the literature. All of these species were subject to the study of Griebeler (2021) that questioned the convexity of the survivorship curve of *T. rex* and that of the other three large tyrannosaurs, but corroborated a convex curve in the ceratopsian. Age-specific survival rates of the hadrosaur most probably follow a composite curve, which the one-parameter survival function of the GTR model is unable to simulate (Eqn 4) and makes it inapplicable to this dinosaur. For the other three large tyrannosaurs, I anticipate that an analogous comparison of the MTR and GTR models would yield rather similar differences in output variables as found for *T. rex*. All four tyrannosaurs not only have large M_{max} and thus AEN, but also rather similar Sm and MaxAge values (Erickson *et al.* 2004; Cullen *et al.* 2020; Griebeler 2021).

Conversely to the four tyrannosaurs, the fossil record provides evidence for a convex survivorship curve in *Psittacosaurus lujiatuensis*. Meng *et al.* (2004) reported a small adult *Psittacosaurus* specimen clustered with 34 juveniles within an area of $0.5 \, m^2$, which could indicate parental care in this taxon and thus makes high premature survival rates likely. *Psittacosaurus lujiatuensis* was about two magnitudes smaller than *T. rex* and was herbivorous. M_{max} sets ρ via M_{eco} and a power law in the GTR and MTR models relates both output variables M_{eco} and ρ (Table 1A; Fig. 1). As the normalization constant ($\log_{10}(\alpha)$; Table 1) used by Marshall *et al.* (2021) is for a carnivorous lifestyle, an application of the GTR model to *P. lujiatuensis* or to any other dinosaur showing a different diet at least requires a revision of this constant. Both models are very sensitive to errors in ρ, and both models use ρ to calculate n, N, p and 1/p.

Neither the MTR nor the GTR model uses an uncertainty distribution on the input variable MaxAge (Table 1A), although a correct aging of a specimen is difficult (Cullen *et al.* 2020). Marshall *et al.* (2021) used the largest age known at that time for *T. rex* (FMNH PR 2081; Erickson *et al.* 2004), but in the meantime Cullen *et al.* (2020) provided a larger estimate for this specimen (33 years). Increasing MaxAge from 28 (Table 1A) to 33 years in the GTR model resulted in a more concave survivorship curve, larger middle values of M_{eco}, g and p, and in smaller values of ρ, n, G, N and 1/p (Table 2; Table S1). Values of E_{Sm}, GRR and v_{Sm} did increase, whereas values of E_0 and l_{Sm} were rather similar across the two MaxAge values (Table 3, Table S2). All these changes demonstrate the sensitivity of the GTR model to the input variable MaxAge.

CONCLUSION

Given the large amount of empirical uncertainty in all input variables, the differences in the middle values of N, p and 1/p found between the GTR and MTR models were moderate (Table 2). Nevertheless, for three main reasons the GTR model is clearly better suited than the MTR model for estimating individual and population level characteristics of *T. rex*: (1) there is much evidence for a reptilian or avian reproductive mode in this tyrannosaur; (2) the vital statistics generated by the MTR model strongly contradict this evidence (see Discussion and Table 3); and (3) it contradicts observed vital statistics of extant large reptiles, birds and mammals (Table 4). Thus, the MTR model does not correctly reproduce the biology of *T. rex* from the individual up to the population level. The GTR model also has advantages with respect to its applicability to other extinct taxa. When ignoring that information on T, $\log_{10}(\alpha)$, A and f is always needed for its application (1) it does not require an accurate survivorship schedule; and (2) it only

requires a growth trajectory and estimates of three life history traits that are either assessable from the trajectory (MaxAge, Sm) or from allometric equations (AEN).

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (https://doi.org/10.1111/pala.12648):

Table S1. Population and preservation characteristics calculated by the GTR model for *T. rex* (MaxAge = 33, Cullen *et al.* 2020).
Table S2. Values of different variables from the vital statistics of *T. rex* populations for the GTR model (MaxAge = 33, Cullen *et al.* 2020).
Appendix S1. R code of the GTR model, and of the algorithms used to calculate the survivorship schedule from a given fecundity schedule and the characteristics of the vital statistics of *T. rex*.

REFERENCES

ARAÛJO, R., CASTANHINHA, R., MARTINS, R. M. S., MATEUS, O., HENDRICKS, C., BECKMANN, F., SCHELL, N. and ALVES, L. C. 2013. Filling the gaps of dinosaur eggshell phylogeny: late Jurassic theropod clutch with embryos from Portugal. *Scientific Reports*, **3**, 1924.

CASTANET, J., FRANCILLON-VIEILLOT, H., MEUNIER, F. J. and DE RICQLÈS, A. J. 1993. Bone and individual aging. 245–283. *In* HALL, B. K. (ed.) *Bone growth*. Bone. Vol. 7. CRC Press.

CLARK, J. M., NORELL, M. A., CHIAPPE, L. M. and AKADEMI, M. S. U. 1999. An oviraptorid skeleton from the Late Cretaceous of Ukhaa Tolgod, Mongolia, preserved in an avianlike brooding position over an oviraptorid nest. *American Museum Novitates*, **3265**, 1–36.

CULLEN, T. M., CANALE, J. I., APESTEGUÍA, S., SMITH, N. D., HU, D. and MAKOVICKY, P. J. 2020. Osteohistological analyses reveal diverse strategies of theropod dinosaur body-size evolution. *Proceedings of the Royal Society B*, **287**, 20202258.

ERICKSON, G. M., ROGERS, K. R. and YERBY, S. A. 2001. Dinosaurian growth patterns and rapid avian growth rates. *Nature*, **412**, 429–432.

ERICKSON, G. M., MAKOVICKY, P. J., CURRIE, P. J., NORELL, M. A., YERBY, S. A. and BROCHU, C. A. 2004. Gigantism and comparative life-history parameters of tyrannosaurid dinosaurs. *Nature*, **430**, 772–775.

ERICKSON, G. M., MAKOVICKY, P. J., INOUYE, B. D. and WINN, A. A. 2006. Tyrannosaur life tables: an example of nonavian dinosaur population biology. *Science*, **313**, 213–217.

ERICKSON, G. M., MAKOVICKY, P. J., INOUYE, B. D., ZHOU, C.-F. and GAO, R.-Q. 2009. A life table for *Psittacosaurus lujiatunensis*: initial insights into ornithischian dinosaur population biology. *The Anatomical Record*, **292**, 1514–1521.

ERICKSON, G. M., MAKOVICKY, P. J., INOUYE, B. D. and WINN, A. A. 2010. A revised life table and survivorship curve of *Albertosaurus sarcophagus* based on the Dry Island mass death assemblage. *Canadian Journal of Earth Sciences*, **47**, 1269–1275.

FANTI, F., CURRIE, P. J. and BADAMGARAV, D. 2012. New specimens of *Nemegtomaia* from the Baruungoyot and Nemegt Formations (Late Cretaceous) of Mongolia. *PLoS One*, **7**, e31330.

FRAZER, N. B. 1984. A model for assessing mean age-specific fecundity in sea turtle populations. *Herpetologica*, **40**, 281–291.

GRIEBELER, E. M. 2021. Dinosaurian survivorship schedules revisited: new insights from an age-structured population model. *Palaeontology*, **64**, 839–854.

GRIEBELER, E. M., KLEIN, N. and SANDER, P. M. 2013. Aging, maturation and growth of sauropodomorph dinosaurs as deduced from growth curves using long bone histological data: an assessment of methodological constraints and solutions. *PLoS One*, **8**, e67012.

HECK, C. T. and WOODWARD, H. N. 2021. Intraskeletal bone growth patterns in the North Island Kiwi (*Apteryx mantelli*): growth mark discrepancy and implications for extinct taxa. *Journal of Anatomy*, **239**, 1075–1095.

HORNER, J. R. 1987. Ecological and behavioral implications derived from a dinosaur nesting site. 50–63. *In* CZERKAS, S. and OLSEN, E. C. (eds) *Dinosaurs past and present. Vol. 2.* University of Washington Press.

KLEIN, N., NEENAN, J. M., SCHEYER, T. M. and GRIEBELER, E. M. 2015. Growth patterns and life-history strategies in Placodontia (Diapsida: Sauropterygia). *Royal Society Open Science*, **2**, 140440.

LEE, A. H. and WERNING, S. 2008. Sexual maturity in growing dinosaurs does not fit reptilian growth models. *Proceedings of the National Academy of Sciences*, **105**, 582–587.

LEHMANN, T. M. and WOODWARD, H. N. 2008. Modelling growth rates for sauropod dinosaurs. *Paleobiology*, **34**, 264–281.

MARSHALL, C. R., LATORRE, D. V., WILSON, C. J., FRANK, T. M., MAGOULICK, K. M., ZIMMT, J. B. and POUST, A. W. 2021. Absolute abundance and preservation rate of *Tyrannosaurus rex*. *Science*, **372**, 284–287.

MARTIN, K. 1995. Patterns and mechanisms for age-dependent reproduction and survival in birds. *American Zoologist*, **35**, 340–348.

MATEUS, O., TAQUET, P., ANTUNES, M. T., MATEUS, H. and RIBEIRO, V. 1998. Theropod dinosaur nest from Lourinhã, Portugal. *Journal of Vertebrate Paleontology*, **18** (suppl. 3), 61A.

MENG, Q., LIU, J., VARRICHIO, D. J., HUANG, T. and GAO, C. 2004. Parental care in an ornithischian dinosaur. *Nature*, **431**, 145–146.

MYHRVOLD, N. P. 2013. Revisiting the estimation of dinosaur growth rates. *PLoS One*, **8**, e819117.

MYHRVOLD, N. P., BALDRIDGE, E., CHAN, B., SIVAM, D., FREEMAN, D. L. and ERNEST, S. K. M. 2015. An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology*, **96**, 3109–3000.

NORELL, M. A., CLARK, J. M., CHIAPPE, L. M. and DASHZEVEG, D. 1995. A nesting dinosaur. *Nature*, **378**, 774–776.

NORELL, M. A., BALANOFF, A. M., BARTA, D. E. and ERICKSON, G. M. 2018. A second specimen of *Citipati osmolskae* associated with a nest of eggs from Ukhaa Tolgod, Omnogov Aimag, Mongolia. *American Museum Novitates*, **3899**, 1–44.

OSBORN, H. F. 1924. Three new Theropoda, *Protoceratops* zone, central Mongolia. *American Museum Novitates*, **144**, 1–12.

PEARL, R. 1928. *The rate of living*. Knopf, 224 pp.

PEARL, R. and MINOR, J. R. 1935. Experimental studies on the duration of life. XIV. The comparative mortality of certain lower organisms. *The Quarterly Review of Biology*, **10**, 60–79.

PIANKA, E. R. 1999. *Evolutionary ecology*. Benjamin-Cummings, 512 pp.

R CORE TEAM. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org

SATO, T., CHENG, Y., WU, X., ZELENITSKY, D. K. and HSIAO, Y. 2005. A pair of shelled eggs inside a female dinosaur. *Science*, **307**, 375.

SCHUCHT, P. J., KLEIN, N. and LAMBERTZ, M. 2021. What's my age again? On the ambiguity of histology-based skeletochronology. *Proceedings of the Royal Society B*, **288**, 20211166.

SCHWEITZER, M. H., WITTMEYER, J. L. and HORNER, J. R. 2005. Gender-specific reproductive tissue in ratites and *Tyrannosaurus rex*. *Science*, **308**, 1456–1460.

SMITH, T. M. and SMITH, R. L. 2006. *Elements of ecology*. Pearson Education, 719 pp.

VARRICHIO, D. J., JACKSON, F., BORKOWSKI, J. J. and HORNER, J. R. 1997. Nest and egg clutches of the dinosaur *Troodon formosus* and the evolution of avian reproductive traits. *Nature*, **385**, 247–250.

VARRICHIO, D. J., JACKSON, F. and TRUEMAN, C. N. 1999. A nesting trace with eggs for the Cretaceous theropod dinosaur *Troodon formosus*. *Journal of Vertebrate Paleontology*, **19**, 91–100.

VARRICHIO, D. J., HORNER, J. R. and JACKSON, F. D. 2002. Embryos and eggs for the Cretaceous theropod *Troodon formosus*. *Journal of Vertebrate Paleontology*, **22**, 564–576.

WERNER, J. and GRIEBELER, E. M. 2013. New insights into non-avian dinosaur reproduction and their evolutionary and ecological implications: linking fossil evidence to allometries of extant close relatives. *PLoS One*, **8**, e72862.

WOODWARD, H. N., PADIAN, K. and LEE, A. H. 2013. Skeletochronology. 187–207. *In* PADIAN, K. and LAMM, E. T. (eds) *Bone histology of fossil tetrapods: Advancing methods, analysis, and interpretation*. University of California Press.

WOODWARD, H. N., FREEDMAN FOWLER, E. A., FARLOW, J. O. and HORNER, J. R. 2015. *Maiasaura*, a model organism for extinct vertebrate population biology: a large sample statistical assessment of growth dynamics and survivorship. *Paleobiology*, **41**, 1–25.

YANG, T.-R., WIEMANN, J., XU, L., CHENG, Y.-N., WU, X.-C. and SANDER, P. M. 2019. Reconstruction of oviraptorid clutches illuminates their unique nesting biology. *Acta Palaeontologica Polonica*, **64**, 581–596.