Trends in embryonic and ontogenetic growth metabolisms in nonavian dinosaurs and extant birds, mammals, and crocodylians with implications for dinosaur egg incubation

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The embryonic metabolism of the saurischian dinosaur *Troodon formosus* and the ornithischian dinosaurs *Protoceratops andrewsi* and *Hypacrosaurus stebingeri* have been determined by using a mass growth model based on conservation of energy and found to be very similar. Embryonic and ontogenetic growth metabolisms are also evaluated for extant altricial birds, precocial birds, mammals, and crocodylians to examine for trends in the different groups of animals and to provide a context for interpreting our results for nonavian dinosaurs. This analysis reveals that the embryonic metabolisms of these nonavian dinosaurs were closer to the range observed in extant crocodylians than extant birds. The embryonic metabolisms of nonavian dinosaurs were in the range observed for extant mammals of similar masses. The measured embryonic metabolic rates for these three nonavian dinosaurs are then used to calculate the incubation times for eggs of 22 nonavian dinosaurs from both Saurischia and Ornithischia. The calculated incubation times vary from about 50 days for *Archaeopteryx lithographica* to about 150 days for *Alamosaurus sanjuanensis*.

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I. INTRODUCTION

Varricchio *et al.* [1] have recently published the first direct measurement of the incubation time of a nonavian theropod dinosaur egg by studying the daily growth of a tooth in a close-to-hatching fossilized embryo of *Troodon formosus*. They found that the tooth had developed for 39 days. Due to the fact that nonavian dinosaurs, extant crocodylians, and extant birds are all archosaurs, Varricchio *et al.* assumed that nonavian dinosaurs established their functional dentition at the same point in embryonic development as modern crocodylians (47% of the incubation time) and determined the incubation time of *T. formosus* to be 74 days. They report that this incubation time is intermediate between the avian and reptilian values (about 44 and 107 days, respectively) based on egg size. Varricchio *et al.* suggest that *T. formosus* attained this accelerated incubation time by brooding their eggs. In earlier work, Varricchio and coworkers [2,3] reported evidence (based on a trace nest with intact eggs) that *T. formosus* brooded their eggs. The eggs of *T. formosus* have been observed to have low porosity [4]. In extant birds, low porosity is found in the eggs of brooding species [5,6]. In their 2018 work, Varricchio *et al.* provide evidence that *T. formosus* brooded their partially buried eggs [1], a practice which would be intermediate between the buried condition of eggs with nest guarding of extant crocodylian species and the brooding of unburied eggs of extant birds. Additional evidence of brooding, including contact incubation, has been reported for *Troodon* as well as the related theropods *Citipati, Deinonychus, Oviraptor*, and *Nemegtomaia* [7–13].

Deeming and coworkers have cast doubt on the hypothesis of contact incubation by theropod dinosaurs [14–17]. In related work, Deeming and Mayr have recently suggested that the pelvic morphology of early Mesozoic birds implies that they were too heavy for contact incubation [18]. Since the vast majority of nonavian dinosaurs were heavier than any bird, their paper questions the suggestion that dinosaurs were able to contact incubate their eggs, with the possible exception of the smallest dinosaurs.

A number of attributes related to avian reproduction have been observed in extinct nonavian dinosaurs [19], including asymmetric eggs [2,20,21], egg shell structure [22,23], and medullary bone [24]. Eggs of extant birds share a number of physical properties, including a hard calcitic shell with a double layer structure, with oviraptorosaurs and troodontids [1]. The eggs of troodontids also share a third external shell layer and more symmetrical eggs with extant birds [1].

The attribution of a number of features of avian reproduction to nonavian dinosaurs as well as the fact that Varricchio *et al.* [1] determined that the incubation time of *T. formosus* is intermediate between the predicted incubation times of extant birds and extant reptiles with eggs of the same mass [25] calls into question the use of extant reptilian embryonic dental development for nonavian dinosaurs. Embryonic development in extant birds is very relevant to the study of embryonic development in extinct dinosaurs since extant birds are living dinosaurs [26,27]. Unfortunately, their lack of teeth means that such data do not exist for extant birds. It is possible that the embryonic dental development of dinosaurs was different than what is observed in extant crocodylians. Consequently, estimating an incubation time for dinosaurs using the crocodylian result might not be accurate. It is also possible that saurischian dinosaurs had a different dental development than ornithischian dinosaurs.

The incubation times of extant reptiles are longer than observed in extant birds [25,28]. Twelve extant members of

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Crocodylia have incubation times ranging between 68 and 99 days [29–39]. The ostrich, *Struthio camelus*, and the emporer penguin, *Aptenodytes fosteri*, have incubation times of 45 and 62 days, respectively [40–42]. The ostrich has the largest egg of any extant bird.

Very long incubation times (ranging from 98 to 272 days) are present in species of *Varanus* [43–51]. The largest species (*Varanus komodoensis*, the Komodo dragon) has an adult mass of about 150 kg and an incubation time of about 225 days [51].

Erickson *et al.* [52] reported the first direct measure of the incubation time of any nonavian dinosaur egg: 83 and 171 days for the ornithischian dinosaurs *Protoceratops andrewsi* and *Hypacrosaurus stebingeri*, respectively. These relatively long incubation times suggested that the extant sister taxon Crocodylia is a better model for embryonic development in ornithischian nonavian dinosaurs than extant birds.

Whether or not these ornithischian incubation times observed by Erickson *et al.* [52] are relevant for the dinosaurs of Saurischia is unclear. The split between Ornithischia and Saurischia is believed to have happened between about 228 and 216.5 million years ago (Ma) [53]. Several lines of evidence suggest that postcranial pneumaticity and air sac lung function were primitive for Saurischia [54,55]. These features are associated with a unidirectional breathing system which is highly efficient at extracting oxygen from air, permitting the possibility of a higher metabolism. Postcranial pneumaticity is not observed in any ornithischians. These results suggest that the metabolism of saurischians might have been different than ornithischians. It should also be noted that extant birds evolved from the theropod clade Paraves. The fact that birds (members of Avialae) first appeared about 165 Ma shows that at least some saurischians had elevated metabolisms perhaps as early as the Middle Jurassic [56,57].

Colonial nesting by dinosaurs has been suggested for the ornithischian dinosaur *Maiasaura* [58] and for the sauropod dinosaur *Saltasaurus* [59–61]. Such colonies in extant birds have shown that these structures provide defense against egg predation since multiple adults are surveying the surroundings at all times. However, nesting colonies have the disadvantage that they cannot be hidden and the adults are confined to the same area during incubation to guard the eggs, and, potentially, to care for the young once they have hatched. While the high mobility of volant birds permit them to travel far in a daily search for food, dinosaurs could not roam large distances without leaving the nesting colony for a long time and had to obtain their sustenance from the surrounding area. This would have been more of an issue for colonies of large species, particularly the sauropods. A high embryonic metabolism for large species of dinosaurs would have been beneficial since that would mean a relatively short incubation time.

The time that the adults were limited to the area of the nesting colony might have exceeded the incubation time in some dinosaurs. Horner [58] has suggested that the young of *Maiasaura peeblesorum* remained in their nests for several months after hatching and were fed by the parents bringing food to the nest.

Nests of *Troodon formosus* show no evidence of trampling of the egg shells nor baby skeletons in the nests, suggesting that the babies were precocial and mobile very shortly after hatching [62,63]. The knee of newly hatched *T. formosus* were observed to be well-formed and capable of supporting full motion [63]. These results imply that *Troodon formosus* left the nest shortly after hatching [62–64].

It should be noted that parents in some extant species fast for extended periods of time while involved in reproduction. A pregnant female of the ovoviviparous species green anaconda (*Eunectex murinus*) does not eat during her seven-month pregnancy [65]. The male emporer penguin (*Aptenodytes forsteri*) does not eat for four months during reproduction [42]. The males of this species incubate the single egg produced by their mates by holding the egg on their feet and covering it with a skin flap. They huddle together during the fierce winter storms of Antarctica. If the adults of some of the dinosaur species that used colonial nesting fasted during reproduction, then the surrounding environment would not have been under such a severe strain.

Modern crocodylians and the animals of *Varanus* do not lay eggs in nesting colonies, though some species guard their nest. *Varanus* hide their individual egg clutches which lowers the probability of egg predation.

The incubation time of an egg is determined by the mass of the newly hatched animal and its embryonic metabolism. In an earlier work [66], a general model for the calculation of the incubation time of any egg based on conservation of energy was developed. Lee [67] used this model with the measured incubation times of *Protoceratops andrewsi* and *Hypacrosaurus stebingeri* [52] to evaluate the embryonic metabolism of these ornithischian dinosaurs.

In this paper, the model of Ref. [67] is used to determine the embryonic metabolic rates of the theropod *Troodon formosus* from the data of Varricchio *et al.* [1], and a reanalysis of the data for the ornithischian dinosaurs *Protoceratops andrewsi* and *Hypacrosaurus stebingeri* [52] is performed. This model [66–68] can determine the average metabolic rate of an organism from its growth data. This determination can be made for either the embryonic growth or ontogenetic growth to determine the average metabolic rate in that period of growth (lasting months for embryonic growth and months to years to decades for ontogenetic growth). For clarity, I will call this metabolism the growth metabolic rate (GMR). Since the GMR averages over the growth of the animal, the measured metabolism corresponds more closely to the field metabolic rate (FMR) than the basal or standard metabolic rates (BMR and SMR, respectively), both of which are measured under controlled conditions of temperature with restricted physical activity.

The FMR is measured by injecting doubly labeled water (with both deuterium and oxygen-18) into an animal in the field. The deuterium is lost only via body water loss by the animal while the oxygen-18 leaves the body in both carbon dioxide (which results from metabolism) and body water. Animals in such studies are recaptured some time later (typically, 1–14 days later) to take the appropriate measurements which yield the field metabolic rate averaged over the period of the measurements.

During FMR measurements, the animals are living in their natural environment and experience a variety of circumstances involving variable temperatures and interactions with other animals. Such changes cause the FMR to be significantly larger than the BMR and SMR. Yodzis and Innes [69], Brose

et al. [70], and Moya-Larano *et al.* [71] have reported that the FMR can be up to three times the BMR. Costa [72] has reported FMR values which are nearly 6 times larger than BMR values for foraging otariids and the bottlenose dolphin.

FMR results for extant bird, mammals and reptiles have been summarized by Nagy *et al.* [73]. Most FMR measurements of birds and mammals are performed on adult specimens who are no longer growing. GMR measurements, by definition, probe the metabolism of the animal during its growth. The necessity of adding new cells during their growth increases their metabolism. Consequently, GMR measurements are expected to yield higher metabolic rates than FMR experiments, particularly for rapidly growing animals.

Diurnal and seasonal temperature fluctuations affect the metabolism and growth of ectothermic animals. In experiments in Louisiana, Chabreck [74] found that the daily temperature variation inside nests of *Alligator mississippiensis* is only 1.2°C while the ambient air had temperature variations of 9.3°C. Consequently, variations in the embryonic metabolism due to changes in temperatures are expected to be less than variations in the ontogenetic growth metabolism. Chabreck also found that nest temperatures averaged 1.4°C warmer than air temperatures. The elevated nest temperature was attributed to the decay of the plant material used in the construction of the nest. The suppression of convective air currents by the nest material would have also contributed to the elevated nest temperature.

In experiments on *Crocodylus porosus* animals with masses between 0.180 and 6.20 kg, Grigg determined that their rate of consumption of oxygen per gram of body mass increased by a factor of 3.5 when the body temperature of the animals was increased from 20 to 33°C [75].

Grigg *et al.* [76] have studied the body temperatures of eleven captive specimens of *Crocodylus porosus* (with masses between 32 and 1010 kg) in a naturalistic setting. Smaller animals had larger variations in body temperature than bigger animals. The daily variations were about 3.5°C for the 32 kg animal and about 1.4°C for the 1010 kg animal. Overall the body temperatures ranged from 25.1 to 28.7°C in the winter and from 28.4 to 33.6°C in the summer.

Seebacher and Grigg [77] studied the body temperature of specimens of *Crododylus johnstoni* (with masses up to about 20 kg) and found that the animals displayed two main patterns of behavior involving being either on land or in the water. The midpoint of the distribution of body temperatures for the animals varied from 29 to 33°C.

The ontogenetic growth data for crocodylians used in this paper come from capture and release measurements. Most of the populations are wild and growth in such populations can be slowed due to a lack of food availability [78]. Social factors are important among crocodylians. Dominant animals displace subordinates from basking sites, limiting their ability to reach the preferred body temperature range [77,79]. These factors lower their growth rate and average metabolism.

In their pioneering work on metabolism, Kleiber [80] and Brody [81] found that the overall metabolic rate of an animal is not directly proportional to its mass. They showed that the organismal metabolic rate, B, for ontogenetic growth in extant animals is related to its mass, M, via a power relationship:

$$B = B_o M^{\alpha}, \tag{1}$$

where B_o is the metabolic prefactor (units of W/kg^{α}) and they reported $\alpha = 3/4$. The fact that α is less than one means that large animals will have a slower metabolism per unit mass than small animals. This size effect on the metabolism can be removed by studying B_o rather than B.

Many studies of the value of α have been published. Heusner [82] found α to be 2/3. However, the mass ranges of his groupings of animals were limited which decreases the reliability to extrapolate his results to larger mass ranges. Nagy *et al.* [73] surveyed the literature of measurements using doubly labeled water to yield the FMR of wild vertebrate animals, including mammals, birds and reptiles. The largest mass of their animals was 100 kg. They determined α to be 0.77 $\pm$ 0.02 for eutherian (placental) mammals, 0.68 $\pm$ 0.02 for birds and 0.89 $\pm$ 0.03 for reptiles. In a study of the standard metabolic rate, White *et al.* [83] included fish, amphibians, reptiles, birds, and mammals, again with masses up to 100 kg. They report α to be 0.68 $\pm$ 0.01 for mammals, 0.64 $\pm$ 0.03 for birds, and 0.76 $\pm$ 0.04 for reptiles. White and coworkers [84] performed a phylogenetically informed analysis of the basal metabolic rate in mammals [84]. Depending on the phylogenetic analysis used, they found that α can vary between about 0.68 and 0.74. Analyzing their data for different masses, they found that α was 0.69 $\pm$ 0.04 for small mammals and 0.76 $\pm$ 0.04 for large mammals. Hayssen and Lacy studied different orders within Mammalia and found variations in α with 0.70 being the average value [85]. McKechnie *et al.* [86] measured the basal metabolic rate in birds and found that α is 0.670 for captive-raised bird and 0.744 for wild caught birds, suggesting a phenotypic dependence for α. Using theoretical arguments about the fractal geometry of the arterial system, West and coworkers have argued that α is 3/4 [87,88]. Dodds *et al.* [89] also used theoretical arguments to argue that $\alpha = 2/3$. Seymour *et al.* [90] have measured the standard metabolic rate in *Crocodylus porsosus* for animals with masses between 0.19 and 389 kg and found that $\alpha = 0.829 \pm 0.013$ (SE). Lee has analyzed the embryonic growth of extant birds and crocodylians using both 3/4 and 2/3 for α and found that $\alpha = 3/4$ yields a superior fit to the experimental data for embryonic growth [66].

The closest extant relatives to nonavian dinosaurs are birds and crocodylians. The reported range of α for these groups of animals is from 0.64 to 0.83. I have considered $\alpha =$ 0.67, 0.75 and 0.83 [66–68] and found that, though the exact results change with α, the trends are remain the same. Because nonavian dinosaurs are now extinct, it is not possible to make a direct determination of the best value of α to use for them. Consequently, I use the intermediate value of $\alpha = 3/4$ for my analysis.

The results for the theropod *Troodon formosus* and for the ornithischian *Protoceratops andrewsi* and *Hypacrosaurus stebingeri* are compared to the embryonic metabolic rates of extant birds, mammals and crocodylians. Comparisons are also made with the ontogenetic growth metabolic rates of nonavian dinosaurs, extant birds, mammals and crocodylians. Modern birds and mammals are endothermic while modern

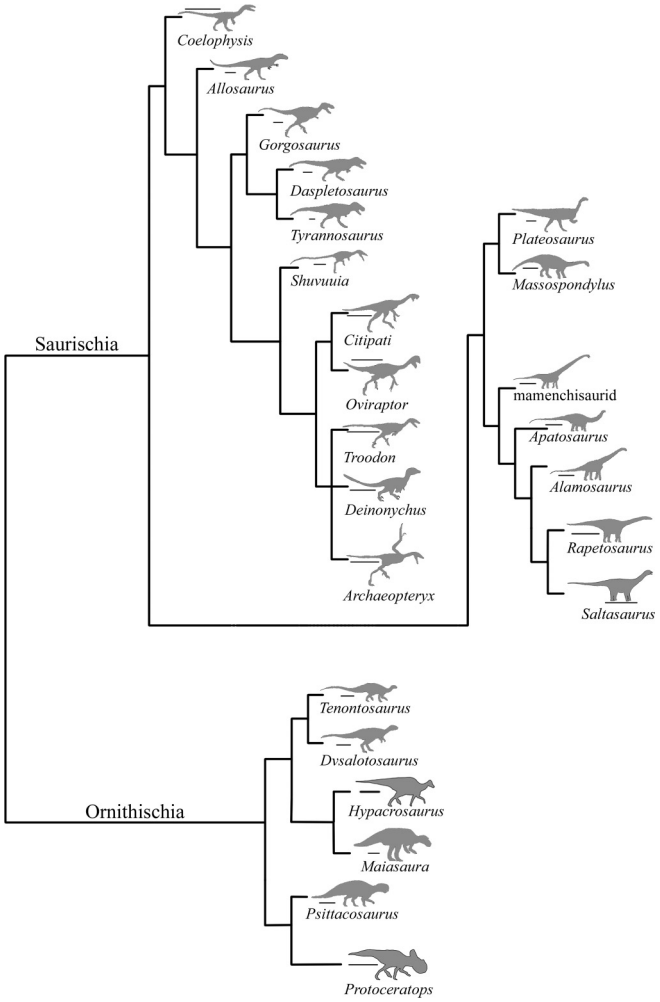

FIG. 1. Cladogram of the dinosaurs of this study.

reptiles are ectothermic. Examining the relationship of embryonic and ontogenetic growth metabolisms for these groups of extant animals provides a context for the interpretation of the results for nonavian dinosaurs.

The observed embryonic metabolism for dinosaurs is then used to calculate the incubation times of 22 nonavian dinosaurs. These dinosaurs include animals from Theropoda, Prosauropoda, Sauropodomorpha, Ornithopoda, and Ceratopsia and come from both the Saurischia and Ornithischia branches of Dinosauria, as shown in the cladogram of Fig. 1 [53,91–102].

Baron *et al.* have recently suggested that Dinosauria is more properly described by three branches: newly defined Saurischia, Ornithischia, and Theropoda [103] rather than the previously defined Saurischia and Ornithischia. If this hypothesis gains wide acceptance, then the results reported here will apply to the newly defined Theropoda and Ornithischia but not the newly defined Saurischia.

II. MODEL

Grady *et al.* [104] and Lee [68] developed models of the mass growth of animals based on conservation of energy to evaluate the metabolism of dinosaurs. Lee [66] extended that model to the growth of embryos. In this approach, the total metabolism, B, of the animal during growth is assumed to provide the necessary power to its cells plus the power needed to create new cells:

$$B = N_c B_c + E_c \frac{dN_c}{dt}. \tag{2}$$

B_c and E_c are the cellular metabolism of an average cell and the energy required to create an average cell, respectively, while N_c is the number of cells. The first term on the right-hand side of Eq. (2) is the metabolism necessary to maintain the living cells while the second term is the metabolism used to grow new cells.

E_c and B_c are assumed to remain unchanged throughout the growth phase. Furthermore, the mass of an average cell, m_c, is assumed to be the same for all animals and to remain constant throughout growth. Bianconi *et al.* [105] determined the number of cells in a 70.0 kg human to be $(3.72 \pm 0.81) \times 10^{13}$, yielding $m_c = (1.88 \pm 0.41) \times 10^{-12}$ kg. Moses *et al.* [106] have determined that the energy required to produce one kilogram of biomass (E_c/m_c) during ontogenetic growth is the same in all animals and is equal to $(5.774 \pm 0.097) \times 10^6$ J/kg. Combining these results yields $E_c = (1.09 \pm 0.24) \times 10^{-5}$ J.

The energy cost of producing a unit mass of cells during embryonic growth is expected to be smaller than during ontogenetic growth since the food is already in a reduced form and need not be digested in the alimentary canal. From $\dot{V}O_2$ measurements of the metabolism of embryos inside eggs, Vleck *et al.* [107] and Whitehead and Seymour [108] have measured the amount of oxygen used during the growth of a variety of bird and crocodylian embryos, respectively. Romanoff [109] has shown that bird egg metabolism is powered almost exclusively by lipids for which one liter of oxygen is equivalent to 19.64 kJ. For bird and crocodylian embryos, the energy required to produce a given mass of cells is $(2.613 \pm 0.128) \times 10^6$ J/kg (SE) [107,108]. It is assumed that this same value is appropriate to use for nonavian dinosaur and mammalian embryonic growth.

The growth of the animal is characterized by its total mass $m(t)$ at time t. Note that $N_c = m/m_c$ and, as discussed earlier, $B = B_o m^\alpha$.

The solution of Eq. (2) is discussed in Refs. [66,68]. The expression for the mass of the animal as a function of time t, $m(t)$ is given by

$$m(t) = M\left\{1 - \left[1 - \left(\frac{m_o}{M}\right)^{(1-\alpha)}\right] e^{-\frac{(1-\alpha)pt}{M^{(1-\alpha)}}}\right\}^{\left(\frac{1}{1-\alpha}\right)}, \tag{3}$$

where m_o is the initial mass of the animal, M is the final adult mass, and the metabolic mass gain parameter $p = m_c B_o / E_c$. Equation (3) is used to fit the mass growth curve for the animal. For ontogenetic growth, m_o, M, and p are all adjusted to find the best fit to the data. For embryonic growth, the initial mass m_o is assumed to be 6.4 mg, the mass of the fertilized ovum [104] and M is fixed to the adult mass of the animal. Only the metabolic mass gain parameter p is allowed to vary.

The value of the growth metabolic factor B_o is then determined from p: $B_o = pE_c/m_c$.

If the embryonic mass growth data is unavailable, the embryonic metabolic prefactor B_o can be determined from

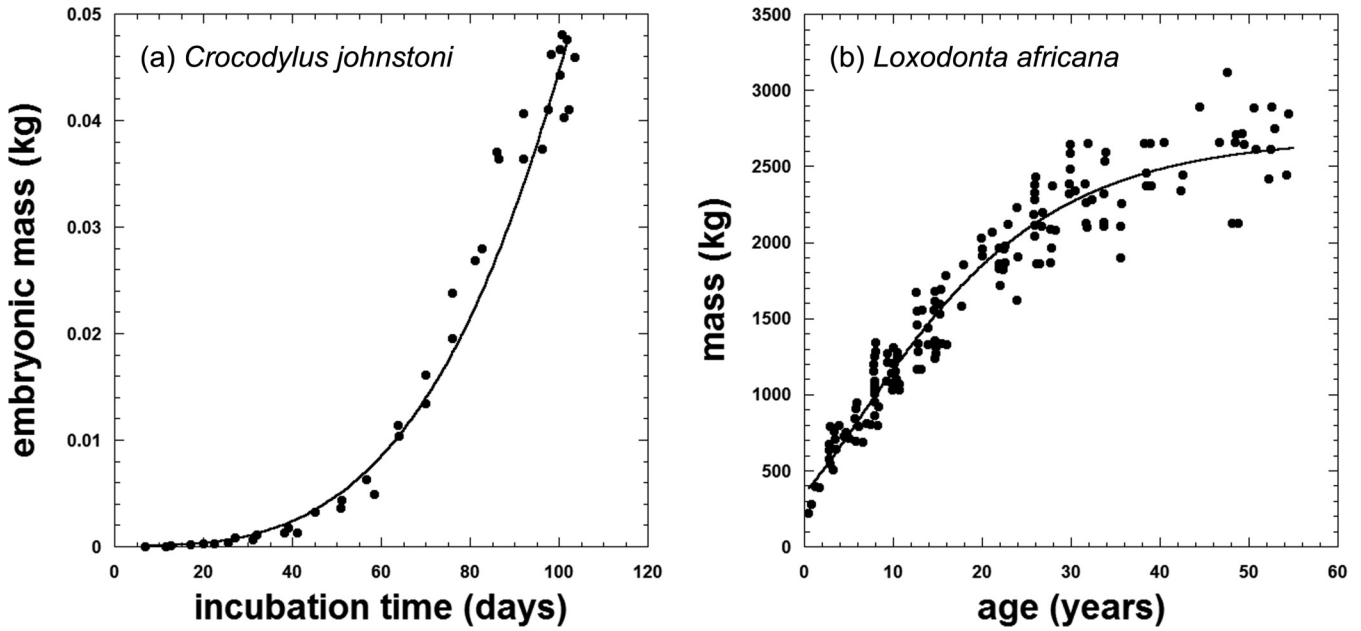

FIG. 2. Mass growth for (a) *Crocodylus johnstoni* embryos at 29°C and (b) *Loxodonta africana* females (right). The mass of the animal as a function of time is shown by the solid circles. The solid line shows the theoretical fit to the data via Eq. (3). The embryonic growth of *Crododylus johnstoni* at 29°C is shown on the left and the data is from Ref. [110]. The ontogenetic growth of *Loxodonta africana* females is shown on the right and the data is from Ref. [111].

Eq. (3) if the hatching mass m_h, hatching time t_h, and the final mass M of the adult animal are known, assuming that the initial mass m_o is the mass of a fertilized ovum (6.4 mg). Equation (3) is solved for the metabolic mass gain parameter p in terms of m_h, t_h, m_o, and M:

$$p = \frac{M^{(1-\alpha)}}{(1-\alpha)t_h} ln\left[\frac{1-\left(\frac{m_o}{M}\right)^{(1-\alpha)}}{1-\left(\frac{m_h}{M}\right)^{(1-\alpha)}}\right]. \tag{4}$$

The metabolic embryonic prefactor is easily determined from Eq. (4), since $B_o = pE_c/m_c$ yields

$$B_o = \frac{E_c M^{(1-\alpha)}}{(1-\alpha)m_c t_h} ln\left[\frac{1-\left(\frac{m_o}{M}\right)^{(1-\alpha)}}{1-\left(\frac{m_h}{M}\right)^{(1-\alpha)}}\right]. \tag{5}$$

The incubation time t_h can be calculated from Eq. (4):

$$t_h = \frac{M^{(1-\alpha)}}{(1-\alpha)p} ln\left[\frac{1-\left(\frac{m_o}{M}\right)^{(1-\alpha)}}{1-\left(\frac{m_h}{M}\right)^{(1-\alpha)}}\right]. \tag{6}$$

III. RESULTS AND DISCUSSION

Theoretical mass growth curves determined via Eq. (3) for *Crocodylus johnstoni* in embryonic growth (incubated at 29°C) and *Loxodonta africana* females in ontogenetic growth in the wild are shown in Fig. 2 with the experimental data [110,111]. The theory is seen to produce an excellent fit to the data.

The incubation of eggs provides another opportunity to test the validity with which this mass growth model determines the metabolism. Since the developing embryo is involved in only the process of growth at a fixed temperature, the factor B_o from our mass growth analysis can be compared directly to the results of $\dot{V}O_2$ measurements on eggs. Whitehead *et al.* [108] have measured the embryonic $\dot{V}O_2$ for *C. johnstoni* at 29 and 31°C and for *C. porosus* at 30°C. Converting these $\dot{V}O_2$ measurements to the metabolic prefactor B_o (using the reported 19.64 J for each liter of O_2 when metabolizing lipids [109]) yields B_o from those measurements. Embryonic mass growth data for *C. johnstoni* at 29 and 31°C have been reported by Whitehead *et al.* [110] and for *C. porosus* at 30°C

TABLE I. Comparison of predictions of the mass growth model for embryonic crocodylians with data from the literature. The metabolic prefactor B_o is calculated in two manners: (1) via the mass growth model described in this paper; and (2) by converting the reported values [110,112] of $\dot{V}O_2$ into the metabolic prefactor B_o. The uncertainties are the standard deviations. The incubation times [calculated using Eq. (6) with the values of p determined by fitting the embryonic mass growth data] are in the third column while the measured incubation times from Ref. [110] for *C. johnstoni* and from Ref. [112] for *C. porosus* are in the fourth column.

	B_o (W/kg$^{3/4}$) (via growth analysis)	B_o (W/kg$^{3/4}$) (from $\dot{V}O_2$ measurements)	predicted incubation (days) (via growth analysis)	measured incubation (days)
C. johnstoni at 29°C	0.545 ± 0.150	0.568 ± 0.111	99.2 ± 1.4	100.9
C. johnstoni at 31°C	0.615 ± 0.169	0.646 ± 0.166	82.8 ± 1.5	81.6
C. porosus at 30°C	0.664 ± 0.182	0.631 ± 0.132	90.5 ± 1.5	91

TABLE II. Embryonic metabolism of *Troodon formosus, Protoceratops andrewsi*, and *Hypacrosaurus stebingeri*. The species, the mass of the egg m_{egg} (measured in kg), the mass of the hatchling m_h (measured in kg), the adult mass M (measured in kg), the observed incubation period t_h^{obs} (measured in days), and the calculated metabolic prefactor B_o (measured in W/kg$^{3/4}$) are given. The mass of the eggs and the observed incubation times are from Ref. [1] for *T. formosus* and from Ref. [52] for *P. andrewsi* and *H. stebingeri*. The adult masses M of *T. formosus, P. andrewsi*, and *H. stebingeri* are from Refs. [68,142,143], respectively. The uncertainties are the standard deviations.

Species	m_{egg} (kg)	m_h (kg)	M (kg)	t_h^{obs}(days)	B_o (W/kg$^{3/4}$)
Troodon formosus	0.314	0.215	52.0 ± 7.3	74	1.21 ± 0.35
Protoceratops andrewsi	0.194	0.136	180 ± 25	83	0.894 ± 0.261
Hypacrosaurus stebingeri	4.251	2.976	4000 ± 560	171	0.980 ± 0.286

by Webb *et al.* [112]. Eq. (3) is used to fit the mass growth data which yields B_o for the same three situations. The results of these analyses are given in Table I. The largest difference for B_o between these two analyses is 5.2%.

As a further test, the fitted values of p from the mass growth data for *C. johnstoni* at 29 and 31°C and for *C. porosus* at 30°C are then used in Eq. (6) to predict the incubation times of these animals using the measured hatchling masses [110,112]. These predictions are then compared to the experimentally observed incubation times [110,112]. As shown in Table I, the predicted incubation times are within 1.6% of the measured incubation times.

The incubation times of the altricial and precocial extant birds of this study were calculated using the value of p determined by fitting the embryonic growth of each bird. The calculated mean incubation time was within 5.7% of the mean of the measured incubation times ($N = 27$).

As discussed earlier, the body temperature of crocodylians in the wild is expected to be lower than the optimum due to diurnal and seasonal variations as well as social interactions with dominant animals which limit the access of subordinant animals to basking sites. These factors plus possible issues with food availability are expected to suppress the GMR relative to the SMR. Seymour *et al.* [90] measured the SMR of captive *Crocodylus porosus* at 30°C via $\dot{V}O_2$ experiments on animals with masses between 0.19 and 389 kg. Converting these measurements yields $B_o = 0.438 \pm 0.118$ W/kg$^{3/4}$ (SD). Using the growth data of Webb and coworkers [113,114] yields $B_o = 0.248 \pm 0.025$ W/kg$^{3/4}$ via the growth model analysis, illustrating the expected suppression in extant crocodylians.

Variability in the ontogenetic growth metabolism of ectotherms is demonstrated by the growth data from various members of Crocodylus. For instance, *Crocodylus niloticus* females at Ngezi, Zimbabwe had an average B_o of 0.137 ± 0.043 W/kg$^{3/4}$ while one female (known as Beadle) from Hwange National Park had a B_o of 0.320 ± 0.101, an increase of a factor of 2.3 [115].

Varricchio *et al.* [1] have reported an incubation time of 74 days for the theropod dinosaur *Troodon formosus*. They also report that the mass of the nearly hatched egg of *Troodon* was 314 g. The mass of the newly hatched *Troodon* is estimated by assuming that the newly hatched nonavian dinosaurs had a mass of 70% of the egg mass, as observed in extant birds [116]. Table II gives the embryonic metabolisms of *Troodon formosus*, *Protoceratops andrewsi*, and *Hypacrosaurus stebingeri* determined from these data by using Eq. (5).

The embryonic metabolisms of these three dinosaur species are compared to the ontogenetic growth metabolisms of 22 dinosaur species [67]. The ontogenetic growth and embryonic metabolisms of extant birds, mammals and crocodylians [41,42,66,110–115,117–141] are determined and used to compare the results of the extinct dinosaurs to those of living animals. All the data for embryonic development by members of Crocodylus were incubated at 30°C. The data at 29 and 31°C in Table I were only used to verify the validity of the growth model and were not used for subsequent analysis. Table III gives the overall results for these different groups of animals.

Table III shows that the mean embryonic metabolic prefactors B_o of these nonavian dinosaurs are closer to the embryonic metabolism of extant crocodylians than extant altricial and precocial birds. This suggests that embryos of nonavian dinosaurs were more like the embryos of extant crocodylians than the embryos of extant birds. This table also shows that the embryonic metabolisms of these nonavian dinosaurs were similar to the embryonic metabolisms of extant mammals.

Table III also shows that the ratio of B_o for ontogenetic growth to embryonic growth is 3 or greater for extant birds and mammals but below 1 for extant crocodylians. This ratio

TABLE III. Metabolisms of extant birds, extant mammals, extant crocodylians and nonavian dinosaurs. The mean metabolic prefactor B_o and its standard error for the ontogenetic growth and embryonic growth of different groups of animals are given. The ratio of the embryonic B_o divided by the ontogenetic growth B_o is given for each group of animals also.

Group	Ontogenetic growth B_o (W/kg$^{3/4}$)	Embryonic B_o (W/kg$^{3/4}$)	Ontogenetic growth B_o/embryonic B_o
Extant altricial birds	15.47 ± 1.61	2.16 ± 0.15	7.16 ± 0.90
Extant precocial birds	9.29 ± 0.98	2.34 ± 0.10	3.97 ± 0.45
Extant mammals	4.78 ± 0.37	1.38 ± 0.09	3.46 ± 0.35
Extant crocodylians	0.266 ± 0.033	0.643 ± 0.021	0.414 ± 0.053
Extinct dinosaurs	0.654 ± 0.089	1.03 ± 0.09	0.635 ± 0.103

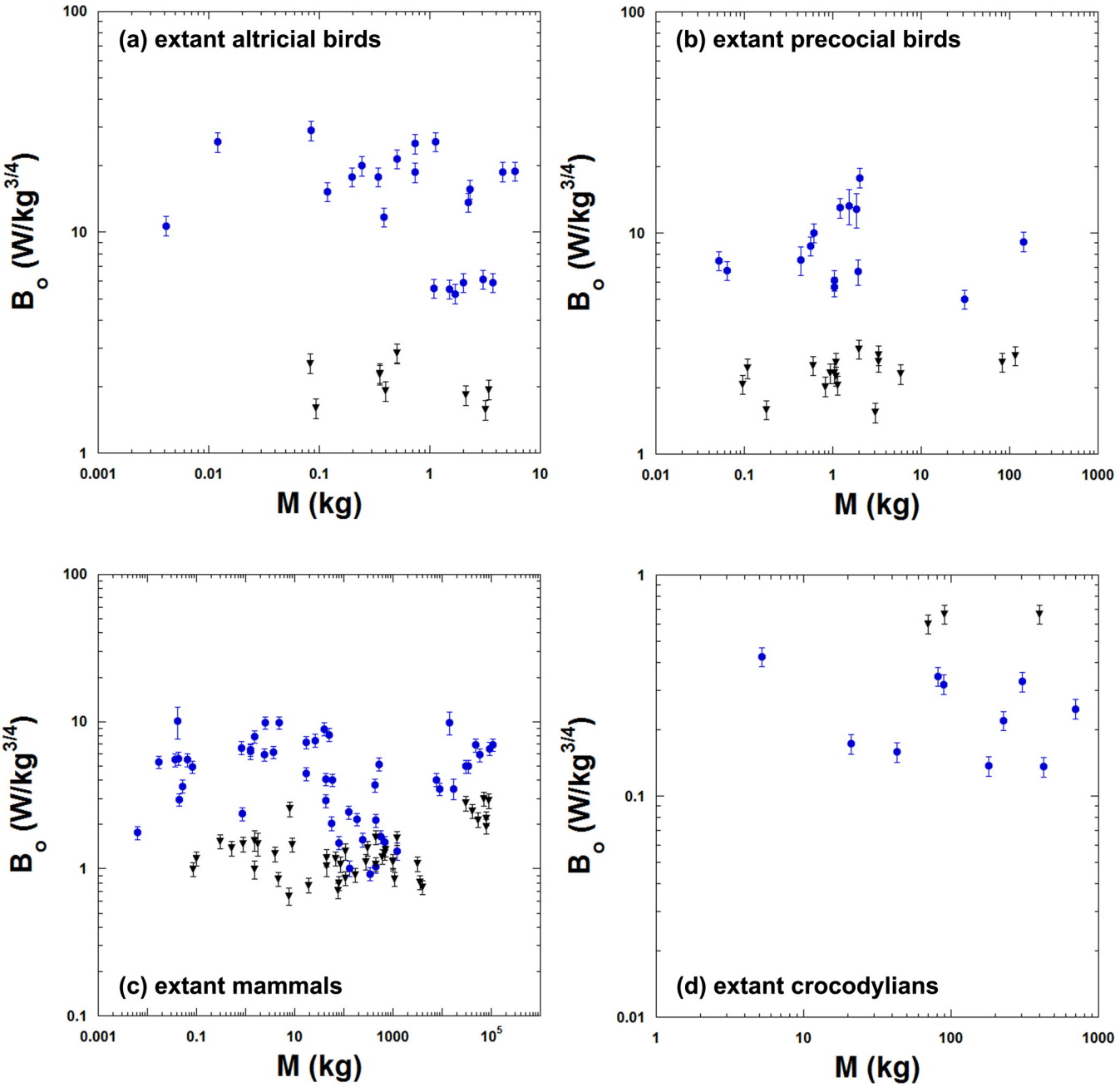

FIG. 3. Embryonic and ontogenetic growth metabolism in extant animals. The metabolic prefactor B_o (in units of $W/kg^{3/4}$) is shown as a function of the mass M (in kilograms) of the adult animal for (a) extant altricial birds, (b) extant precocial birds, (c) extant mammals, and (d) extant crocodylians. The data are shown by downward pointing triangles for the embryonic animals and by circles for the ontogenetic growth animals.

for the nonavian dinosaurs of this study is also less than 1. These results suggest that nonavian dinosaur embryos were more like extant crocodylians than extant birds.

Figure 3 shows the embryonic and ontogenetic growth metabolic prefactor B_o of four groups of extant animals: altricial birds, precocial birds, mammals, and crocodylians. Juvenile and adult birds and mammals use endothermy to maintain a relatively high body temperature T_B in a relatively narrow range via physiological thermoregulation. This permits endotherms to be active throughout the year and to occupy every part of the planet. However, endothermy requires the animal to consume large amounts of food.

Extant reptiles use ectothermy which allows their body temperature to vary as the temperature of the environment fluctuates. On average, the metabolic rate of an ectothermic animal is lower than in an endothermic animal. An ecothermic animal requires much less food than an endothermic animal of the same mass. However, an ectotherm will become inactive if the environmental temperature remains low for an extended period of time, causing an ectotherm to be vulnerable to predation by endotherms.

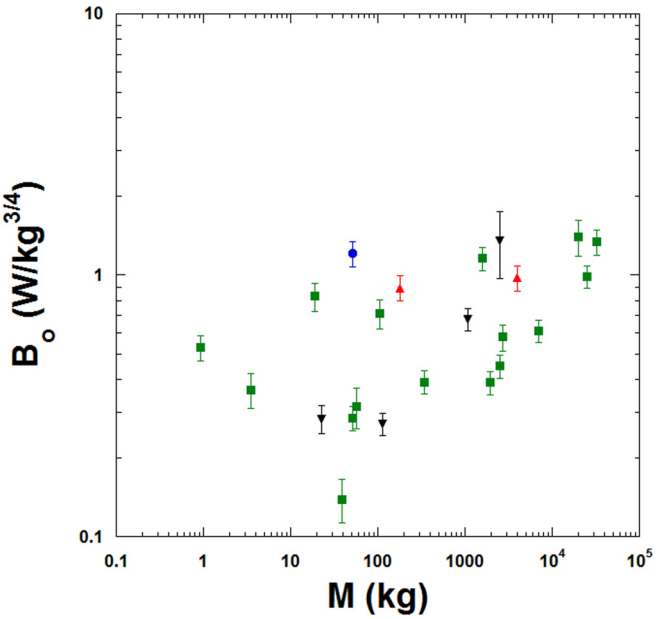

FIG. 4. Embryonic and ontogenetic growth metabolism of the dinosaurs of this study. The metabolic prefactor B_o (in units of W/kg$^{3/4}$) is shown as a function of the adult mass M (in kilograms). For saurischian dinosaurs, the circle shows the datum for embryonic metabolisms while the squares show the data for ontogenetic growth metabolism. For ornithischian dinosaurs, the upward-pointing triangles show the data for embryonic metabolisms while the downward-pointing triangles show the data for ontogenetic growth metabolism.

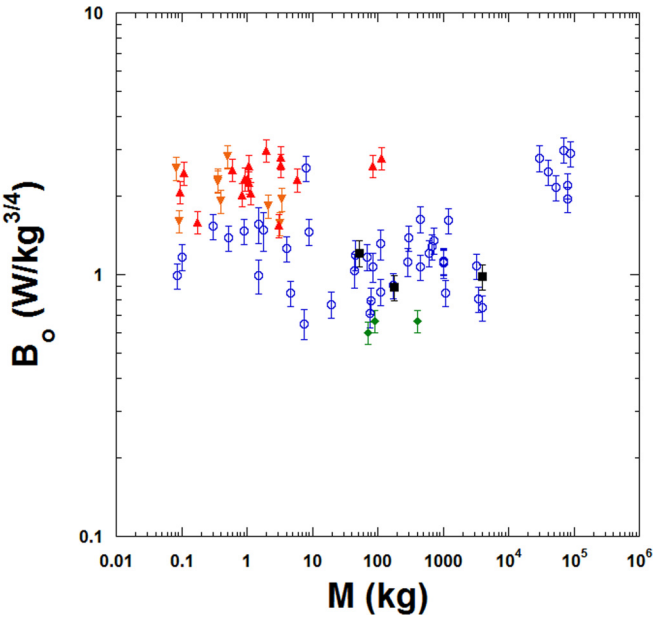

FIG. 5. Embryonic metabolism in the animals of this study. The embryonic metabolic prefactor B_o (in units of W/kg$^{3/4}$) is shown as a function of the adult mass M (in kilograms). The symbols are the data for the different groups: altricial birds—downward-pointing triangles; precocial birds—upward-pointing triangles; mammals—open circles; crocodylians—diamonds; extinct dinosaurs—squares.

Erickson *et al.* [144] was the first to suggest that the mass growth rate of nonavian dinosaurs indicated that dinosaurs regulated their body temperature by a mechanism intermediate between endothermy and ectothermy. Grady *et al.* [104] found support for the suggestion of Erickson *et al.* by determining that the metabolism of nonavian dinosaurs was intermediate between endothermy and ectothermy.

Other results support the suggestion that nonavian dinosaurs were endotherms. Seymour [145] studied aerobic and anaerobic power generation in *Crocodylus porosus*, a large estuarine crocodile which can attain masses in excess of 400 kg. His results suggest that ectothermic dinosaurs would have lacked the power generation capability and endurance of endothermic mammals [145]. This is important evidence since nonavian dinosaurs were the dominant land animals for most of the Mesozoic Era. He interpreted this result to show that nonavian dinosaurs were endothermic.

Reid [146,147] pioneered the use of bone histology and growth rates to inform the discussion of the temperature-regulation mechanism of nonavian dinosaurs. His work showed that nonavian dinosaurs were unlike extant ectotherms and similar to extant endotherms. Padian and Horner [148] also reported similar observations.

Figure 3 shows the same trends as in Table III. The embryonic B_o is smaller than the ontogenetic growth value for altricial birds, precocial birds and mammals. In contrast, the embryonic prefactor B_o is larger than the ontogenetic growth B_o in crocodylians.

Extant birds have a very high metabolism during their ontogenetic growth development. Since volant birds spend a significant fraction of their life airborne to collect food and to avoid terrestrial predators, it is important that birds grow to maturity rapidly to attain full-flight abilities at the earliest time possible. Altricial birds are observed to have a higher ontogenetic growth metabolism than precocial birds since they are hatched at a less well-developed state. Consequently, altricial birds need to grow at a faster rate than precocial birds.

Figure 4 shows that the relationship of the embryonic and ontogenetic growth metabolic prefactor B_o in nonavian dinosaurs is the same as observed in extant crocdylians: the embryonic metabolism is, on average, higher than the ontogenetic growth metabolism. However, there is overlap between these data sets for nonavian dinosaurs. This same figure also shows that embryonic metabolisms are the same for the two branches of Dinosauria. Likewise, the ontogenetic growth metabolisms are also the same for the two branches of Dinosauria.

Figure 5 compares the embryonic metabolisms for the different groups of animals. We see that the general trends are that the birds have the highest embryonic metabolism. In general, the mammals have the next highest embryonic metabolism. The embryonic metabolism of the crocodylians is the lowest. There is overlap between the extant groups.

This figure also shows that, for the mass range between 10 and 10 000 kg, the embryonic metabolic prefactor B_o of the nonavian dinosaurs are near the middle of mammal range. The nonavian dinosaur values are above the values observed for extant crocodylians and below the values observed for extant birds. However, the dinosaur results are closer to the crocodylian values than the bird values. Therefore, we find

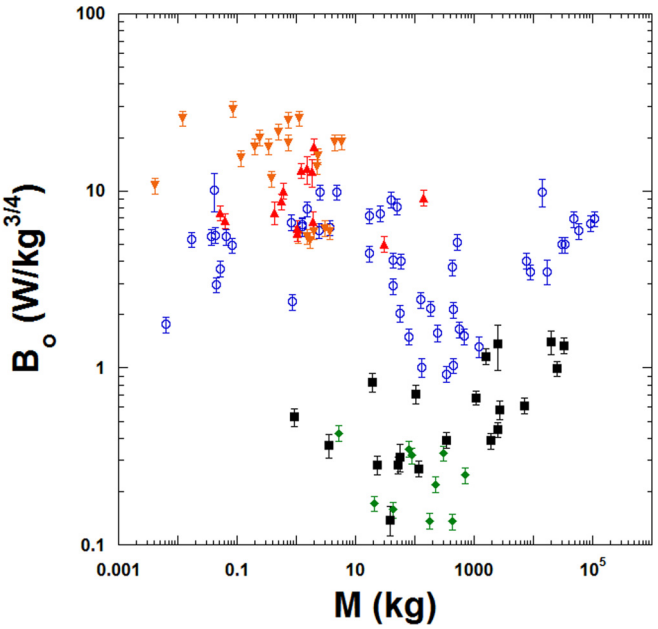

FIG. 6. Ontogenetic growth metabolism in the animals of this study. The ontogenetic growth metabolic prefactor B_o (in units of W/kg$^{3/4}$) is shown as a function of the adult mass M (in kilograms). The symbols are the data for the different groups: altricial birds—downward-pointing triangles; precocial birds—upward-pointing triangles; mammals—open circles; crocodylians—diamonds; extinct dinosaurs—squares.

the embryonic metabolism of nonavian dinosaurs to be more like extant crocodylians than extant birds.

An examination of the ontogenetic growth metabolisms of these animals is shown in Fig. 6. The birds have the highest ontogenetic growth metabolisms, though there is some overlap with the mammalian results. There is no overlap between the metabolisms of extant mammals and extant crocodylians: the crocodylian ontogenetic growth metabolism is clearly lower than the mammalian metabolism. Interestingly, the ontogenetic growth metabolisms of the dinosaurs are intermediate between the mammalian and crocodylian values. This result is consistent with the earlier suggestion that nonavian dinosaurs regulated their body temperature via a mechanism intermediate between endothermy and ectothermy [68,104,144].

The brooding ability of nonavian dinosaurs would have been affected by their temperature-regulation mechanism. Extant birds are endothermic animals with some of the highest metabolisms that are observed in modern animals. Many brooding birds produce elaborate nests that are very effective thermal insulators [149]. With their high body temperature and well-insulated nests, their eggs are kept at a high temperature throughout incubation.

As shown in Fig. 6, nonavian dinosaurs have a significantly lower metabolism than extant birds and their average body temperature T_B would have been lower than the average T_B of extant birds. Consequently, brooding nonavian dinosaurs would not have been able to incubate their eggs at temperatures as high as modern birds. This would have resulted in an embryonic metabolism in nonavian dinosaurs which was lower than observed in extant birds. This is the trend observed in this work.

Deeming and coworkers [14–17] have suggested that nonavian dinosaurs were unable to contact incubate their eggs. If correct, brooding by dinosaurs would have been even less efficient at warming the eggs. Therefore, the embryonic metabolism of nonavian dinosaurs are expected to have been lower than observed in extant birds.

It would have been exceedingly difficult for medium- and large-sized dinosaurs to have brooded their eggs. With masses up to 30 000 kg, the adults would have been too large to put even a small fraction of their weight on their eggs. Such large animals would also have found it difficult to have sufficient dexterity to avoid crushing their own eggs while moving.

Rather than brooding, medium- and large-sized dinosaurs are believed to have buried their eggs, probably with vegetation which would have released heat as it decayed. Such behavior is observed in modern crocodylians, though some nests have very little organic matter in them [150].

The incubation time of an egg is determined by the mass of the fertilized ovum, the mass of the hatchling and its average embryonic metabolism via Eq. (6). Table IV lists the incubation times determined in this manner for the dinosaurs of this study. The mass of the fertilized ovum is assumed to be 6.4 mg, as in Ref. [104]. The hatchling mass m_h is determined by using the results of Dolnik [151] and Deeming and Birchard [116] to relate the hatchling mass m_h to the adult mass M of the dinosaur. The embryonic metabolic prefactor B_o used for the nonavian saurischian dinosaurs was 1.21 W/kg$^{3/4}$, the value determined for *Troodon formosus* in this study. The average metabolic prefactor B_o of ornithischian dinosaurs *P. andrewsi* and *H. stebingeri* (0.937 W/kg$^{3/4}$) was used to calculate the incubation times for the ornithischian dinosaurs.

From Table IV, we see that the incubation times for saurischian dinosaurs range from 51 to 123 days and range from 88 to 146 days for the ornithischian dinosaurs.

Dinosaurs that provide active care for their eggs and/or young would be restricted to remaining in the vicinity of their eggs until they hatch. Gregarious behavior has been reported for a number of dinosaur taxa, including ceratopsids [153–155], ornithopods [58,156,157], theropods [157–164], and sauropods [157,165–167]. Gregarious behavior in extant animals includes herding for mutual protection of prey species, such as wildebeests (*Connochaetes taurinus*) and zebras (*Equus quagga*), as well as pack hunting by predatory species, such as lions (*Panthera leo*) and wolves (*Canis lupus*). Matriarch-based herding among African elephants (*Loxodonta africana*) provides protection for the newly born and young juveniles of the herd. Colonial nesting is observed among a number of extant birds, including tufted puffins (*Fratercula cirrhata*), herons (such as *Ardea alba modesta*), bank swallows (*Riparia riparia*), and weaverbirds (*Philetairus socius*).

Most gregarious behavior observed in extant animals involve, to some degree, care for the young by the adults. A significant part of that care is providing protection from predation. Such care is most needed at the very beginning of life, that is, when the juvenile is newly hatched or born. We assume that, at least, some of the nonavian dinosaurs displaying gregarious behavior also provided care to their

TABLE IV. Ontogenetic growth metabolism and predicted incubation times of dinosaurs. The adult mass M (in kg), the hatchling mass m_h (in kg), the metabolic prefactor B_o (in $W/kg^{3/4}$) and the predicted incubation times t_h^{pre} (in days). The embryonic metabolic prefactor B_o used for the nonavian saurischian dinosaurs was 1.21 $W/kg^{3/4}$ determined in this study for *Troodon formosus*. The average metabolic prefactor B_o of ornithischian dinosaurs *P. andrewsi* and *H. stebingeri* (0.937 $W/kg^{3/4}$) was used to calculate the incubation times for the ornithischian dinosaurs.

Species	M (kg)	m_h (kg)	Ontogenetic growth B_o ($W/kg^{3/4}$)	t_h^{pre} (days)
Theropoda				
Tyrannosaurus rex	7000 ± 980	2.06 ± 0.13	0.612 ± 0.061	123 ± 30
Daspletosaurus torosus	2700 ± 378	1.33 ± 0.09	0.580 ± 0.067	111 ± 27
Gorgosaurus libratus	2500 ± 350	1.28 ± 0.08	0.449 ± 0.045	110 ± 27
Allosaurus fragilis	1930 ± 270	1.17 ± 0.07	0.388 ± 0.039	107 ± 26
Citipati osmolskae	105 ± 15	0.298 ± 0.019	0.713 ± 0.088	79 ± 19
Deinonychus antirrhopus	57.0 ± 8.0	0.225 ± 0.014	0.315 ± 0.056	74 ± 18
Troodon formosus	52.0 ± 7.3	0.215 ± 0.014	0.284 ± 0.030	74 ± 18
Oviraptor philoceratops	39.0 ± 5.5	0.189 ± 0.012	0.139 ± 0.026	72 ± 17
Coelophysis rhodesiensis	19.0 ± 2.7	0.136 ± 0.009	0.830 ± 0.101	67 ± 16
Shuvuuia deserti	3.5 ± 0.5	0.0623 ± 0.0040	0.364 ± 0.055	57 ± 14
Archaeopteryx lithographica	0.93 ± 0.13	0.0339 ± 0.0022	0.528 ± 0.060	51 ± 12
Prosauropoda				
Plateosaurus engelhardti	1600 ± 224	1.04 ± 0.07	1.16 ± 0.12	105 ± 26
Massospondylus carinatus	340 ± 48	0.511 ± 0.033	0.391 ± 0.039	89 ± 22
Sauropoda				
Alamosaurus sanjuanensis	32 600 ± 4,600	4.17 ± 0.27	1.34 ± 0.15	146 ± 35
mamenchisaurid	25 100 ± 3,500	3.70 ± 0.24	0.990 ± 0.099	142 ± 34
Rapetosaurus krausei[a]	20 500 ± 2,800	3.40 ± 0.21	–	140 ± 34
Apatosaurus	20 000 ± 2,800	3.33 ± 0.21	1.40 ± 0.22	138 ± 34
Saltasaurus loricatus[a]	6870 ± 970	2.04 ± 0.13	–	123 ± 30
Ornithopoda				
Maiasaura peeblesorum	2500 ± 350	1.28 ± 0.08	1.36 ± 0.39	142 ± 35
Tenontosaurus tilletti	1080 ± 151	0.870 ± 0.056	0.678 ± 0.057	130 ± 32
Dysalotosaurus lettowvorbecki	115 ± 16	0.310 ± 0.020	0.270 ± 0.027	103 ± 25
Ceratopsia				
Psittacosaurus mongoliensis	23.0 ± 3.2	0.148 ± 0.010	0.282 ± 0.034	88 ± 21

[a]The hatchling mass m_h of *Rapetosaurus krausei* has been reported by Curry Rogers *et al.* [152]. The adult mass M of this sauropod was calculated by using the result of Deeming and Birchard [116] to relate the hatching mass m_h to the mass of the egg, m_{egg}, and then the result of Dolnik [151] was used to relate m_{egg} to the adult mass M. Conversely, the adult mass M of *Saltasaurus loricatus* from Ref. [101] was used with the results of Deeming and Birchard [116] and [151] to determine its hatching mass. The uncertainties are the standard deviation.

eggs and/or newly hatched young. If this were the case, then the adult dinosaurs would have remained in the vicinity of their eggs until they hatched and, perhaps, for some time thereafter.

Evidence does exist of dinosaurs providing care to their young. *Maiasaura peeblesorum* nested in colonies and are believed to have brought food to their young in their nests for a period of several months [58,168]. With their calculated incubation time of about 140 days, *Maiasaura* would have been restricted to the nesting area for more than half a year (roughly 200 days). Large ornithischian dinosaurs have been suggested to have made migrations of about 3000 km from lower latitude nesting sites to higher latitude feeding areas in polar regions [169–171]. Such a long incubation time appears to be inconsistent with *Maiasaura* making very long annual migrations.

There is evidence that the young of the prosauropod *Massospondylus carinatus* remained in their nests for a period of couple months after hatching [172–174]. This suggests that their young were altricial and that the parents actively cared for the young. Our calculated incubation time for *M. carinatus* of about 3 months plus a couple of months of care implies that *M. carinatus* almost half a year in the same vicinity, assuming that the young were incapable of travel until a couple of months old.

The calculated incubation time of about 123 days for *Tyrannosaurus rex* indicates that *T. rex* adults were restricted in their movement for the 4 months of incubation. If the adults continued their usual amount of eating, this restriction of movement might have been a significant burden on the local ecosystem. These large carnivores needed large quantities of food. It is possible that the parents restricted their food intake during this time. That would have diminished the strain on the ecosystem, but at the cost of the health of the adults themselves. Rivas [65] has reported that female *Eunectes murinus* are weakened by their long fast while pregnant and at an increased risk of death.

It is possible that not all species of dinosaurs were gregarious. Roach and Brinkman [175] have presented evidence of intraspecific aggression by *Deinonychus antirrhopus*, possibly including cannibalism. Such behavior is observed in the extant *Varanus komodoensis*. However, most reports of the social behavior of nonavian dinosaurs report gregarious behavior.

Large nesting colonies nests have been found for the sauropod titanosaur *Saltasaurus loricatus* [59–61,176]. The gregarious nature of their nesting behavior is shown by the close spacing of the clutches, the high density of the clutches and their continuity over different breeding seasons [176]. Such a nesting colony would have attracted predators and, consequently, the parents presumably guarded the nesting colony until the eggs were hatched and the young were able to leave the area. The nests in these colonies are spaced about the length of an adult dinosaur, consistent with the adults laying their eggs at the same time. Trackways provide evidence that some sauropods formed herds [157,165–167]. As shown in Table IV, the incubation time was about 120 days. Even if the young were fully capable of movement upon hatching, these large sauropods were restricted in their movements for about 4 months a year. Given the large amount of food required by the adults, the vegetation of the neighboring areas must have been impacted negatively.

Recall that the extant reptilian embryonic dental development was used to determine the incubation period of *Troodon formosus*. The fact that the resulting incubation is intermediate to the avian and reptilian values suggests that the embryonic dental development of *T. formosus* was probably faster than in extant reptiles since extant birds have a higher embryonic development. Therefore, the incubation time of *T. formosus* was probably shorter than the reported 74 days [1]. A shorter incubation time for *T. formosus* means a higher embryonic metabolism than calculated in this paper. That higher metabolism would mean shorter incubation times for the saurischian dinosaurs in Table IV.

IV. SUMMARY

The embryonic metabolism of the theropod dinosaur *Troodon formosus* and the ornithischian dinosaurs *Proterceratops andrewsi* and *Hypacrosaurus stebingeri* have been determined to be near the average value observed in extant mammals of similar masses. Given the relationship of nonavian dinosaurs to both extant crocodylians and birds, it is noteworthy that their embryonic metabolism is more similar to extant crocodylians than extant birds. These average embryonic metabolisms were then used to calculate the incubation times for 22 dinosaurs from both Sauischia and Ornithischia. The calculated incubation times vary from about 50 days for *Archaeopteryx lithographica* to about 150 days for *Alamosaurus sanjuanensis*.

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