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Relative growth rates of predator and prey dinosaurs reflect effects of predation

Lisa Noelle Cooper[1,2], **Andrew H. Lee**[3,*], **Mark L. Taper**[4] and **John R. Horner**[5]

[1]*Department of Anatomy, Northeastern Ohio Universities College of Medicine, Rootstown, OH 44272, USA*
[2]*School of Biomedical Sciences, Kent State University, Kent, OH 44242, USA*
[3]*College of Osteopathic Medicine, Ohio University, Athens, OH 45701, USA*
[4]*Department of Ecology, and* [5]*Museum of the Rockies, Montana State University, Bozeman, Montana 59717, USA*

Hadrosaurs grew rapidly, and quantifying their growth is key to understanding life-history interactions between predators and prey during the Late Cretaceous. In this study, we longitudinally sampled a sequence of lines of arrested growth (LAGs) from an essentially full-grown hadrosaur *Hypacrosaurus stebingeri* (MOR 549). Spatial locations of LAGs in the femoral and tibial transverse sections of MOR 549 were measured and circumferences were calculated. For each bone, a time series of circumference data was fitted to several stochastic, discrete growth models. Our results suggest that the femur and the tibia of this specimen of *Hypacrosaurus* probably followed a Gompertz curve and that LAGs reportedly missing from early ontogeny were obscured by perimedullary resorption. In this specimen, death occurred at 13 years and took approximately 10–12 years to reach 95 per cent asymptotic size. The age at growth inflection, which is a proxy for reproductive maturity, occurred at approximately 2–3 years. Comparisons with several small and large predatory theropods reveal that MOR 549 grew faster and matured sooner than they did. These results suggest that *Hypacrosaurus* was able to partly avoid predators by outgrowing them.

Keywords: stochastic growth model; life history; predator–prey interaction; dinosaur

1. INTRODUCTION

Hadrosaurs were large herbivorous dinosaurs that became abundant and diverse during the Late Cretaceous (Horner *et al.* 2004). Part of their success may be attributed to their rapid growth rates; early histological studies of the hadrosaurs *Hypacrosaurus* and *Maiasaura* suggest that they were among the fastest growing dinosaurs (Horner *et al.* 1999, 2000; Erickson *et al.* 2001). Lines of arrested growth (LAGs), which are presumably annual markers of bone growth (Castanet *et al.* 1993), do not appear regularly in those hadrosaur long bones until they are approximately half-grown, and even essentially full-grown ones only show a maximum of eight LAGs. In addition, those bones that are fully grown show tightly spaced peripheral LAGs and reduced tissue vascularity (i.e. external fundamental system (EFS)), which suggest that growth to asymptotic body length (7 m) in *Hypacrosaurus* and *Maiasaura* required a minimum of eight years (Horner *et al.* 1999, 2000).

Only rapid growth rates could have produced such large body size in a relatively short period of time. Initial estimates of bone deposition rates calculated from inter-LAG thicknesses in 'late juveniles' range from 20 to 80 μm d^{-1} (Horner *et al.* 2000; Padian *et al.* 2001), which are comparable to rates found in rapidly growing ratites (Castanet *et al.* 2000) and penguins (de Margerie *et al.* 2004). In addition, early estimates of the accumulation in body mass of *Maiasaura* suggest that, during the fifth year of growth, growth rates reached a maximum of 1042 kg yr^{-1} (Erickson *et al.* 2001). If accurate, the relative mass accumulation increased by 166 per cent

during that time. Among dinosaurs in which mass accumulation has been modelled (Erickson & Tumanova 2000; Erickson *et al.* 2001, 2004; Bybee *et al.* 2006; Lee & Werning 2008), only the much smaller *Shuvuuia* shows a greater relative growth rate (RGR; 201% per year albeit based on only three observations).

These results for hadrosaurs, however, are questionable. Sensitivity of age estimation to methodological bias was demonstrated only recently (Horner & Padian 2004), so an age of 6–8 years for a fully grown *Hypacrosaurus* or *Maiasaura* could be an underestimate. Error from potentially biased age estimates coupled with a paucity of available data (i.e. three observations of *Maiasaura* taken from Horner *et al.* (2000)) produced a biologically unrealistic growth trajectory in which multi-year growth to asymptotic body mass (1500 kg) occurred almost entirely during the final year (Erickson *et al.* 2001). These results warrant a reanalysis of the growth of hadrosaurs.

Here, we analyse the skeletal growth of a hadrosaur, *Hypacrosaurus stebingeri* (Museum of the Rockies: MOR 549). Although bones of this specimen preserve only a partial record of bone growth biased towards late ontogeny, that partial record is unusually long (approx. 6–8 years depending on the bone analysed; figure 1) and terminates with an EFS (Horner *et al.* 1999), which marks a growth asymptote. By longitudinally sampling this record of ontogeny, we can directly assess the temporal sequence of growth and avoid confounding intraspecific variation with variation related to temporal trends (Diggle *et al.* 2002). The method proposed here specifically reconstructs the growth trajectory of a single individual, which is exceptional in the number of LAGs preserved in its long bones, and we make no attempt to address

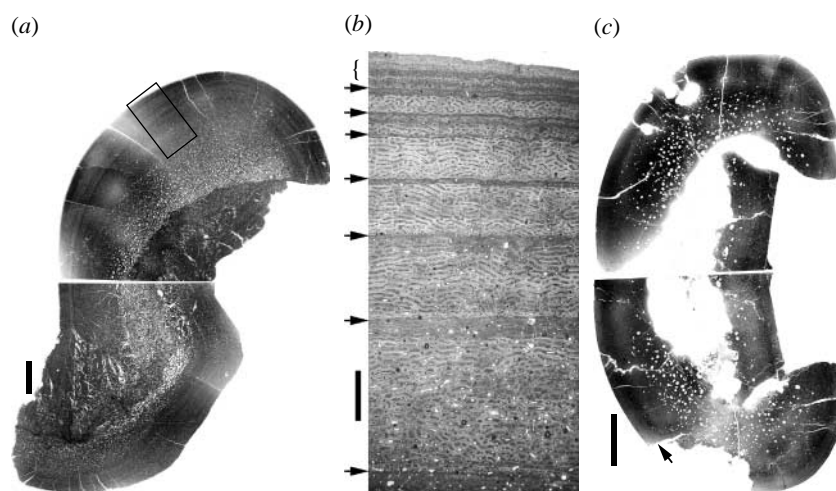* Author for correspondence (alee712@gmail.com).

Figure 1. Histology of the femur of *H. stebingeri*. (*a*) Roughly concentric LAGs in the femoral cortex of MOR 549; the cancellous medulla has obscured the earliest LAGs. (*b*) Details of (*a*) showing all of the preserved LAGs (arrows) in the femur; the bracket marks an EFS or growth asymptote. (*c*) LAG (arrow) in the femur of MOR 355. Scale bars, (*a*,*c*) 10 mm and (*b*) 1 mm.

intraspecific variation in growth. Instead, our goal is to reconstruct the growth trajectory of MOR 549 in order to gain insights into how growth and life-history traits varied between *Hypacrosaurus* and carnivorous dinosaurs during the Late Cretaceous. Life-history theory suggests that prey species should experience rapid growth if juvenile mortality (caused mainly by predation) is high and resources are plentiful (or readily available) (Arendt & Reznick 2005). Because (i) *Hypacrosaurus* was coeval with several carnivorous dinosaurs ranging from small to large theropods (Weishampel *et al.* 2004), and (ii) both juveniles and fully grown individuals were eaten by theropods (Horner 1994; Varricchio 2001; Farlow & Holtz 2002), we predict that *Hypacrosaurus* grew faster and matured sooner than coeval theropods.

2. MATERIAL AND METHODS

(a) *Reconstructing the growth of* Hypacrosaurus

We reanalysed the femoral and tibial mid-diaphyseal transverse sections from the type specimen of *H. stebingeri* (MOR 549), which were reported previously by Horner *et al.* (1999). Those sections preserve seven to eight LAGs. Because each LAG represents the periosteal surface of the bone during a depositional pause in growth, a temporal sequence of LAGs within a single bone provides a high-resolution means of tracking increases in bone circumference throughout ontogeny (Bybee *et al.* 2006). Although the circumference of LAGs can be measured directly using digital macrophotography techniques (Bybee *et al.* 2006), these femoral and tibial transverse sections show some localized deformation. Thus, we used an equation by Ramanujan (1914) to calculate the LAG circumference from the major and minor radii of each LAG. This approach is justified because at mid-diaphysis, (i) the transverse sectional shapes of less deformed femora and tibiae approximate an ellipse (figure 1*c*) and (ii) the LAGs are approximately concentric (figure 1*a*).

For each LAG, the lengths of major and minor radii were calculated by taking the difference between the major or minor radius of the bone and the corresponding distance from the bone perimeter to the LAG (figure 1*b*). These distances were measured directly from the transverse

sections under a microscope using Omnimet Image Analysis System (Buehler, Lake Bluff, IL, USA). To test the accuracy of calculated circumferences of this specimen and account for curf loss during sectioning, we compared the actual mid-diaphyseal circumferences of femora and tibiae of this specimen measured before the specimen was sectioned. Measured and calculated circumferences differed only by 5 per cent, so we increased all calculations of LAG circumferences accordingly. Table 1 lists calculated LAG circumferences for the femur and the tibia.

The earliest portions of a LAG record are often obscured or obliterated by medullary expansion (figure 1*a*,*c*), so an unbiased estimation of age must first involve the reconstruction of any obliterated LAGs. There are several methods to account for these missing LAGs (a process called retrocalculation), and they fall into two major classes: (i) overlapping LAGs from successively larger ontogenetic stages (Chinsamy 1993; Castanet 1994; Erickson *et al.* 2001; Bybee *et al.* 2006) and (ii) using various distances between adjacent LAGs (Horner & Padian 2004; Klein & Sander 2007; Lee & Werning 2008). Here, we propose a third class of retrocalculation that uses regression analysis to determine which growth model best fits a sequence of LAG circumferences within a bone. Thus, the growth model itself reconstructs the destroyed LAGs, and thus the length of time missing from a bone (figure 2).

Sequential LAG circumferences within a single bone are not independent observations, so they were fitted to first-order difference equations that take into account the dependency between successive observations. These difference equations are analogous to the stochastic, discrete-time, process-error models that are used in studies of population growth (Dennis & Taper 1994; Dennis *et al.* 2006). We used several equations including the discrete-time linear model as well as the discrete-time Richards model and three of its special forms. Equations for the linear and Richards models are, respectively,

$$C_{t+1} = C_t \times \exp(K/C_t + \varepsilon_t) \tag{2.1}$$

and

$$C_{t+1} = C_t \times \exp(A^{1-m} \times K/(1-m) \times C_t^{m-1} - K/(1-m) + \varepsilon_t), \tag{2.2}$$

Table 1. Dimensions of LAGs and their estimated ages for the femur and the tibia of MOR 549.

element	LAG circumference (mm)	estimated age[a] (years)	estimated age[b] (years)	estimated age[c] (years)	estimated age[d] (years)	estimated age[e] (years)	best estimated age (years)
femur	336	32	5	7	17	7	7
	359	33	6	8	18	8	8
	373	34	7	9	19	9	9
	383	35	8	10	20	10	10
	390	36	9	11	21	11	11
	393	37	10	12	22	12	12
	395	38	11	13	23	13	13
parameters		2	3	3	3	4	
ΔAIC_c		20	0.5	0	4	30	
tibia	236	16	4	6	13	11	6
	269	17	5	7	14	12	7
	295	18	6	8	15	13	8
	312	19	7	9	16	14	9
	331	20	8	10	17	15	10
	336	21	9	11	18	16	11
	341	22	10	12	19	17	12
	342	23	11	13	20	18	13
parameters		2	3	3	3	4	
ΔAIC_c		15	4	2	0	14	

[a] Linear.
[b] Monomolecular.
[c] Gompertz.
[d] Logistic.
[e] Richards.

where C_t is the circumference at time t; C_{t+1} is the circumference at time $t+1$; A is the asymptotic bone circumference; K is the instantaneous RGR; and ε_t is the process error that is distributed normally with a mean of 0 and a variance of σ^2. The m parameter controls the shape of the sigmoidal curve, and the Richards model reduces to length-based forms of the monomolecular, Gompertz and logistic models when m equals 0, approximately 1 and 4, respectively. These values of m differ from those of other studies (Seber & Wild 1989; Lei & Zhang 2004) because we modelled growth in circumference (a measure of length) as opposed to growth in mass (a measure of length^3). Custom scripts were written in R v. 2.6.2 to estimate parameter values using least-squares regression and generate parametric bootstrapped 95% confidence intervals (CIs).

Models differ in their complexity and how well they fit the data, so we assessed evidential support for each model using the small sample form of Akaike's information criterion (AIC_c; Hurvich & Tsai 1989) and Schwarz's information criterion (SIC; Schwarz 1978). Both methods produced nearly identical information criterion difference values (ΔAIC_c and ΔSIC), so only ΔAIC_c values are reported (table 1). Generally, a stronger model is statistically distinguishable from a weaker one if the difference in their ΔAIC_c is at least 3, which is equivalent to a realized p-value of 0.051 (Taper 2004). When we were unable to distinguish between models (e.g. linear versus Gompertz), we selected the more biologically informative model of the pair (e.g. Gompertz).

To estimate the age at death, equations (2.1) and (2.2) were integrated with respect to time, resulting in the following equations (Lei & Zhang 2004):

$$C(t) = a + Kt \qquad (2.3)$$

and

$$C(t) = A\left[1 - \left(1 - \frac{a^{1-m}}{A^{1-m}}\right)\exp(-Kt)\right]^{1/(1-m)}, \qquad (2.4)$$

where a is the femoral and tibial circumference at hatching (31 and 25 mm, respectively).

(b) Interspecific comparisons of life-history traits

This specimen of *Hypacrosaurus* was coeval with several theropods from the Two Medicine Formation including the maniraptoran *Troodon formosus* and the tyrannosaurids *Albertosaurus* sp., *Gorgosaurus* sp. and *Daspletosaurus torosus* (Weishampel *et al.* 2004). To act as a proxy for the Two Medicine *Albertosaurus*, we selected the growth data of *Albertosaurus sarcophagus* from the Horseshoe Canyon Formation (Erickson *et al.* 2004, 2006). Those data can be readily detransformed into raw circumferential measures of the femur, which tend to reflect trends in the overall growth of the body (Owens *et al.* 1993). Although the growth data of the larger *Daspletosaurus* (Erickson *et al.* 2004) can also be readily detransformed into femoral circumference, it is not meaningful to fit three observations to a sigmoidal growth trajectory. Instead, because growth rate shows a positive correlation with body size in tyrannosaurids (Erickson *et al.* 2004), we used the growth data ($n=8$) of the much larger and geologically younger *Tyrannosaurus rex* (Erickson *et al.* 2004; Horner & Padian 2004) as an upper-limit proxy for the growth of *Daspletosaurus*.

The original growth data of *Albertosaurus* and *Tyrannosaurus* consist of independent observations (i.e. cross-sectional sampling of terminal age and circumference data from several individuals), so we performed nonlinear regressions using the integrated growth equations (equations (2.3) and (2.4)), which are observation-error models. We reparametrized equation (2.4) to calculate the age of growth inflection (Seber & Wild 1989), which coincides generally with sexual maturity in amniotes (Brody 1964),

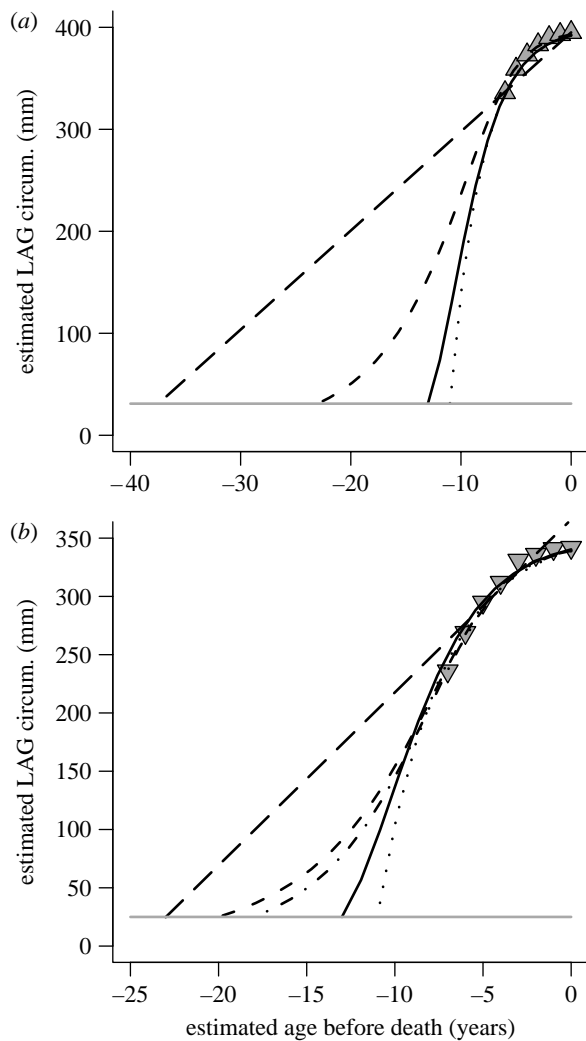$$C(t) = A[1 + (m-1)\exp(-K(t-I))]^{1/(1-m)} + \varepsilon_t, \qquad (2.5)$$

Figure 2. Models used to retrocalculate the age at death of MOR 549. (*a*) Femur; the Richards model is virtually identical to the Gompertz model and is not presented for clarity. (*b*) Tibia. Long dashed line, linear; short dashed line, logistic; dot-dashed line, Richards; solid line, Gompertz; dotted line, monomolecular; grey line neonatal circumference.

where C is the femoral circumference; t is the estimated age; A is the asymptotic circumference; m is the shape parameter (see §2*a*); K is the instantaneous RGR; I is the age at growth inflection; and ε_t is the observation error in C that is distributed normally with a mean of 0 and a variance of σ^2. To reduce any unevenness in variance (heteroscedascity), growth data were weighted with a power function if the improvement was statistically significant.

Interspecific comparisons of life history were assessed using three traits: age at growth inflection (I); RGR; and time required to grow to 95 per cent asymptotic size ($t_{95\%}$). These three traits were either extracted directly from parameter estimates (equation (2.5)) or calculated using the following equations:

$$I = \frac{1}{K}\ln\left[\left(\frac{1}{m-1}\right)\left(\frac{a}{A}\right)^{1-m} - 1\right], \qquad (2.6)$$

$$\mathrm{RGR} = K/m, \qquad (2.7)$$
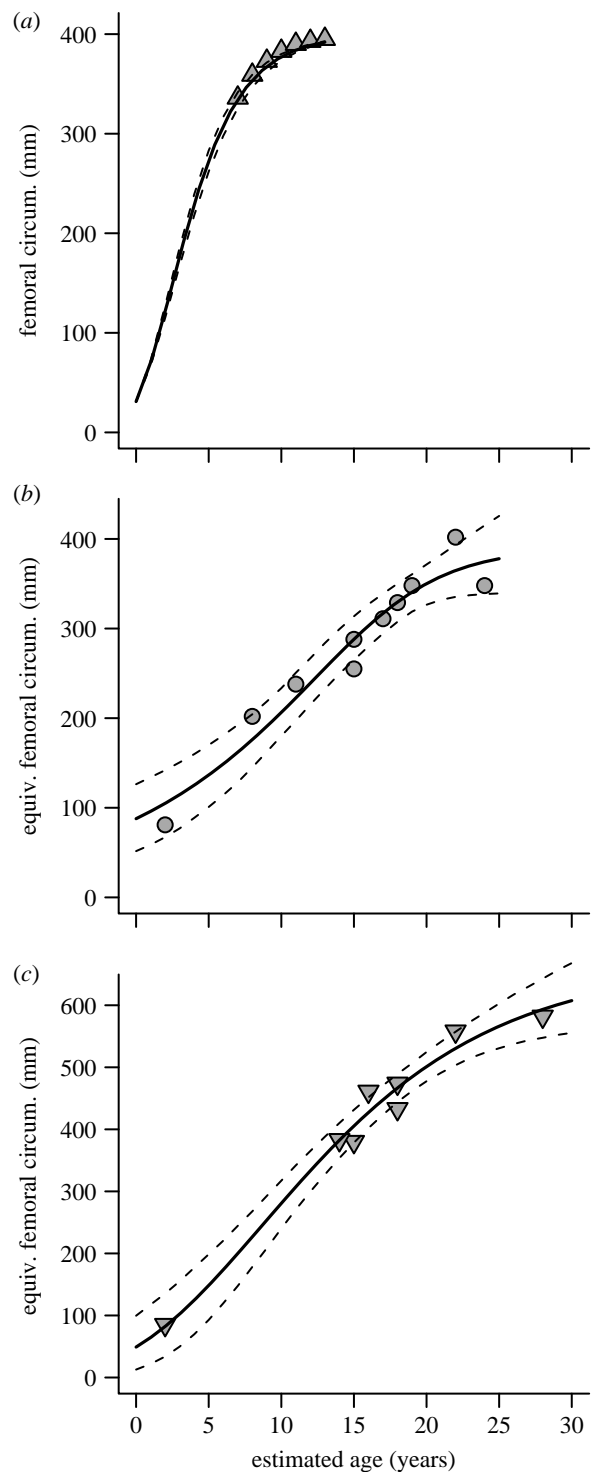
$$t_{95\%} = I + 3/K. \qquad (2.8)$$

Figure 3. Femoral growth trajectories. (*a*) *Hypacrosaurus*. (*b*) *Albertosaurus*. (*c*) *Tyrannosaurus*. Dashed lines are 95% confidence bands.

Parametric bootstrapping (*sensu* Dennis & Taper (1994)) was performed to propagate parameter uncertainty into calculations of life-history traits and generate 95% CIs. Comparisons of life-history traits were performed using the two-tailed *t*-test.

3. RESULTS
(a) *Age estimate of* Hypacrosaurus
Age estimates for the femur and the tibia of MOR 549 span a similar range (table 1). Femoral age estimates range from 11 to 38 years. Among the range of estimates, an

age of 13 years (Gompertz model) is the best supported one, although an age of 11 years (monomolecular model) has nearly as much support ($\Delta AIC_c = 0.5$). Furthermore, both of these femoral age estimates have overwhelmingly more support than an age of 38 years (linear model; $\Delta AIC_c = 20$). The data from the tibia show a range of age from 11 to 23 years. The best supported age of the tibia is 20 years (logistic model). However, an age of 13 years (Gompertz model) has nearly as much support ($\Delta AIC_c = 2$). That femoral circumferential growth follows a Gompertz model whereas tibial circumferential growth follows a logistic model is not surprising because those bones differ in shape. However, they should reveal the same estimate age. Thus, we selected the Gompertz model to represent the growth of *Hypacrosaurus* because it is the best supported model that gives a concordance in estimated age (13 years) between the femur and the tibia (figure 3a).

(b) *Life-history traits of* Hypacrosaurus

The transition from growth acceleration to deceleration (i.e. the growth inflection point) occurred for the femur of *Hypacrosaurus* at 2.5 years (CI 2.3–2.6) and in the tibia at 2.8 years (CI 2.5–3.3) after hatching. At these ages, the femur and the tibia experienced their maximum circumferential RGRs of 38 per cent per yr (CI 36–40) and 34 per cent per yr (CI 30–39), respectively. In absolute terms, maximum circumferential growth rates for the femur and the tibia were 56 mm yr^{-1} (CI 53–59) and 44 mm yr^{-1} (CI 39–49), respectively. These absolute circumferential growth rates suggest that, at their maximum, the femur and the tibia deposited new periosteal bone tissue at approximate rates of 24 and 19 µm d^{-1}, respectively. After the growth inflection, circumferential growth rates slowed progressively, and 95 per cent asymptotic size for the femur and the tibia occurred at ages of 10 years (CI 10–11) and 12 years (CI 10–13), respectively. Although circumferential growth continued until death for another 3 years in the femur and 1 year in the tibia, circumferential accumulation was less than 5 per cent during that period. This suggests that this specimen of *Hypacrosaurus* was effectively fully grown at death.

(c) *Life-history traits of* Albertosaurus *and* Tyrannosaurus

Linear models are only marginally better supported than sigmoidal models when describing the femoral circumferential growth of *Albertosaurus* and *Tyrannosaurus*. For example, a linear model is virtually indistinguishable from a logistic model ($\Delta AIC_c = 0.1$) when describing *Albertosaurus* growth data or from a Gompertz model when describing *Tyrannosaurus* growth data ($\Delta AIC_c = 0.9$). These sigmoidal models show nearly as much support as linear models and allow the inference of far more life-history traits, so we selected them to represent the femoral circumferential growth of *Albertosaurus* (figure 3b) and *Tyrannosaurus* (figure 3c).

Growth inflections in *Albertosaurus* and *Tyrannosaurus* occurred at ages of 12 years (CI 10–18) and 9 years (CI 7–12), respectively. These ages precede slightly, albeit insignificantly, ages at inflection based on estimated body mass (Erickson *et al.* 2004; Lee & Werning 2008). At inflection, the femoral RGR was 7 per cent per yr

(CI 4–10) for *Albertosaurus* and 11 per cent per yr (CI 7–16) for *Tyrannosaurus*. Absolute femoral circumferential growth rates for *Albertosaurus* and *Tyrannosaurus* were 16 mm yr^{-1} (CI 12–23) and 27 mm yr^{-1} (CI 22–35), respectively. These rates suggest that radial deposition of periosteal bone tissue in femora of *Albertosaurus* and *Tyrannosaurus* was approximately 7 and 12 µm d^{-1}, respectively. Growth to 95 per cent femoral circumference in *Albertosaurus* and *Tyrannosaurus* took 23 years (CI 18–34) and 36 years (CI 27–51), respectively.

4. DISCUSSION AND CONCLUSIONS

(a) *Life-history comparisons between* Hypacrosaurus *and Late Cretaceous predators*

The growth and life history of *Hypacrosaurus* differ strikingly from those of representative coeval theropods. A biologically and statistically justified reconstruction of femoral circumferential growth for MOR 549 suggests an age at death of 13 years. This age estimate is 5 years older than the previously published minimum estimate, which did not account for the number of LAGs lost to perimedullary resorption (Horner *et al.* 1999). By contrast, by an age of 13 years, the similarly sized theropod *Albertosaurus* was only half-grown (figure 3). Furthermore, femoral growth rates reached their maximum significantly earlier in *Hypacrosaurus* than in either *Albertosaurus* or even far larger tyrannosaurids such as *Tyrannosaurus* ($p < 0.001$). When standardized for differences in size and shape of the growth trajectory (see equation (2.7)), the femoral circumference of *Hypacrosaurus* still increased three to five times faster than either theropod ($p < 0.001$). Whether *Hypacrosaurus* also grew relatively faster than small coeval theropods such as *Troodon* cannot currently be addressed with confidence because published reconstructions do not present CIs or the raw data to rerun the original analysis (Erickson *et al.* 2007). However, if the data and reconstructions are robust and CIs are narrow, then *Hypacrosaurus* might have grown twice as fast as *Troodon* when accounting for differences in size and growth trajectories. That *Hypacrosaurus* outpaced the growth of small to large coeval and predatory theropods is consistent with expectations from life-history theory, which suggests that growth exceeding species-specific critical size reduces the risk of mortality (Arendt & Reznick 2005). It may be that *Hypacrosaurus* grew faster than its predators to quickly attain a defensive size refuge.

(b) *Longitudinal sampling improves growth trajectory reconstruction*

Our growth model of MOR 549 predicts that six LAGs were lost to medullary expansion and osteonal remodelling. To test the model, we compared the predicted circumferences of these LAGs with those in a smaller (and presumably younger) *Hypacrosaurus* femur (MOR 355; figure 1c). MOR 355 has an approximate mid-diaphyseal circumference of 213 mm. Given a specimen of this size, our model predicts three deposited LAGs, whose circumferences are 62, 125 and 194 mm sequentially. The two smaller predicted LAG circumferences fall within the medullary space that has an approximate circumference of 127 mm. However, the single LAG preserved in MOR 355 is located approximately 1 mm deep to the

periosteal surface (figure 1c) and has a circumference of 207 mm. That the observed LAG circumference is within 6 per cent of the predicted value and that MOR 355 shows none that are larger suggest tentative support for the growth reconstruction of MOR 549 and its general application for the species.

Growth rates change during ontogeny, so sigmoidal curves are appropriate as descriptions of growth. However, the traditional cross-sectional sampling of bones from different individuals is insufficient to resolve subtle changes in growth rate. Resolution of these subtle changes is important if the goal is to infer biologically important events from growth data such as the ages at growth inflection and growth completion. For example, the cross-sectional dataset of *Tyrannosaurus* shows a weak trend towards an upper asymptote, although the oldest specimen does shows an EFS, which is histological evidence of a growth asymptote. However, because the dataset reports only the terminal ages and sizes of individuals, a biologically informative Gompertz model is statistically indistinguishable from a simpler but less informative linear one. Had the dataset included an annual progression of LAG circumferences towards the upper asymptote, the constraint of a Gompertz growth trajectory would have been certainly stronger. Thus, reconstructions of growth trajectories benefit from a longitudinal data sampling approach (e.g. Bybee *et al.* 2006; Erickson *et al.* 2007).

(c) *Sexual maturity of* Hypacrosaurus

Growth spanning several years coincides with an early onset of reproductive maturity (Lee & Werning 2008). Although this suggests that *Hypacrosaurus* probably became reproductively mature while still growing, there is no independent evidence of that maturity (i.e. brooding: Erickson *et al.* 2007; or medullary bone: Lee & Werning 2008). In the absence of that evidence, recent studies have suggested that the age of inflection, at which point growth rates just begin to slow, reflects the onset of maturity (Erickson *et al.* 2007; Lee & Werning 2008). If so, *Hypacrosaurus* became mature at an age of 2–3 years. At this age, individuals were already of moderate size (approx. 40% asymptotic femoral circumference) and had a mean femoral length and circumference of 450 and 195 mm, respectively. Together with RGRs exceeding those of coeval small and large predators, early reproductive maturity would have increased lifetime reproductive success of *Hypacrosaurus*.

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