



# DINOSAURIAN SURVIVORSHIP SCHEDULES REVISITED: NEW INSIGHTS FROM AN AGE-STRUCTURED POPULATION MODEL

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**Abstract:** Little is known of dinosaur population biology due to insufficient information on age-dependent fecundities and mortalities. So far, survivorship curves (SC) of only six dinosaurs (four tyrannosaurs, one ceratopsian, one hadrosaur) have been erected from bone assemblages of aged specimens. They indicate high survival throughout most of their life with presumably higher mortalities after hatching and increasing mortalities towards its end. However, none of these studies recognized that to infer a reliable SC for a taxon, the assemblage must preserve a stationary age distribution (i.e. one which is stable, with constant population size over time as overall fecundities match mortalities, hereafter SAD population). To assess SCs of these dinosaurs, I built a simple population model with age-dependent fecundities and survival rates. Its three input parameters are maximum longevity, age at sexual maturation and maximum annual offspring number, for which information exists on these dinosaurs. As bone

histological studies and scaling relationships provide estimates on these parameters, my model is also applicable to other extinct taxa. Modelling suggests that bone assemblages did not preserve SAD populations. SCs determined for SAD populations of *Albertosaurus sarcophagus*, *Gorgosaurus libratus*, *Daspletosaurus torosus* and *Tyrannosaurus rex* indicated that low mortalities followed high mortalities in early life or that mortality rates were rather constant throughout their life. In *Psittacosaurus lujiatunensis*, modelling suggests low mortalities throughout most of its life that increase towards its end. Due to its simplicity, my model was unable to render composite SCs, specifically the sigmoidal shape previously predicted for *Maiaasaura peeblesorum*.

**Key words:** life-history strategy, fecundity, stationary age-structure, attritional bone assemblage, catastrophic bone assemblage, bone histology.

AGE-SPECIFIC fecundities and mortalities determine the growth rate of a population and reveal important ecological and evolutionary insights as they reflect the life-history strategy of a species and the environment that shaped it over evolutionary time (Stearns 1992; Pianka 1999). For instance, natural selection in saturated environments favours a high intraspecific competitive ability and a low population growth rate (K-selection), whereas in heterogeneous environments intraspecific competition is reduced and a high growth rate is favoured (r-selection, Pianka 1999).

From a demographic perspective, the deaths in a population always have to be compensated for by births to enable long-term population and species survival (Stearns 1992; Pianka 1999). A female's reproductive output is age-dependent. In extant species annual fecundities can increase (e.g. fish, reptiles), decrease (e.g. small birds) with age or show a maximum within an animal's life (e.g. in large mammals and humans fecundity increases with age and shows a senescence-driven die-off towards the end of life) (Pianka 1999; Case 2000; Smith & Smith 2006).

With respect to deaths in a population, ecologists distinguish between three basic idealized curves on age-dependence of species survival ( $\log_{10}$ -transformed probability of surviving from birth to a given age, standardized for an initial cohort of 1000 individuals; Pearl 1928; Pearl & Minor 1935). The convex survivorship curve (type 1) assumes high survival throughout most of the life with mortalities considerably increasing towards its end. Such survivorship curves (SC) have been observed in human populations in highly industrialized countries or populations of captive animals. In contrast, species with linear SCs (type 2) show a comparatively constant mortality risk throughout their life. For small, short-lived birds, mammals and lizards, linear SCs have been found. Species with concave SCs (type 3) experience high mortalities at the beginning of their life, followed by low mortalities towards its end. SCs of large, long-lived reptiles are consistent with a concave shape (Pianka 1999; Case 2000; Smith & Smith 2006).

For a few dinosaurs, researchers have established age distributions from bone assemblages to infer their SCs.

Erickson *et al.* (2006) were the first to present dinosaurian SCs (i.e. for the North American tyrannosaurs *Albertosaurus sarcophagus*, *Dasplatosaurus torosus*, *Gorgosaurus libratus* and *Tyrannosaurus rex*). Their study followed that on the ceratopsian *Psittacosaurus lujiatunensis* from China (Erickson *et al.* 2009). The most recent is from Woodward *et al.* (2015) on the hadrosaur *Maiasaura peeblesorum* from Montana, USA. Erickson *et al.* (2010) later added four further specimens to their 2006 published *Albertosaurus sarcophagus* sample ( $n = 22$ , Erickson *et al.* 2006), but sample sizes of *Psittacosaurus lujiatunensis* ( $n = 80$ ) and *Maiasaura peeblesorum* ( $n = 50$ ) were still substantially larger than those of the four tyrannosaurs (*Albertosaurus sarcophagus*:  $n = 22$ , *Dasplatosaurus torosus*:  $n = 14$ , *Gorgosaurus libratus*:  $n = 39$ , *Tyrannosaurus rex*:  $n = 31$ ). Erickson *et al.* (2006, 2009, 2010) derived convex SCs for tyrannosaurs and *Psittacosaurus lujiatunensis*, and hypothesized a moderate mortality rate for their first two years of life (for which they had no specimens) as seen in extant vertebrate carnivores. These authors concluded that the SCs of these species are consistent with those of long-lived birds and mammals. Woodward *et al.* (2015) established a sigmoidal-shaped SC (a moderate mortality rate in the first year of life being documented by specimens in their sample is followed by a long period of a rather constant low rates) for *Maiasaura peeblesorum*.

A few studies inspired by Erickson *et al.* (2006) aimed at improving the accuracy and biological correctness of dinosaurian SCs inferred from bone assemblages. Steinsaltz & Orzack (2011) developed a method using 95% confidence intervals around the estimated age-specific survival rates. Erickson *et al.* (2006, 2009, 2010) had applied bootstrap analysis to statistically assess inaccuracies in SCs. Steinsaltz & Orzack (2011) questioned the convex SCs hypothesized for tyrannosaurs, as they demonstrated that between 50 and 100 individuals are required for a reasonable statistical power to infer a convex SC. Ricklefs (2007) assessed aging rates (average mortality per year) from the SCs of the tyrannosaurs (Erickson *et al.* 2006) and showed that although tyrannosaurs are more closely related to birds than to mammals, their rates resembled those seen in present-day large terrestrial mammals and humans. More recently, Weon (2015) applied biodemographical analysis to the updated *Albertosaurus sarcophagus* dataset (Erickson *et al.* 2010). He challenged Ricklefs (2007) by showing that this tyrannosaur's SC was more similar to that of modern big birds than to eighteenth-century humans.

So far, all studies on dinosaurian SCs have ignored the fact that bone assemblages must comprise a stationary age distribution (i.e. the population has an age distribution which is stable in shape over time, with a size that does not change over time; hereafter SAD population); this is

required to infer reliable information on aging and even life-history strategies of species (Stearns 1992; Pianka 1999; Case 2000). It is well known that the population's growth rate affects its age distribution and vice versa (Pianka 1999; Case 2000). With respect to the stability of age distributions, Erickson *et al.* (2006) only discussed taphonomic problems for their tyrannosaur bone assemblages, that is to say, only a catastrophic assemblage (e.g. from flash floods, volcanic burial) provides a representation of the population's age distribution at a single moment (preserved individuals coexisted and deaths occurred randomly with respect to age). However, they did not note that in this situation it could indeed be possible that the population was increasing or decreasing when the catastrophic event happened. Contrary to a catastrophic assemblage, in an attritional assemblage in which the young and old individuals are the most abundant (i.e. a bimodal distribution) because they are most susceptible to mortality (Voorhies 1969), preserved individuals that did not coexist; bones are from a wide temporal and spatial range. In this case, a stationary age distribution would imply that the bone assemblage must be a sample of a population showing a constant size over the time span during which bones accumulated. This is very unrealistic given that this span could be huge, perhaps millions of years. Erickson *et al.* (2006) ruled out attritional assemblages for their tyrannosaurs as they had left-skewed age distributions (higher age classes dominate; but see Steinsaltz & Orzack 2011, who showed that a positive size-dependent fossilization rate could result in left-skewed age distributions). Conversely, Erickson *et al.* (2009) and Woodward *et al.* (2015) argued that the right-skewed age distributions of *Psittacosaurus lujiatunensis* and *Maiasaura peeblesorum* (in which younger age classes dominate) indicate that these assemblages were not attritional, because a standing crop population of the cervid *Odocoileus virginiana* had a right-skewed distribution (Voorhies 1969).

Here, I present a mathematical model for an age-structured population, using a fecundity schedule as input. Given that fecundities and mortalities determine a population's growth rate, I use the model to predict the survivorship schedule and the growth rate of a population both fitting together at best a given empirical SC under the given fecundity schedule. It thus allows a check of whether a sampled age distribution could come from a SAD population. The model is further used to calculate the SC of a SAD population given a fixed fecundity schedule. My model is very simple and designed to be applicable to extinct taxa and to assess the position of their SC within the concave to convex spectrum. It is parametrized by three life history traits only and makes use of a two-parameter family function on fecundity schedules and a one-parameter family function on the survivorship schedule. Information on the model's three input parameters maximum longevity (inferable from

their published SCs, Erickson *et al.* 2004, 2006, 2009, 2010; Woodward *et al.* 2015), age at sexual maturation (inferable from their growth curves relating age to body size, Erickson *et al.* 2001, 2009; Woodward *et al.* 2015) and maximum annual offspring number (inferable from allometric regressions relating this trait to their body mass, Werner & Griebeler 2013) is fortunately assessable for all six dinosaurs for which SCs have already been established and which are revisited herein.

First, I use my model to demonstrate how the population growth rate and fecundity schedule alter the SC of a population. Next, I apply it to 20 extant species (reptiles, birds and mammals). Specifically, I use it to check whether age distributions of sampled field populations of these species were from SAD populations and then predict their SCs given that they form SAD populations. Then I check whether the latter SCs indeed conform to literature expectations. With the first two analyses, I aim to question whether my model works for extant species and to identify sources of error when inferring SCs of extant and extinct taxa from my model.

I next show with my model that SCs established from dinosaurian bone assemblages were not from SAD populations. This result strongly questions the correctness of the previously published position of these dinosaurs within the concave to convex SC spectrum. I then use the model to determine the SCs of SAD populations of the six dinosaurs. Contrary to literature expectations, the derived SCs were concave to linear for the tyrannosaurs *Albertosaurus sarcophagus*, *Gorgosaurus libratus*, *Dasplatosaurus torosus* and *Tyrannosaurus rex*, whereas the published convex SC of *Psittacosaurus lujiatuensis* was corroborated. The model predicted a concave SC for *Maiasaura peeblesorum* which captures its high mortalities in the first years of life well, but failed to render the sigmoidal-shaped SC published by Woodward *et al.* (2015) due its simplicity.

Finally, I conclude that when good estimates on its input parameters exist, my model calculates much more reliable SCs for extinct taxa than expected from bone assemblage analysis due to the taphonomic problems of the latter.

## MATERIAL AND METHOD

### *The model*

My age-structured population model derives changes in a population's size between one year and the next from age-specific mortality and age-specific birth rates all assumed to be constant over time. It does not distinguish between individuals of different sexes and thus implicitly assumes an equal sex ratio for the population. The population's net reproductive rate ( $R_0$ ) is defined as the average number of class zero offspring produced by an

average newborn individual during its entire lifetime.  $R_0$  is the sum of products of  $l_x$  and  $m_x$ :

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \quad (1)$$

where age  $x$  is a natural number (years),  $l_x$  the probability that an individual survives from birth ( $x = 0$ ) to a given age  $x$  ( $>0$ ) and  $m_x$  the number of births given by an individual of age  $x$  (within one year).

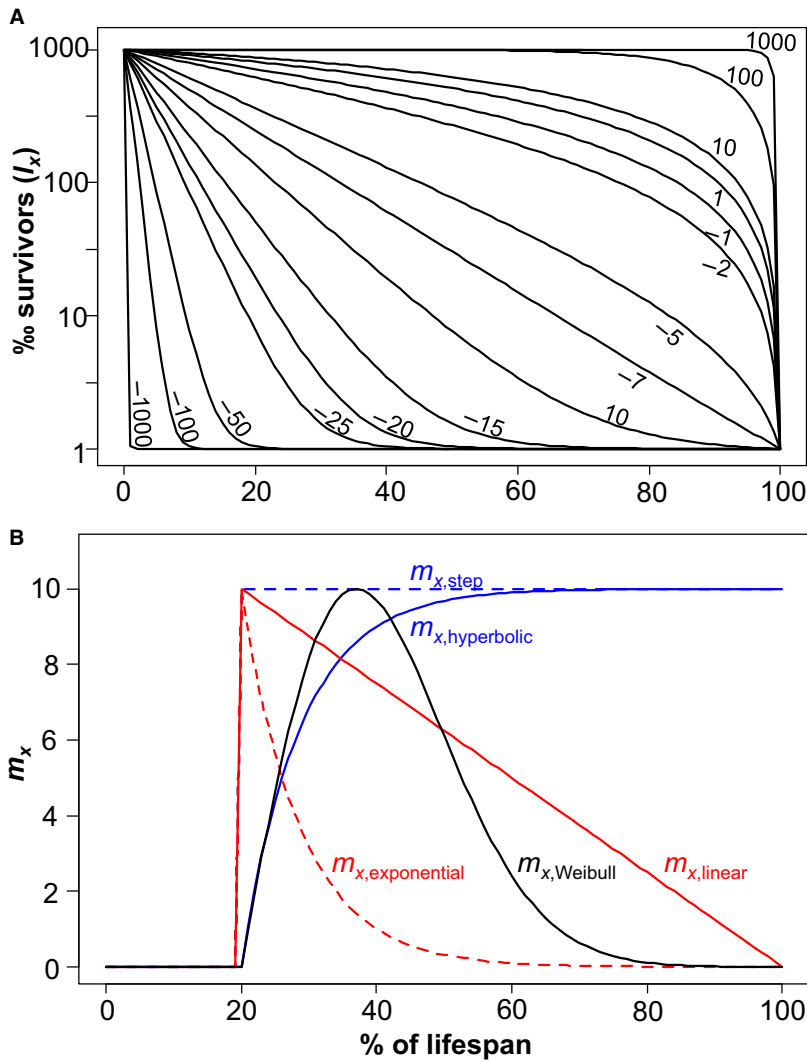
Once a population has attained a stable age distribution,  $R_0$  equals the geometric growth rate. When  $R_0$  is greater than one, the population is exponentially increasing, when  $R_0$  equals one, it is constant in size (i.e. it is a SAD population), and when  $R_0$  is smaller than one, the population is exponentially decreasing (Stearns 1992; Pianka 1999; Case 2000). My simple population model ignores fluctuations in the population's growth rate  $R_0$  caused by environmental factors (e.g. weather, predators) that alter fecundities and mortalities over time. In natural populations  $R_0$  values larger or smaller than one are only realized for short time periods and no population is able to exponentially increase or decrease forever. Thus averaged across time there is no growth in a population.

*Modelling of age-specific survival ( $l_x$ ).* I used a function for age-specific survival rates  $l_x$  that is able to capture the shape of each of the three generalized SCs (convex, linear, concave; Pearl 1928; Pearl & Minor 1935). To keep it as simple as possible, I parametrized it using a single parameter ( $l_x$  shape parameter,  $\lambda$ ) directly controlling the SC's shape and thus the position of the SC within the concave to convex spectrum. Given the  $\log_{10}$ -transformed  $l_x$  axis,  $\lambda$  values around  $-7$  yield linear shaped, larger values convex and smaller values concave shaped SCs (Fig. 1A).

$$l_x = 1 + \frac{\exp(\lambda \cdot x) - 1}{1 - \exp(\lambda)} (1 - 0.001) \quad (2)$$

In Equation 2,  $\lambda$  ( $\neq 0$ ) is this  $l_x$  shape parameter and  $x$  is the standardized age of an individual (real number,  $0 \leq x \leq 1$ ). The raw values of ages are natural numbers and range between zero and the maximum longevity (maxL, years) observed in the population. I obtained standardized ages by dividing the raw age by maxL. The value 0.001 corresponds to one surviving individual out of an initial cohort of 1000 individuals (Pianka 1999; Case 2000).

*Modelling age-specific fecundities ( $m_x$ ).* For age-specific fecundities  $m_x$ , I considered five different functions ( $m_x$  models). Functions relate a fecundity value  $m_x$  to an individual's age  $x$  (natural number,  $0 \leq x \leq \text{maxL}$ , Fig. 1B). All functions assume  $m_x = 0$  for sexually immature individuals (age  $x <$  age at sexual maturation, ASM) and make use of a maximum fecundity value ( $m_{\text{max}} > 0$ ).



**FIG. 1.** The survival function (A, Eqn 2) and the five  $m_x$  models (B, Eqns 3–7) used by my age-structured population model. Age is shown as percentage of maximum longevity (% of lifespan), which was arbitrarily set to 100 (years). A, shape parameter,  $\lambda$ , values used by curves are indicated; age-specific survival  $l_x$  is given on a logarithmic scale for a cohort of 1000 individuals (% survivors); note that a linear SC is seen for  $\lambda$  around  $-7$  (see main text). B, the five  $m_x$  models:  $m_{x,step}$ ,  $m_{x,hyperbolic}$ ,  $m_{x,linear}$ ,  $m_{x,exponential}$  and  $m_{x,Weibull}$ ; in all models, maximum annual offspring number  $m_{max}$  was arbitrarily set to 10 and age at sexual maturation ASM to 20 years.

They cover the broad spectrum of shapes of fecundity curves found in extant animals.

The step function assumes a constant fecundity ( $m_{max}$ ) after the individual has passed ASM.

The second function establishes a hyperbolic increase in  $m_x$  for sexually mature individuals.  $m_{max}$  is the asymptote of this function:

$$m_{x,hyperbolic} = \begin{cases} 0 & 0 \leq x < ASM \\ m_{max} - m_{max} \exp\left(\frac{\log\left(\frac{0.001}{m_{max}}\right)}{\max L - ASM}(x - ASM)\right) & ASM \leq x \end{cases} \quad (4)$$

$$m_{x,step} = \begin{cases} 0 & 0 \leq x < ASM \\ m_{max} & ASM \leq x \end{cases} \quad (3)$$

This is the simplest  $m_x$  model relating fecundity  $m_x$  to age ( $x \geq 0$ ). It was suggested for several bird species (Martin 1995).

The fecundity schedules of red deer studied on the island of Rhum off Scotland (Lowe 1969), of the loggerhead sea turtle (Frazer 1984) and of some birds (Martin 1995) are consistent with a hyperbolic function.

Conversely, the linear function assumes  $m_{max}$  at ASM and models a linear decrease in  $m_x$  throughout the rest of an individual's life:

$$m_{x,linear} = \begin{cases} 0 & 0 \leq x < ASM \\ m_{max} - \frac{m_{max}}{maxL - ASM}(x - ASM) & ASM \leq x \end{cases} \quad (5)$$

White Leghorn domestic chicken (Pianka 1999) and other birds (Martin 1995) show a linear decrease in fecundity with an increasing age in their reproductive phase.

The exponential function also assumes  $m_{max}$  at ASM, but establishes an exponential decrease in  $m_x$  with increasing age for sexually mature individuals:

For insects such as the rice weevils (Birch 1948) and the

$$m_{x,exponential} = \begin{cases} 0 & 0 \leq x < ASM \\ m_{max} \exp\left(\frac{\log\left(\frac{0.001}{m_{max}}\right)}{maxL - ASM}(x - ASM)\right) & ASM \leq x \end{cases} \quad (6)$$

human louse (Pianka 1999) an exponential fecundity schedule was observed.

Finally, I chose a Weibull (density) function to implement an optimum curve for age-specific fecundities for sexually mature individuals:

$$m_{x,Weibull} = \begin{cases} 0 & 0 \leq x < ASM \\ \frac{m_{max}}{max} \left\{ \alpha \beta^{-\alpha} (x - ASM)^{\alpha-1} \exp\left(-\left(\frac{x - ASM}{\beta}\right)^\alpha\right) \right\} & ASM \leq x \end{cases} \quad (7)$$

It makes use of a shape parameter  $\alpha > 0$  and a scale parameter  $\beta > 0$ . In my formulation, the factor  $(m_{max}/max)$ , with max being the maximum value of the original Weibull function, changes this function's co-domain from  $[0, max]$  to  $[0, m_{max}]$ . For my study, I chose  $\alpha = 2.0$  and  $\beta = 0.3 \cdot (maxL - ASM)$  (Fig. 1B) as this parameter combination yields a curve similar to that which Keyfitz & Flieger (1968) observed for humans. An optimum curve on age-specific fecundities was further reported for some birds (Martin 1995) and the Asian elephant (Olsen & Wiese 2000).

*Sensitivity analysis on  $R_0$ ,  $m_{max}$ , ASM,  $m_x$  model with respect to SC shape*

To better understand the interplay between  $R_0$ , fecundity schedules (all five  $m_x$  models are parametrized by  $m_{max}$  and ASM; see Eqns 3–7) and the shape of the SC ( $\lambda$ ), I carried out a sensitivity analysis with my model. I inspected three growth scenarios: a shrinking population ( $R_0 = 0.5$ ), a constant-sized population ( $R_0 = 1$ , i.e. a SAD population) and an increasing ( $R_0 = 2$ ) population, for a hypothetical

species with maxL fixed to 100 years. For each of the three growth scenarios, I considered different fecundity schedules. ASM values used in fecundity schedules were 1, 5, 10 ... 95 years and  $m_{max}$  values were 5, 10 ... 100 offspring per year. Each of the combinations of ASM and  $m_{max}$  was evaluated for each of my five  $m_x$  models (Eqns 3–7). This resulted in 6000 combinations (i.e. 3  $R_0$ ; 20 ASM; 20  $m_{max}$ ; 5  $m_x$  model) for which the model was evaluated. Specifically, for each combination, I calculated with my model the  $\lambda$  value of the survival function (Eqn 2) by numerically solving Eqn 1 for the given  $R_0$  value (0.5, 1.0 and 2.0) and

the given fecundity schedule (ASM,  $m_{max}$ ,  $m_x$  model) (see below).

*Application of the model to populations of extant species and dinosaurs*

*Extant species studied and maxL, ASM and  $m_{max}$  values used in modelling.* Unlike extinct taxa, in extant species taphonomic problems with age distribution samples are absent and much better information on model parameters ASM, maxL and  $m_{max}$  exists. I, thus studied 20 extant vertebrates for which I found SCs in the literature to check whether my model can predict their SCs. These species comprised six reptiles, seven birds and seven mammals. The modelled reptiles were the desert night lizard (*Xantusia vigilis*; Zweifel & Lowe 1966), the Nile crocodile (*Crocodylus niloticus*; Blomberg *et al.* 1982), the pond slider (*Trachemys scripta*; Gibbons & Semlitsch 1982), the painted turtle (*Chrysemys picta*; Frazer *et al.* 1991), the Texas tortoise (*Gopherus berlandieri*; Hellegren *et al.* 2000) and the loggerhead sea turtle (*Caretta caretta*; Frazer 1983). All avian species studied were from Deevey (1947). These were the European robin (*Erithacus rubecula*), the song thrush (*Turdus philomelos*), the American robin (*Turdus migratorius*), the common black bird (*Turdus merula*), the common starling (*Sturnus vulgaris*), the northern lapwing (*Vanellus vanellus*) and the European herring gull (*Larus argentatus*). The mammalian species were the Dall sheep (*Ovis dalli*; Deevey 1947), the warthog (*Phacochoerus aethiopicus*; Spinage 1972), the impala (*Aepyceros melampus*; Spinage 1972), the zebra (*Equus quagga boehmi*; Spinage 1972), the African buffalo

(*Syncerus caffer*; Spinage 1972), the white-tailed deer (*Odocoileus virginianus*; Quick 1962) and the hippo (*Hippopotamus amphibius*; Millar 1988).

I further applied my model to four other vertebrate species covering the concave to convex spectrum. They were used in Erickson *et al.* (2006) as reference for dinosaurian SCs. These were the American alligator (*Alligator mississippiensis*, concave), the osprey (*Pandion haliaetus*, linear), the human (*Homo sapiens*, convex) and the African bush elephant (*Loxodonta africana*, convex).

To parametrize the survivorship function (Eqn 2) and the  $m_x$  models (Eqns 3–7) for each of these extant species, I extracted estimates for maxL, ASM and  $m_{\max}$  from the papers that reported their SCs. When this was not feasible, I referred to the online database AnAge (Tacutu *et al.* 2013). Neither of these sources provided information on  $m_{\max}$  for five reptiles (*Crocodylus niloticus*, *Alligator mississippiensis*, *Trachemys scripta*, *Chrysemys picta*, *Caretta caretta*) and four birds (*Erithacus rubecula*, *Turdus philomelus*, *Turdus merula*, *Vanellus vanellus*). For these reptiles, I extracted the adult body mass reported in the database AnAge (Tacutu *et al.* 2013) and then calculated the ratio of the allometrically predicted annual clutch mass and egg mass (reptile model; Eqn 8, below) to estimate  $m_{\max}$  as annual fecundity. For the birds, I adopted this procedure, but applied the bird model on annual fecundity (Eqn 9, below). Sources and values of maxL, ASM and  $m_{\max}$  (plus adult body mass when  $m_{\max}$  was allometrically estimated) of all extant species studied are listed in (Table S1). I did not find a fecundity curve ( $m_x$  model,  $m_{\max}$ , ASM) for any of the extant species in the literature and therefore considered each of my five  $m_x$  models (Eqns 3–7) for all of them.

*Dinosaurs studied and maxL, ASM and  $m_{\max}$  values used in modelling.* I studied the four tyrannosaurs *Albertosaurus sarcophagus*, *Daspletosaurus torosus*, *Gorgosaurus libratus* and *Tyrannosaurus rex* (Erickson *et al.* 2006, 2010), the ceratopsian *Psittacosaurus lujituenensis* (Erickson *et al.* 2009) and the hadrosaur *Maiasaura peeblesorum* (Woodward *et al.* 2015). I compiled the values needed as input for my model from the literature or estimated them from the dinosaurs' adult body masses (see below). Their maximum longevities (maxL) were read off from the published SCs. For their ASM and adult body mass, I referred to published growth curves from bone histological studies (Erickson *et al.* 2001 for tyrannosaurs; Erickson *et al.* 2009 for *Psittacosaurus lujituenensis*; Woodward *et al.* 2015 for *Maiasaura peeblesorum*). For an estimate of dinosaur adult body mass, I used the asymptotic body mass from its growth curve and for its ASM the age at which the curve's inflection point is seen. Evidence for inferring sexual maturity from a growth curve's inflection point exists in reptiles and amphibians (Reiss 1989; Kupfer *et al.* 2004; Lee & Werning 2008). I

estimated  $m_{\max}$  of each dinosaur from its adult body mass using both the reptile and bird model from Werner & Griebeler (2013). These authors established allometries for reptiles (crocodiles and tortoises) and birds (Struthioniformes, Tinamiformes, Galliformes and Anseriformes) that relate adult body mass (BM, in g) to egg mass (EM, in g) and to annual clutch mass (ACM, in g), respectively. I then derived  $m_{\max}$  as the ratio of the allometrically predicted annual clutch mass and egg mass for each dinosaur. For egg mass and annual clutch mass, Werner & Griebeler (2013) showed that in theropods (*Troodon formosus*, *Oviraptor philoceratops*, *Citipati osmolskae*, *Lourinhanosaurus antunesi*) traits conform best to those of similar-sized or scaled-up extant birds, in sauropodomorphs (*Megaloolithus patagonicus*, *Megaloolithus mammillare*, *Massospondylus carinatus*) to extant reptiles and in hadrosaurs (*Maiasaura peeblesorum*, lambeosaurine dinosaur) to both extant clades. The allometric regressions from Werner & Griebeler (2013) used for the six dinosaurs revisited herein are

Reptile model:

$$\begin{aligned}\log_{10}(\text{EM}) &= -1.622 + 0.328 \cdot \log_{10}(\text{BM}) \\ \log_{10}(\text{ACM}) &= -0.695 + 0.690 \cdot \log_{10}(\text{BM})\end{aligned}\quad (8)$$

Bird model:

$$\begin{aligned}\log_{10}(\text{EM}) &= -1.235 + 0.746 \cdot \log_{10}(\text{BM}) \\ \log_{10}(\text{ACM}) &= -0.363 + 0.726 \cdot \log_{10}(\text{BM}).\end{aligned}\quad (9)$$

As the regression on avian egg mass (Eqn 9) against adult body mass predicts physiologically absurd egg masses for large dinosaurs, I always set egg mass to 5 kg when Equation 9 predicted a larger egg mass than 5 kg. Egg masses of the largest dinosaurs, the sauropods, are estimated to have been around 5 kg (Deeming 2006; Hechenleitner *et al.* 2016).

*SCs and SAD populations.* To assess whether empirical SCs of extant species and extinct dinosaurs were from SAD populations, I determined with my model for each taxon and for each of the five  $m_x$  models (Eqns 3–7, ASM and  $m_{\max}$  fixed given for the species; Tables S1, S3) the combination of  $R_0$ ,  $m_x$  model and  $\lambda$  yielding a SC fitting best to its empirical SC (for extant species erected from the sampled age distribution of the population; for dinosaurs erected from their bone assemblage). For dinosaurs studied herein, I always considered both the reptile and bird model on  $m_{\max}$  (Eqns 8, 9) for each  $m_x$  model. Out of the studied dinosaurs, Werner & Griebeler (2013) had only *Maiasaura peeblesorum* in their dinosaur sample and for this hadrosaur, reproductive traits conformed more or less to both (Werner & Griebeler 2013).

Finally, I applied an Akaike information approach to establish an overall  $R_0$  and  $\lambda$  value across  $m_x$  models for

each taxon. Only for dinosaurs, this was separately done for the reptile and for the bird model. Following Symonds & Moussalli (2011), I first calculated for each of the five  $m_x$  models the residual sum of squares (RSS) across all ages  $x$  ( $0 \leq x \leq \text{maxL}$ ) from the best SC derived under the respective  $m_x$  model (set of  $l_x$  values, values are obtained from evaluating Equation 2 for each age  $x$  assuming the best  $\lambda$  value,  $0 \leq x \leq \text{maxL}$ , predicted  $l_x$  values) and from the empirical SC of the taxon (set of  $l_x$  values, values read off for ages  $x$  from the SC erected from the age distribution,  $0 \leq x \leq \text{maxL}$ , observed  $l_x$  values). The residual value for a given age  $x$  is the difference between its observed  $l_x$  value and its predicted  $l_x$  value. For each  $m_x$  model, I then calculated the small sample size corrected AIC value (AICc) from its RSS. Next, I calculated the Akaike weight ( $w$ ) from these AICc values for each of the five  $m_x$  models, which I finally used for averaging  $R_0$  and  $\lambda$  values across  $m_x$  models considered for taxa.

To calculate SCs expected for SAD populations ( $R_0 = 1$ ) of extant species and extinct dinosaurs, using my model, I calculated for each of the five  $m_x$  models the best  $\lambda$  value yielding a growth rate  $R_0 = 1$ . Only for the dinosaurs, I repeated this for both the reptile and bird model (Eqns 8, 9) on parameter  $m_{\text{max}}$  for all five  $m_x$  models.

#### Evaluation of the model

I implemented my age-structured population model in R (v.3.5.2; R Core Team 2018; Griebeler 2021). Numerical solving of Eqn 2 for a given  $R_0$  value and a given fecundity schedule (ASM,  $m_{\text{max}}$ ,  $m_x$  model) to determine the best  $\lambda$  value was done with the bisection method (Press *et al.* 1992), which is a simple root-finding-algorithm (Press *et al.* 1992).

When checking whether SCs of extant species and extinct dinosaurs come from SAD populations,  $R_0$  was systematically altered in 0.01 steps within the interval  $[-25, 25]$  and the  $\lambda$  value was optimized by the bisection method for each of these  $R_0$  values. For optimization of  $\lambda$ , the normalized root-mean-square deviation (RMSD) on the predicted (set of  $l_x$  values, predicted for all ages  $x$  using the  $\lambda$  value under consideration,  $0 \leq x \leq \text{maxL}$ ) and the observed SC (set of  $l_x$  values, values read off for ages  $x$  from the SC erected from the age distribution,  $0 \leq x \leq \text{maxL}$ ) was minimized. RMSD is the ratio of the standard deviation of the residuals (=  $l_x$  value predicted -  $l_x$  value observed for an age  $x$ ,  $0 \leq x \leq \text{maxL}$ ) and the mean of all observed  $l_x$  values (observed  $l_x$  values of ages  $x$  are averaged over all ages  $x$ ,  $0 \leq x \leq \text{maxL}$ ). The final best combination of  $R_0$  and  $\lambda$  for the observed SC was that yielding the overall smallest RMSD value across all  $R_0$  values and  $\lambda$  values evaluated. I conducted this search for the best combination of  $R_0$  and  $\lambda$  fitting the observed SC in terms of minimizing RMSD for each of my five  $m_x$  models.

For estimating the  $\lambda$  value of a SAD population for extant species and extinct dinosaurs (of the hypothetical species in the sensitivity analysis) under a given fecundity schedule and a given  $m_x$  model, the bisection algorithm searched for the best  $\lambda$  value yielding  $R_0$  for the given fecundity schedule. This procedure was again conducted for each of the five  $m_x$  models.

The initial bisection interval of  $\lambda$  was always  $[-999, 1000]$  (Fig. 1A). I assumed that this algorithm had converged when the bisection interval, and thus the error interval of  $\lambda$ , was smaller than 0.01. The final  $\lambda$  value was the average value of the lower and upper limit of this interval. Due to the assumed narrowness of the error interval, SCs derived for the final  $\lambda$  value, for the lower limit and for the upper limit were virtually identical. The bisection interval was halved in each iteration step. The accuracy of  $R_0$  was always  $\pm 0.01$ .

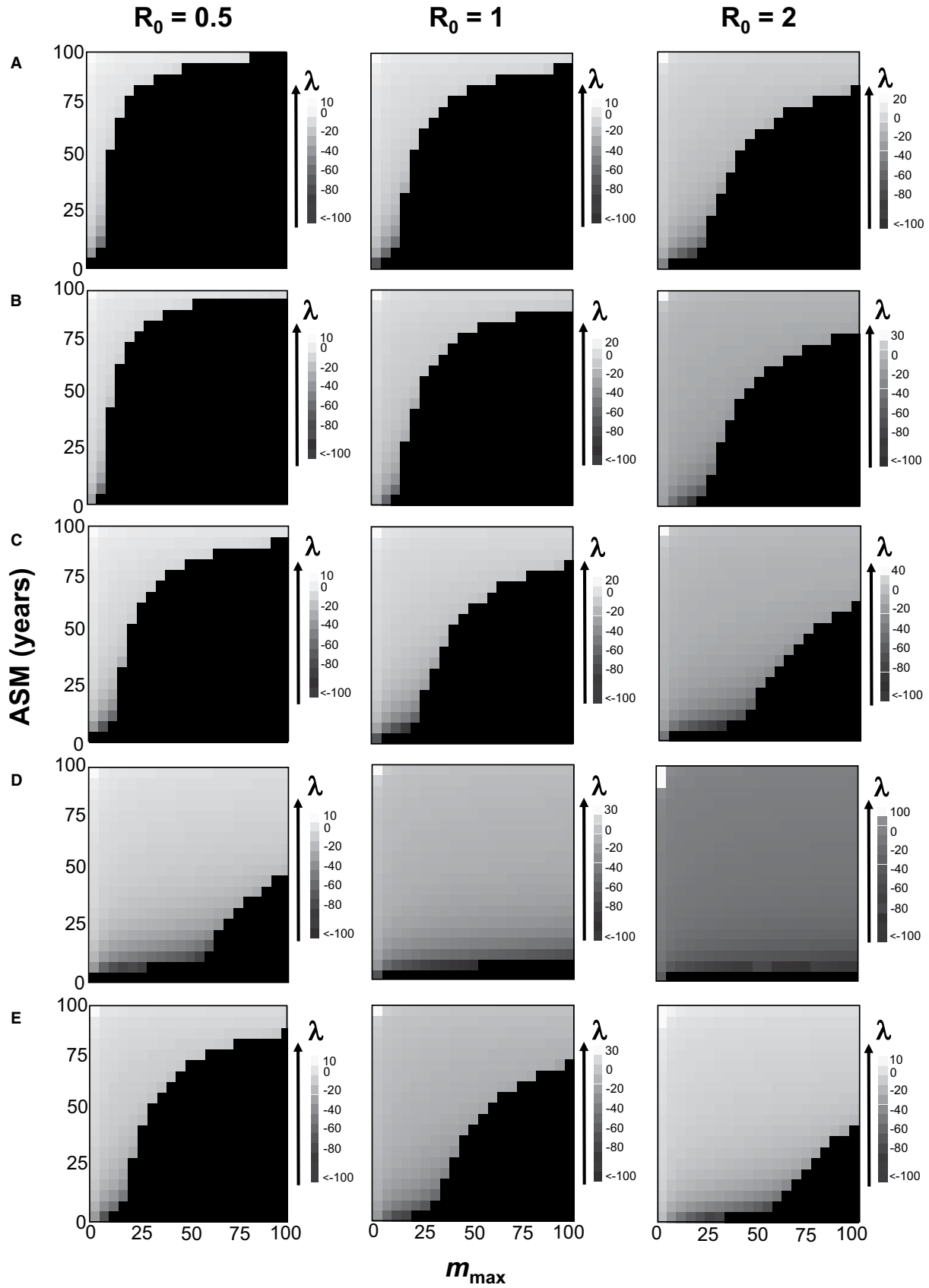
## RESULTS

### *Sensitivity analysis on $R_0$ , $m_{\text{max}}$ , ASM and $m_x$ model used with respect to SC shape ( $\lambda$ )*

My sensitivity analysis indicated a strong influence of both the population growth  $R_0$  and the fecundity schedule ( $m_{\text{max}}$ , ASM,  $m_x$  model) on the shape of the SC ( $\lambda$ ) determined from my model (Fig. 2). Given a specific combination of  $m_{\text{max}}$ , ASM and  $m_x$  model, the derived  $\lambda$  value was smallest for the shrinking population, intermediate for the SAD population (constant size), and highest for the increasing population. For all three  $R_0$  scenarios,  $\lambda$  values decreased with increasing  $m_{\text{max}}$ . An earlier maturation within an individual's life (ASM) resulted in a smaller  $\lambda$  value than a later maturation. Given a specific ASM and  $m_{\text{max}}$  value,  $\lambda$  values were smallest for the  $m_{x,\text{step}}$  and  $m_{x,\text{hyperbolic}}$  models (Fig. 2A, B). They were only slightly larger for the  $m_{x,\text{linear}}$  and  $m_{x,\text{Weibull}}$  models than for the  $m_{x,\text{step}}$  and  $m_{x,\text{hyperbolic}}$  models (Fig. 2A–C, E) and they were clearly the largest for the  $m_{x,\text{exponential}}$  model (Fig. 2D).

### *Application of the model to populations of extant species and dinosaurs*

*Extant species.* None of the SCs of studied extant species was from a SAD population (Fig. S1) and the published age distribution samples were more or less unsuitable for assessing the position of species within the concave to convex SC spectrum. While calculated  $R_0$  values averaged across the five  $m_x$  models indicated that populations of the reptilian species *Xantusia vigilis* ( $R_0 = 0.688$ ), *Chrysemys picta* (0.018) and *Caretta caretta* (0.704) were shrinking, they suggested that populations of *Crocodylus*





**FIG. 2.** Sensitivity analysis of the interplay between the fecundity schedule assumed, the population growth rate ( $R_0$ ) and shape of the SC ( $\lambda$ ). The  $\lambda$  value of the SC (Eqn 2) was determined for different combinations of maximum annual offspring number ( $m_{\max}$ ), age at sexual maturation (ASM) and  $R_0$ . Each combination of  $m_{\max}$  and ASM was evaluated for each of five  $m_x$  models (rows A–E; Eqns 3–7; Fig. 1B) for a shrinking ( $R_0 = 0.5$ ), constant-sized ( $R_0 = 1$ ) and an increasing ( $R_0 = 2$ ) population (the three columns). Maximum longevity was always arbitrarily set to 100 years. Models: A,  $m_{x,\text{step}}$ ; B  $m_{x,\text{hyperbolic}}$ ; C,  $m_{x,\text{linear}}$ ; D  $m_{x,\text{exponential}}$ ; E,  $m_{x,\text{Weibull}}$ . Arrows indicate increasing  $\lambda$  values and thus an increasing convexity of the derived SC. Note varying scales of  $\lambda$  values.

*niloticus* (1.389), *Trachemys scripta* (2.764) and *Gopherus berlandieri* (2.160) were increasing in size (Table S1A). When assessing their SCs in SAD populations,  $\lambda$  values inferred indicated a linear to convex SC, irrespective which  $m_x$  model I assumed for the species, except for *Crocodylus niloticus* (Fig. S1A; Table S2A). *Crocodylus niloticus* always had a concave SC (Fig. S1A; Table S2A).

All empirical SCs of bird species were from considerably increasing populations ( $2.878 \leq R_0 \leq 7.744$ ), except for *Larus argentatus* (Table S1B). The latter population was comparatively slightly shrinking in size (0.884). For all bird species, SCs of SAD populations determined under the different  $m_x$  models were linear to concave, except again for *Larus argentatus* (Fig. S1B; Table S2B). The latter raptor is the largest in my sample and had a convex SC under all five  $m_x$  models.

In studied mammals, published SCs of *Phacochoerus aethiopicus* ( $R_0 = 4.902$ ) and *Hippopotamus amphibius* (6.025) were from substantially increasing populations. Those of *Aepyceros melampus* (1.630), *Equus quagga boehmi* (1.646) and *Ovis dalli* (1.680) were from moderately increasing populations and those of *Odocoileus virginians* (0.840) and of *Syncerus caffer* (0.364) were from shrinking populations (Table S1C).

SCs determined for SAD populations of mammals were concave to convex (Fig. S1C; Table S2C). Depending on the  $m_x$  model used, the smallest mammals in my sample *Ovis dalli*, *Phacochoerus aethiopicus* and *Aepyceros melampus* had moderately concave to slightly convex SCs and the midsized *Equus quagga boehmi* a linear to convex SC. The SCs of the largest mammal in my sample *Hippopotamus amphibius* were moderately concave to linear. The SCs of the midsized *Odocoileus virginians* and of the large *Syncerus caffer* were clearly convex for all  $m_x$  models.

The SCs calculated for SAD populations of the four extant vertebrate species used as references for dinosaurs in Erickson *et al.* (2006) matched literature expectations (Fig. 3; Table S2D). The SC of *Homo sapiens* was convex, that of *Loxodonta africana* linear to convex, that of *Pan-dion haliaetus* linear to concave and that of *Alligator mississippiensis* concave.

**Dinosaurs.** Calculated dinosaurian  $R_0$  indicated that bone assemblages were not from SAD populations, irrespective of whether I used a reptile or bird model on their fecundity schedule. Very large  $R_0$  values ( $15.410 \leq R_0 \leq 24.924$ ,

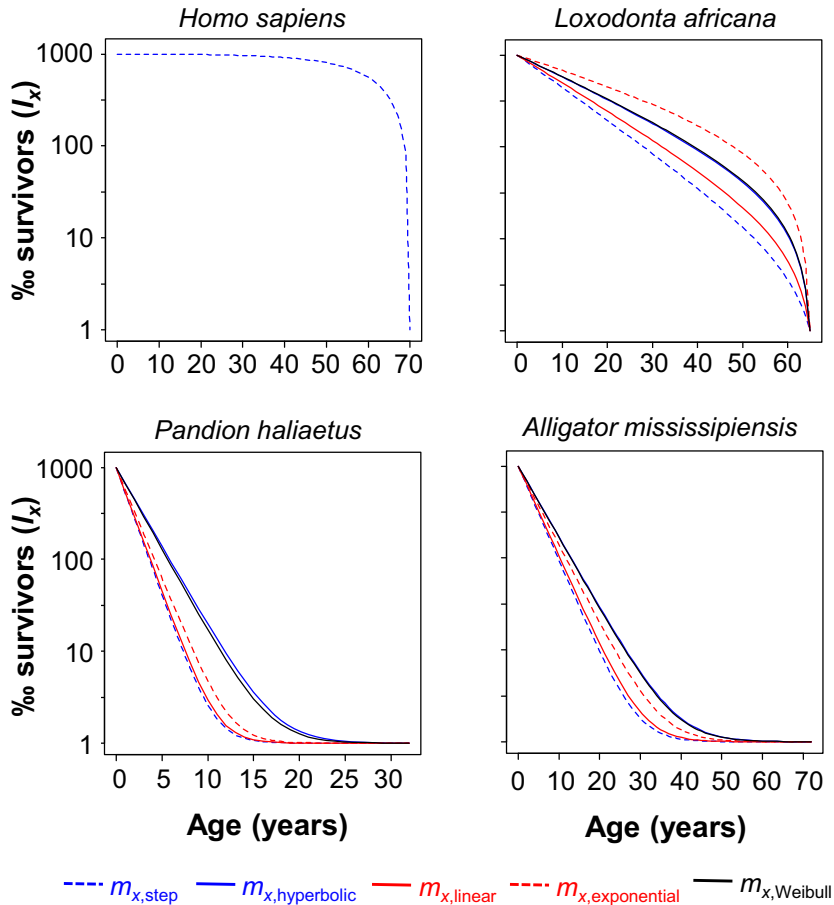
where  $R_0$  is the mean number of offspring given per individual within its life) indicated that all bone assemblages conform to substantially increasing populations (Fig. 4; Table S3). As such  $R_0$  values clearly contradict that bone assemblages resemble SAD populations ( $R_0 = 1$ ) they are inadequate for drawing conclusions on the shape of the dinosaur's SC and thus of the SC's position within the concave to convex spectrum. *Psittacosaurus lujiatuensis* was the only exception. Under the bird model the best  $R_0$  value was comparatively close to one (1.786) (Fig. 4; Table S3), whereas under the reptile model, its population was clearly increasing (8.070).

SCs calculated for dinosaurian SAD populations were linear to concave, with the bird model yielding more convex SCs than the reptile model for a given  $m_x$  model. *Psittacosaurus lujiatuensis* (Fig. 4; Table S4) was the only exception, its SC was convex under the bird and reptile model for all five  $m_x$  models considered. The updated bone assemblage on *Albertosaurus sarcophagus* (Erickson *et al.* 2010) resembled the results obtained from the somewhat smaller sample (Erickson *et al.* 2006; Fig. S2A).

## DISCUSSION

### Sensitivity analysis

*Quality of bone assemblages for establishing SCs (SAD population).* Studies so far conducted on dinosaurian SCs were only aware that bone assemblages should not be attritional (individuals coexisted) in order to avoid an overrepresentation of young and old age classes in the age distribution sample (Voorhies 1969). However, authors did not check whether assemblages were from SAD populations, that is, that the age distribution of the population is stable and the population's growth rate ( $R_0$ ) equals one. My sensitivity analysis clearly shows that  $R_0$  considerably affects the shape of the derived SC ( $\lambda$ ). Given a fixed fecundity schedule ( $m_{\max}$ , ASM,  $m_x$  model) increasing populations ( $R_0 > 1$ ) have larger  $\lambda$  values and thus more convex SCs than shrinking populations ( $R_0 < 1$ ) (Fig. 2). In increasing populations, young individuals comprise the most frequent age classes and such populations therefore have highly right-skewed age distributions, whereas those of shrinking populations are left-skewed as the older age classes dominate (Pianka 1999). Conversely, given a fixed



**FIG. 3.** Modelled SCs of SAD populations of four extant vertebrates. Species are expected to cover the complete concave (*Alligator mississippiensis*) to convex (*Homo sapiens*) SC spectrum. Each of the five  $m_x$  models ( $m_{x,step}$ ,  $m_{x,hyperbolic}$ ,  $m_{x,linear}$ ,  $m_{x,exponential}$ ,  $m_{x,Weibull}$  model, Eqns 3–7; Fig. 1B) were considered for each of species. For *Homo sapiens* the bisection algorithm solving Equation 2 for  $R_0 = 1$  failed to find a  $\lambda$  value for any  $m_x$  model except for  $m_{x,step}$ . Note that different  $m_x$  models can produce identical SCs (Table S2D) and then curves are overprinted. For accuracies of  $\lambda$  values used by SCs refer to Table S2D.

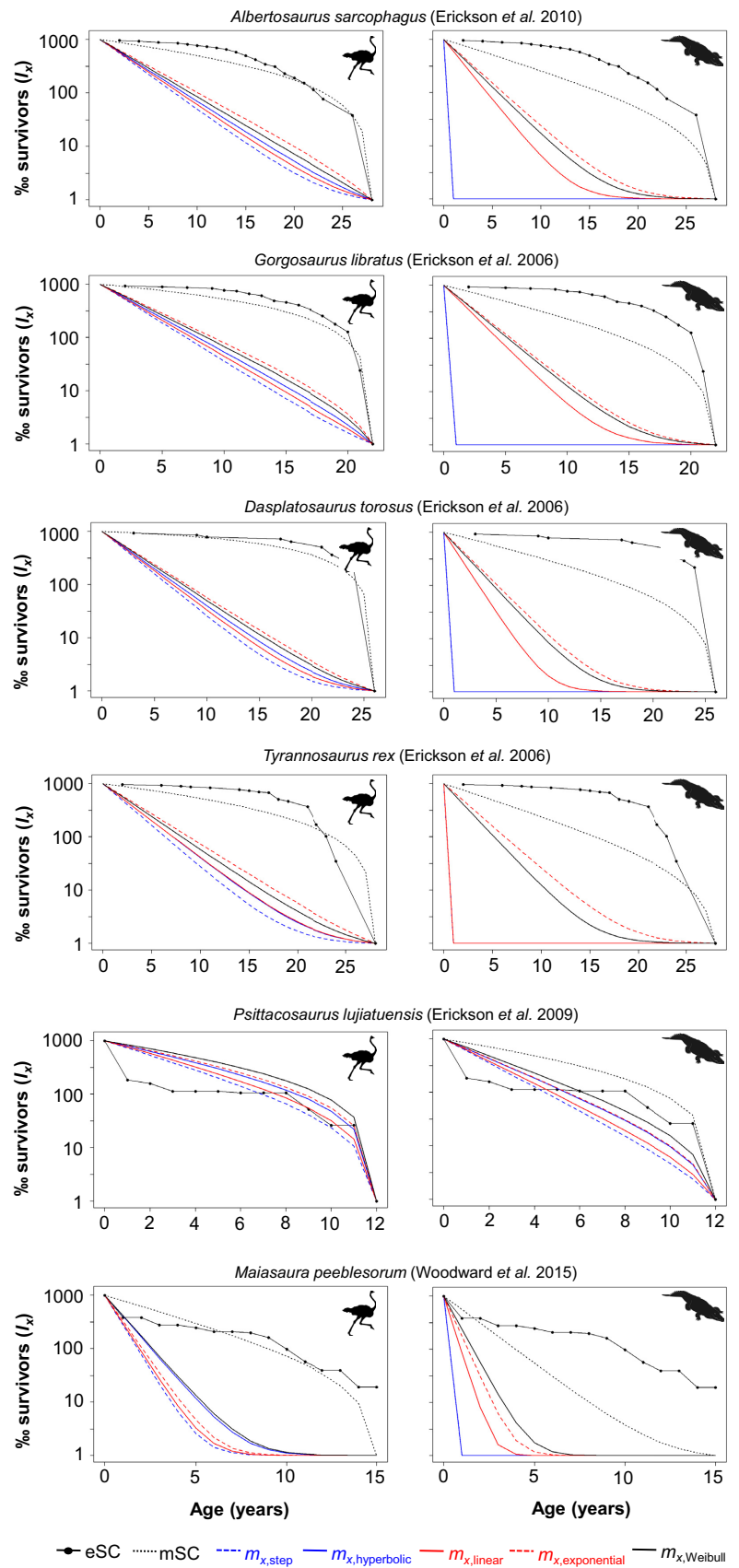
$R_0$  (i.e.  $R_0 = 1$ , a SAD population), right-skewed age distributions indicate high overall fecundities in adult age classes that result in more concave SCs, whereas left-skewed distributions indicate low fecundities that result in more convex SCs (Pianka 1999). As in fossil populations, including those of the dinosaurs studied herein (Erickson *et al.* 2006, 2009; Woodward *et al.* 2015), juveniles are most likely to be underrepresented in number, their age distributions tend to be left-skewed. Thus, as  $R_0$  is unknown for fossil populations, their left-skewed age distribution could either indicate a shrinking population or low fecundities when assuming that the distribution is from a SAD population. In the first case the population's SC will move towards the concave end of the spectrum, whereas in the second it will move towards the convex end.

*Sensitivity of calculated SCs to the fecundity schedule assumed.* The modelling approach I used to check whether an age distribution is stationary (SAD population), requires most accurate fecundity schedules for the taxon. This is clearly demonstrated in my sensitivity analysis as it indicates a strong effect of  $m_{max}$ , ASM and  $m_x$  model on the  $\lambda$  value yielding a given overall

population growth rate  $R_0$  (Fig. 2). The  $\lambda$  values decreased with increasing  $m_{max}$ , irrespective of which combination of ASM value and  $m_x$  model I assumed (Fig. 2). Parameter  $m_{max}$  sets the level of births given per individual in a population. The more births occur, the more deaths are needed to match a given  $R_0$ . The decrease in  $\lambda$  with increasing  $m_{max}$  implies that an overestimation of  $m_{max}$  (too large) will move a population's SC towards the concave end of the spectrum, whereas an underestimation (too small) will move it towards the convex end.

For a given  $m_{max}$  and  $m_x$  model, earlier maturation resulted in smaller  $\lambda$  values than those for a later maturation (Fig. 2). ASM constrains how many newborns a mature individual can potentially have within its life (the area under the age-specific fecundity curve is confined by ASM and maxL; Fig. 1B). At the population level, an early maturation results in more births than a later one and implies smaller  $\lambda$  values than a later maturation in order to match a given  $R_0$ . Thus, analogous to  $m_{max}$ , an overestimation of a species' ASM will move the SC towards the convex end, whereas an underestimation towards the concave end of the spectrum.

**FIG. 4.** Modelled SCs of the four tyrannosaurs as well as of the ceratopsian *Psittacosaurus lujiatuensis* and the hadrosaur *Maiasaura peeblesorum* using both the reptile (right column; Eqn 8) and bird (left column; Eqn 9) models on  $m_{max}$  from Werner & Griebeler (2013) and each of the five  $m_x$  models (Eqns 3–7, Fig. 1B). In each case, the SC was erected from the bone assemblage (eSC). The mSC in each plot uses the  $\lambda$  value derived from Akaike weights based averaging across the five  $m_x$  models. Averaged  $\lambda$  values were from checking whether the eSC could come from a SAD population ( $R_0 = 1$ ) for each of the five  $m_x$  models (Eqns 3–7) is also shown. For detailed information on model parameter values assumed for species and modelled SCs with their accuracy, see Tables S3–S4. The model revealed very similar SCs (Fig. S2A) for the updated bone assemblage of *Albertosaurus sarcophagus* (Erickson *et al.* 2010) when compared to those derived from the original dataset (Erickson *et al.* 2006). Note that in some cases SCs are overprinted due to their very similar  $\lambda$  values. Silhouettes are from PhyloPic (Public Domain Dedication license (CC0 1.0); <http://phylopic.org/>); by Becky Barnes and Ferran Sayol, respectively.



In my sensitivity analysis, the  $m_x$  model chosen also strongly affected the  $\lambda$  values determined for a given combination of  $m_{\max}$  and ASM (Fig. 2). The  $\lambda$  values were smallest for the  $m_{x,\text{step}}$  and  $m_{x,\text{hyperbolic}}$  models, somewhat larger for the  $m_{x,\text{linear}}$  and  $m_{x,\text{Weibull}}$  models and were clearly the largest for the  $m_{x,\text{exponential}}$  model. Given the identical  $m_{\max}$  and ASM values, this ranking of  $m_x$  models reflects differences in the total number of newborns that an individual of a given age could potentially give within the rest of its life (area under the age-specific fecundity curve confined by this age and maxL; Fig. 1B). This reproductive output is highest under the  $m_{x,\text{step}}$  and lowest under the  $m_{x,\text{exponential}}$  model. Under the  $m_{x,\text{hyperbolic}}$  model it is somewhat smaller than under the  $m_{x,\text{step}}$  model and under the  $m_{x,\text{linear}}$  model it is somewhat higher than under the  $m_{x,\text{Weibull}}$  model. As a larger reproductive output results in more births in a population than a smaller one, deaths must be more frequent in the first situation than in the second in order to match the given  $R_0$  of the population.

#### SCs of extant species and limitations on the model's applicability

*Checking for SAD populations.* Empirical SCs of the 20 extant species conformed best either to shrinking or increasing populations, except for *Larus argentatus* and *Odocoileus virginians*. The  $R_0$  value averaged across  $m_x$  models of the latter two species was much closer to one (Table S1; *Larus argentatus*: 0.884, *Odocoileus virginians*: 0.840). Thus, even for extant species, the problem of sampling an age distribution that is from a SAD population is evident. However, field studies often reveal only a snapshot of a population's age-structure. While my model assumes that fecundities and mortalities of populations are constant over time, those of natural populations vary due to fluctuations in abiotic and biotic environmental conditions experienced by populations (e.g. weather conditions or predator abundance may vary from year to year). However, the development of methodical improvements on inferring reliable SCs for extant species is out of the scope of this study.

For one reptile (*Trachemys scripta*), six out of seven birds (all except *Erithacus rubecula*) and two out of seven mammals (*Odocoileus virginians*, *Hippopotamus amphibius*) RMSD values were comparatively small (smaller than 0.1) and suggest a very good fit of the modelled to the empirical SC (Fig. S1; Table S1). The other 11 taxa uncover several limitations to the applicability of my model:

1. Life history traits of species are plastic with respect to environmental conditions experienced by populations

(Promislow & Harvey 1990; Ricklefs 2000; Morrison & Hero 2003; Blank & Lamouroux 2007; Parker & Andrews 2007). Finding estimates of traits parametrizing their fecundity schedules was difficult in all species. My sensitivity analysis suggests that each of these can considerably affect the shape of the SC ( $\lambda$ ; Fig. 2).

2. My one-parameter family survival Equation 2 is unable to model composite curves of the three generalized SCs (concave, linear, convex). An implementation of such SCs requires further model parameters (e.g. the equation used in Weon & Je 2011 makes use of an age-dependent  $l_x$  shape parameter), which is particularly problematic when the number of age classes of a species is comparatively small (i.e. the species' maximum longevity (maxL) is small). *Crocodylus niloticus* and *Erithacus rubecula* had the largest RMSD values across all extant species studied (*Crocodylus niloticus*:  $0.412 \leq \text{RMSD} \leq 0.431$ , *Erithacus rubecula*: 0.216; Table S1). Their empirical SCs show a concave phase at the beginning of their life, followed by a linear phase in the middle and an exponential phase towards the end of their life (Fig. S1).
3. For nine species, a further important source of error is that the maximum longevity from the empirical SC is clearly smaller than their true maximum longevity. This was seen in four reptiles (*Xantusia vigilis*, *Trachemys scripta*, *Gopherus berlandieri*, *Caretta caretta*) and five mammals (*Phacochoerus aethiopicus*, *Aepyceros melampus*, *Equus quagga boehmi*, *Syncerus caffer*, *Hippopotamus amphibius*). Their true SCs will be more convex than the ones determined from my model herein.

*Calculated SCs of SAD populations.* Nevertheless, given all the limitations listed above, SCs of SAD populations modelled for extant species matched more or less well literature expectations with respect to their position within the concave to convex spectrum (Figs S1, S3).

In reptiles, modelled curves were linear to convex, except for *Alligator mississippiensis* and *Crocodylus niloticus* (with the composite empirical SC). The concave SC observed for *Alligator mississippiensis* (irrespective which  $m_x$  model I assumed) is consistent with the observation that the largest reptiles show concave SCs, whereas small and short-lived reptiles have linear SCs (Pianka 1999; Case 2000; Smith & Smith 2006). Indeed, for all  $m_x$  models my results predicted a linear SC for the small-sized tortoises *Trachemys scripta* and *Chrysemys picta* as well as for the mid-sized tortoise *Gopherus berlandieris*. For the small lizard *Xantusia vigilis* and the very large turtle *Caretta caretta* it is likely that the substantial underestimation of their true maximum longevity explains their unexpected convex shaped SCs (Fig. S1A).

For all bird species, modelled SCs were concave, except for *Larus argentatus* and *Turdus migratorius* (Fig. S1B). *Larus argentatus* was the largest bird in my sample and had a convex SC under all  $m_x$  models, whereas that of the similar-sized, but longer-lived *Pandion haliaetus* were always concave (Fig. 3; Table S2D). For *Turdus migratorius*, a linear SC was only found for the  $m_{x,Weibull}$  model, whereas those derived from all other  $m_x$  models were concave. Contrary to all other bird species studied, the raptor *Larus argentatus* matures late compared to its maximum life span (in the middle of its maximum lifespan) and has a low annual fecundity (three eggs; Table S1). This is consistent with a more K-selected life-history strategy in this raptor and with the convex SC calculated for this species. The five songbirds studied and *Vanellus vanellus*, however, become sexually mature in their first or second year of life (maximum longevities are between 7 and 12 years; Table S1) and show a considerably higher fecundity (7 up to 12 eggs; Table S1) than *Larus argentatus*. This indicates a more r-selected life-history strategy and a more concave SC for all six of these bird species. Early reproduction within life also questions the correctness of the  $m_{x,Weibull}$  model yielding a linear SC for *Turdus migratorius*, whereas the  $m_{x,step}$  and  $m_{x,linear}$  model yielded a concave SC is corroborated in small birds (Martin 1995; Pianka 1999). Given that the SC plotted in Erickson *et al.* (2006) was erected from a SAD population, the other raptor (*Pandion haliaetus*) indicates a substantial mortality during the early phase of its life (concave), a broad linear phase in the middle of life, and a short convex phase towards its end. The survivorship function of my model (Eqn 2) is unable to capture such a complex survivorship schedule.

From the literature (Pianka 1999; Case 2000; Smith & Smith 2006), I expected a linear SC for the small, short-lived mammals and a convex SC for the large mammals. The smallest mammals in my sample (*Ovis dalli*, *Phacochoerus aethiopicus* and *Aepyceros melampus*) had moderately concave to slightly convex SCs and the midsized *Equus quagga boehmi* a linear to convex SC depending on the  $m_x$  model used. The SCs of the midsized *Odocoileus virginians* and of the large *Syncerus caffer* were clearly convex. *Homo sapiens* had a convex SC and that calculated for *Loxodonta africana* was convex, too. The SCs modelled for the large *Hippopotamus amphibius* were moderately concave to linear. Thus, all predicted SCs of mammals conform to literature expectations (Fig. 3; Fig. S1), except for *Hippopotamus amphibius*. The life table in Millar (1988) used in my study on the hippo lacks information on survival of individuals of ages less than than four years (Fig. S1) and does not show the high mortalities between birth and one year (45%; Owen-Smith 1992) reported for this species. These high mortalities of young indicate that the true SC of this species is again a composite curve.

#### SCs of the six dinosaurs studied

I next applied my model to the six dinosaurs subject to this study (Erickson *et al.* 2006, 2009, 2010; Woodward *et al.* 2015). Modelling clearly demonstrated that dinosaur bone assemblages were from substantially increasing populations ( $8.070 \leq R_0 \leq 24.924$ ) and that they had not preserved SAD populations. The only exception was seen for *Psittacosaurus lujiatuensis* under the bird model on  $m_{max}$  for which my model yielded a  $R_0$  value comparatively close to one (1.786). For *Psittacosaurus lujiatuensis*, the SC of the SAD population was convex under both the bird and reptile model for all  $m_x$  models corroborating Erickson *et al.* (2009). For all of the other five dinosaurs, SCs calculated for SAD populations were linear to concave, with the reptile model resulting in more concave SCs than the bird model. Linear to concave SCs derived herein contradict fairly convex (tyrannosaurs; Erickson *et al.* 2006, 2010) and sigmoidal-shaped SCs (*Maiasaura peeblesorum*; Woodward *et al.* 2015) published for these dinosaurs before.

When checking for SAD populations, dinosaurian  $\lambda$  values were always smaller under the reptile than under the bird model on  $m_{max}$  (Tables S3, S4), which is consistent with the larger annual egg numbers ( $m_{max}$ ) seen in similar-sized reptiles than in birds and the results of my sensitivity analysis (Fig. 2). Changing the  $m_x$  model for a dinosaur altered modelled  $\lambda$  values less than applying a reptile or a bird model on  $m_{max}$  (Fig. 4). All these observations stress again the need for precise fecundity schedules with which to assess dinosaurian SCs but such information on dinosaur taxa is generally rare or simply not preserved in the fossil record (e.g. number of clutches per year). Except for *Maiasaura peeblesorum*, for none of the six dinosaurs studied herein egg masses or clutches sizes are known and for all including *Maiasaura peeblesorum* the best allometric model on annual egg number is unknown (Werner & Griebeler 2013). On the other hand, at least for inferring dinosaurian ASM from growth curves reliable evidence exists. Histological studies reported medullary bone, a distinct indicator of reproductive maturity, in several dinosaurs. This ephemeral bony tissue forms before ovulation in the marrow cavities of birds as a calcium source for eggshelling. It was described in a single specimen of the tyrannosaur *Tyrannosaurus rex* (Schweitzer *et al.* 2005), in another saurischian dinosaur, *Allosaurus*, and in the iguanodontid *Tenontosaurus* (Lee & Werning 2008). Lee & Werning (2008) showed for these three taxa that ages at reproductive maturity as indicated by medullary bone coincide with ages at which growth acceleration turns into deceleration (inflection point of the growth curve). These authors further concluded a reptile-like reproduction strategy (reproductive maturity occurs while growth continues) and ruled out a bird-like strategy (reproductive maturity occurs after growth has stopped) for the three taxa. They further argued

that the strong correlation in amniotes between relatively early reproduction and high adult mortality (Tinkle *et al.* 1970; Promislow & Harvey 1990, 1991) suggests that all these extinct taxa also experienced a high adult mortality. Thus, the concave SCs that I determined under a reptile model for all dinosaurs add further support to a reptile-like reproduction strategy at least in *Tyrannosaurus rex*. However, some medium and large-sized mammals also start to reproduce before being fully-grown (e.g. female elephants; Owen-Smith 1992) but similar-sized reptiles become sexually mature later than similar-sized mammals (Hallmann & Griebeler 2018) and usually have lower maximum longevities than similar-sized mammals (Western & Ssemakula 1982; Hallmann & Griebeler 2018). Reptiles must thus have higher annual offspring numbers than similar-sized mammals (Werner & Griebeler 2011, 2013) in order to balance deaths by births in a population ( $R_0 = 1$ ). Further, a mammalian aging and reproduction strategy (as suggested by Ricklefs 2007) leading to a convex SC is unlikely in tyrannosaurs as both the reptile and the bird models (Eqns 8, 9) reveal higher annual egg numbers than a mammal model for large similar-sized species (Werner & Griebeler 2011; Hallmann & Griebeler 2018).

Concave to linear SCs obtained for *Maiasaura peeblesorum* under the reptile and bird model are consistent with the high mortality within the first year of life (89.9%) observed by Woodward *et al.* (2015). For this hadrosaur, these authors further suggested that the early high mortality (concave shape) is followed by a period of low mortality (linear to convex shape), the latter eventually ending in senescent attrition (note maximum longevity is not documented in their sample). On the one hand my survivorship function (Eqn 2) is unable to capture the situation of having concave, linear or convex shapes at different phases within an animal's life and thus my model is unable to directly check the conclusion of Woodward *et al.* (2015). The composite curve suggested by these authors is consistent with the comparatively large RMSD values derived from my model (Table S3). On the other hand, my model suggests that the SC erected by these authors was from a substantially increasing population ( $21.223 \leq R_0 \leq 24.704$ ; Table S3) and thus indicates that young individuals are clearly overrepresented in their bone assemblages. This artefact might question whether this hadrosaur really experienced two different phases of mortality at the beginning of its life. A larger maximum longevity than that documented in the bone assemblage would move the SC of *Maiasaura peeblesorum* calculated by my model towards the convex end of the spectrum.

Out of my dinosaur sample, the small ceratopsian *Psittacosaurus lujiatuensis* had clearly convex SCs under the bird model, whereas the SCs from the reptile model were less, but still convex (Fig. 4). For this dinosaur Zhao *et al.* (2013) reported a juvenile-only cluster with clear evidence

of different ages (five 2-year olds and one 3-year old). Authors interpreted it as a close-knit, mixed-age herd either for protection against predators or as putative helpers at the parental nest. The more or less convex SCs inferred from my model indicate low mortalities within the first years of life in *Psittacosaurus lujiatuensis*, which are consistent with both interpretations of this cluster (Zhao *et al.* 2013).

## CONCLUSION

This study presents an age-structured population model to assess age-specific survival and even life-history strategies of dinosaurian taxa when making assumptions about their age-specific fecundities. As information on dinosaurian survivorship and fecundity schedules is scarce, it only makes use of three life-history traits (maximum longevity, age at sexual maturation, maximum annual offspring number), two-parameter family equations on fecundity schedules and a one-parameter family equation on the survival schedule. My sensitivity analysis shows that the accuracy of an inferred SC depends considerably on the model parameter values used and the  $m_x$  model chosen. Bone assemblages of all six dinosaurs revisited herein clearly did not preserve SAD populations (except for *Psittacosaurus* under the bird model on maximum annual offspring number) and were thus inadequate for inferring their SCs. As bone assemblages are unlikely to be from a constant-sized population, the application of my model is a much better approach to assess the position of dinosaurian SCs within the concave to convex spectrum, given that good estimates of model input parameters are available. Fortunately, information on the three life-history traits used by my model is steadily increasing from bone histological studies and the discovery of new fossils. My results strongly question published fairly convex SCs on the four tyrannosaurs (Erickson *et al.* 2006, 2010) and a K-selected life-history strategy with low fecundities suggested for them previously. It provides further evidence of a reptile-like reproduction strategy in *Tyrannosaurus rex* (Lee & Werning 2008) and for a convex SC in *Psittacosaurus lujiatuensis* (Erickson *et al.* 2009). The position of *Maiasaura peeblesorum* within the concave to convex SC spectrum could not be successfully evaluated as its bone assemblage suggests a (sigmoidal) composite SC (Woodward *et al.* 2015).

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## DATA ARCHIVING STATEMENT

Data for this study including all R scripts used for modelling dinosaurs and extant species are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.5mkkwh765>

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## SUPPORTING INFORMATION

Additional Supporting Information can be found online (<https://doi.org/10.1111/pala.12576>):

**Fig. S1.** Modelled survivorship curves of six extant reptiles (A), seven birds (B) and seven mammals (C).

**Table S1.** Modelling results on whether empirical survivorship curves of six extant reptile, seven bird, and seven mammal species are from SAD populations.

**Table S2.** Survivorship curves modelled for SAD populations of studied extant reptiles, birds and mammals.

**Fig. S2.** Modelled survivorship curves of the four tyrannosaurs *Albertosaurus sarcophagus*, *Gorgosaurus libratus*, *Dasplatosaurus torosus*, *Tyrannosaurus rex* (A), and of the ceratopsian *Psittacosaurus lujiatunensis* and the hadrosaur *Maia-saura peeblesorum* (B).

**Table S3.** Modelling results on whether bone assemblage based survivorship curves of the six dinosaurs studied are from SAD populations.

**Table S4.** Survivorship curves modelled for SAD populations of studied six dinosaurs.

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