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Evolutionary drivers of reproductive output variation among amniotes, and the origins of large offspring in birds

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Birds and mammals mostly produce clutches with small numbers of large individual offspring compared to non-bird reptiles, including dinosaurs on the bird-stem lineage. Existing hypotheses for this variation propose links between relative offspring size and large brains or high metabolic rates, but remain incompletely tested. We characterize the allometries of reproductive output traits (clutch mass, clutch size and individual offspring mass) and evaluate their correlates using phylogenetic regressions across 2857 living and extinct amniote species. Across amniotes, species with larger relative brain sizes have larger individual offspring, fewer offspring or both. This signifies a higher maternal investment per offspring in large-brained species, exemplified by birds and mammals. In dinosaurs, large egg sizes evolved shortly before the origin of the bird crown group, coinciding with an evolutionary increase in relative brain mass and suggesting that evolutionary increases in egg/neonate size evolved due to a requirement for greater investment per offspring with increasing brain size. These egg size increases may explain changes to dinosaur nest structure and pelvic anatomy along the bird-stem lineage. Our results provide insights into the evolutionary pressures shaping reproductive strategies and brain size across amniotes, underscoring the significance of these traits in the broader context of amniote diversification.

Supplementary material is available online at
<https://doi.org/10.6084/m9.figshare.c.8526205>.

1. Introduction

The transmission of genetic material from parents to offspring is central to the mechanisms of natural selection and the concept of Darwinian fitness. Therefore, natural selection should result in life history and reproductive traits that maximize lifetime reproductive success [1–7]. Here, we analyse patterns of variation in clutch/litter mass, egg/neonate mass and clutch/litter size. We refer to these collectively as ‘reproductive output traits’ and to the allometric relationships of these reproductive output traits to body size as ‘reproductive output scaling’. Assuming that the energetic investment made in a single clutch or litter is held constant, there is a trade-off between clutch/litter size and the energetic investment in each individual egg or neonate. Hence, the reproductive output of land vertebrates (amniotes) varies between clutches comprising larger numbers of smaller individual offspring, as seen in many living reptiles, especially turtles [8,9] and clutches comprising a smaller number of larger individual offspring, as seen in placental mammals and birds [6,10]. An end-member example of this is the blue whale (*Balaenoptera musculus*), which produces a single offspring every 2–3 years with a neonatal body mass of roughly 2500 kg (1.6% of the adult female mass [11]). In contrast, the hawksbill sea turtle (*Eretmochelys imbricata*) produces an average clutch of 158 proportionally small eggs [12], weighing about 29 g each (0.019% of the adult female mass [13]). These represent the extremes of a continuum of reproductive investment that exhibits phylogenetic, ecological and allometric variation—with reproductive output traits per clutch within a species therefore resulting from multiple factors. Mammal [7,14,15] and bird [16,17] species generally have smaller counts of larger offspring as body size increases (i.e. reverse allometry of clutch or litter size), whereas turtles [18,19], crocodylians [20,21] and squamates [22,23] typically lay larger numbers of proportionally smaller eggs as adult body size increases [6].

There is relatively little evidence for the reproductive output traits of extinct species. However, exceptional examples are known for various groups, including stem-mammals [24], extinct birds [25–28] and especially non-avian dinosaurs, which are members of the bird-stem lineage [29–34]. Different groups of non-avian dinosaurs had different reproductive output traits, spanning from very large numbers of proportionately small eggs in sauropods [35–38] to smaller numbers of proportionately larger eggs in theropods [39]. They also ranged from an almost complete lack of parental presence beyond the egg-laying stage in sauropods [40] to potentially extensive pre-hatching parental care, such as communal nests [39], and post-hatching parental care, such as contact incubation [41,42], in groups that are closely related to birds such as oviraptorid and troodontid theropods [39]. Fossil nests are known only from a few groups of non-avian dinosaurs, mostly theropods and sauropodomorphs. Most observed clutches contain large numbers of relatively small individual offspring, similar to living reptiles but differing from birds and mammals [43,44].

The considerable variation of reproductive output traits described above results from approximately 310 million years of evolution since the divergence of all living land vertebrates (amniotes) from their most recent common ancestor, at the mammal–reptile split. Various hypotheses have been proposed to explain this variation and might explain why birds and mammals evolved their specific reproductive strategies. Most can be classified as either energetic hypotheses or physiological hypotheses. These include the effects of energetic investment in brain size [45–47] and the effects of physiological parameters such as basal metabolic rate (BMR) [48–50]. These are described in more detail below and are not necessarily mutually exclusive. A central goal of the current work is to evaluate the applicability of these hypotheses on broad phylogenetic scales, as explanations of variation in reproductive output traits across amniotes, including both living and extinct groups. Dinosaurs also show a unique combination of the traits proposed to explain variation in reproductive output traits among living amniotes—they have relatively small brain sizes, often similar to non-avian reptiles [51–55] (figure 1), but relatively high metabolic rates closer to those of mammals than to living reptiles [56–60] (figure 2; metabolic rates of extinct species cannot be measured directly, and here are proxied by estimated maximum growth rate). This unique trait combination provides a potentially useful test of brain-related and metabolism-related explanations of variation in reproductive output traits among amniotes.

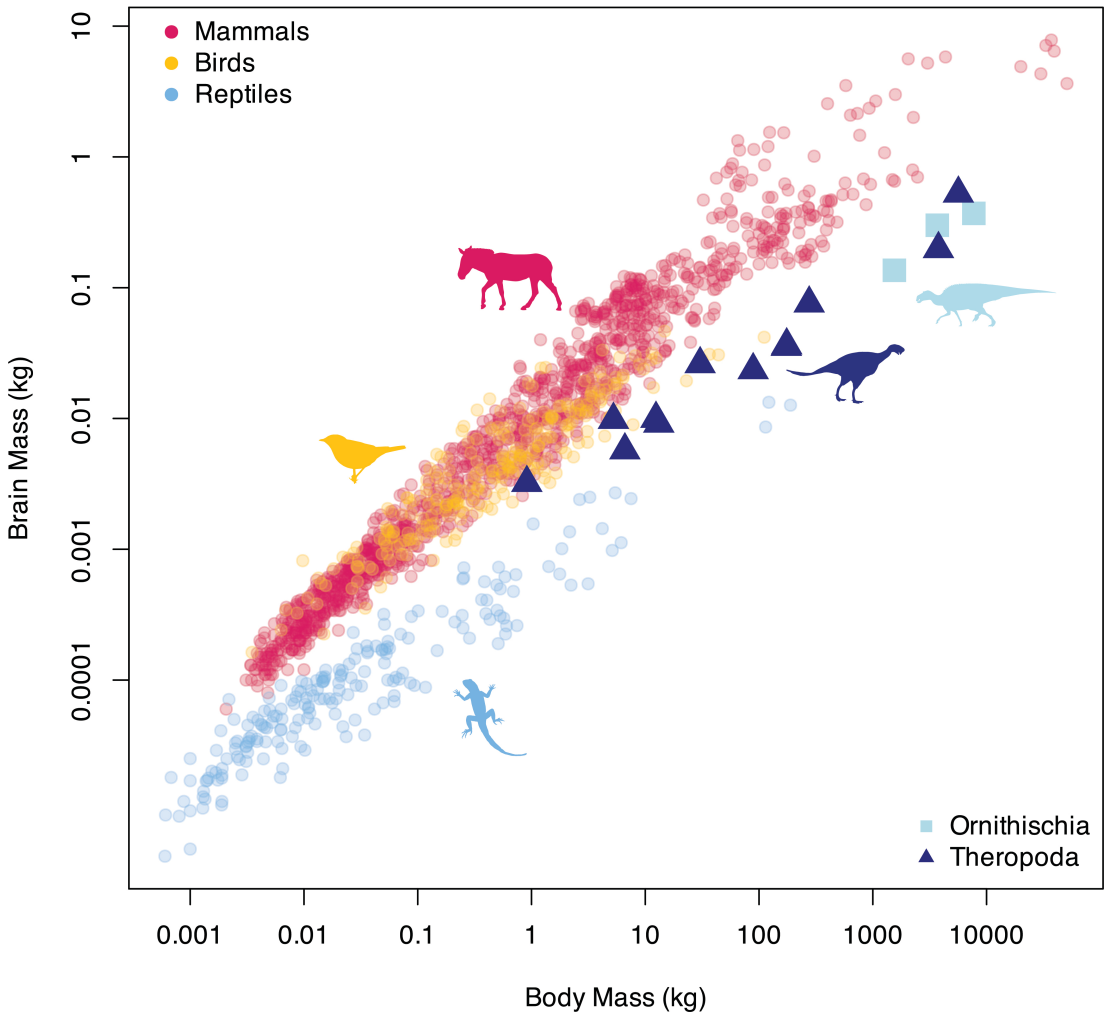


Figure 1. Plot of extant amniote groups and extinct non-avian theropod and ornithischian brain mass against body mass. The data in this plot are informative rather than interpretive and are intended to highlight the intermediate nature of hypothesized non-avian dinosaur brain size relative to extant groups. This does not impact analyses, results, or macroevolutionary interpretations, and so we present the data in its original publication form without regression lines. Silhouettes highlight *Agama agama* (Natalie Claunch; CC0 1.0), *Equus africanus* (Steven Traver; CC0 1.0), *Maiasaura peeblesorum* (Scott Hartman; CC BY-NC-SA 3.0), *Oviraptor philoceratops* (Matt Martyniuk; CC BY-NC-SA 3.0) and *Sylvia borin* (Martin Bulla; CC BY 4.0).

1.1. Proposed explanations of variation in reproductive scaling among amniotes

1.1.1. Brain size

Relative brain size (i.e. brain size relative to body mass) has been posited to impact life-history parameters and, ultimately, reproductive output. The energy trade-off hypothesis postulates a trade-off between brain growth and energetically costly aspects of body maintenance, such as growth and reproduction, due to the increased metabolic cost of a relatively larger brain [45,47,61]. Comparative studies of both birds and mammals show that species with a large relative brain size generally have smaller clutches/litters of relatively larger eggs/neonates. Relative egg/neonate mass is positively correlated with relative brain size in birds and mammals [45], relative litter size is negatively correlated with relative brain size in mammals [46,62,63] and in mammals that produce only one offspring, species with relatively larger brains have long developmental durations [62]. Increased metabolic investment in offspring is positively correlated with relative brain size in birds (incubation time [64,65]) and mammals (gestation/lactation periods [62,66]). Experimental studies in a precocial bird (*Coturnix japonica*) have also shown a negative relationship between reproductive investment (through manipulating prenatal provisioning) and maternal cerebellum size [67]. These studies provide support for the

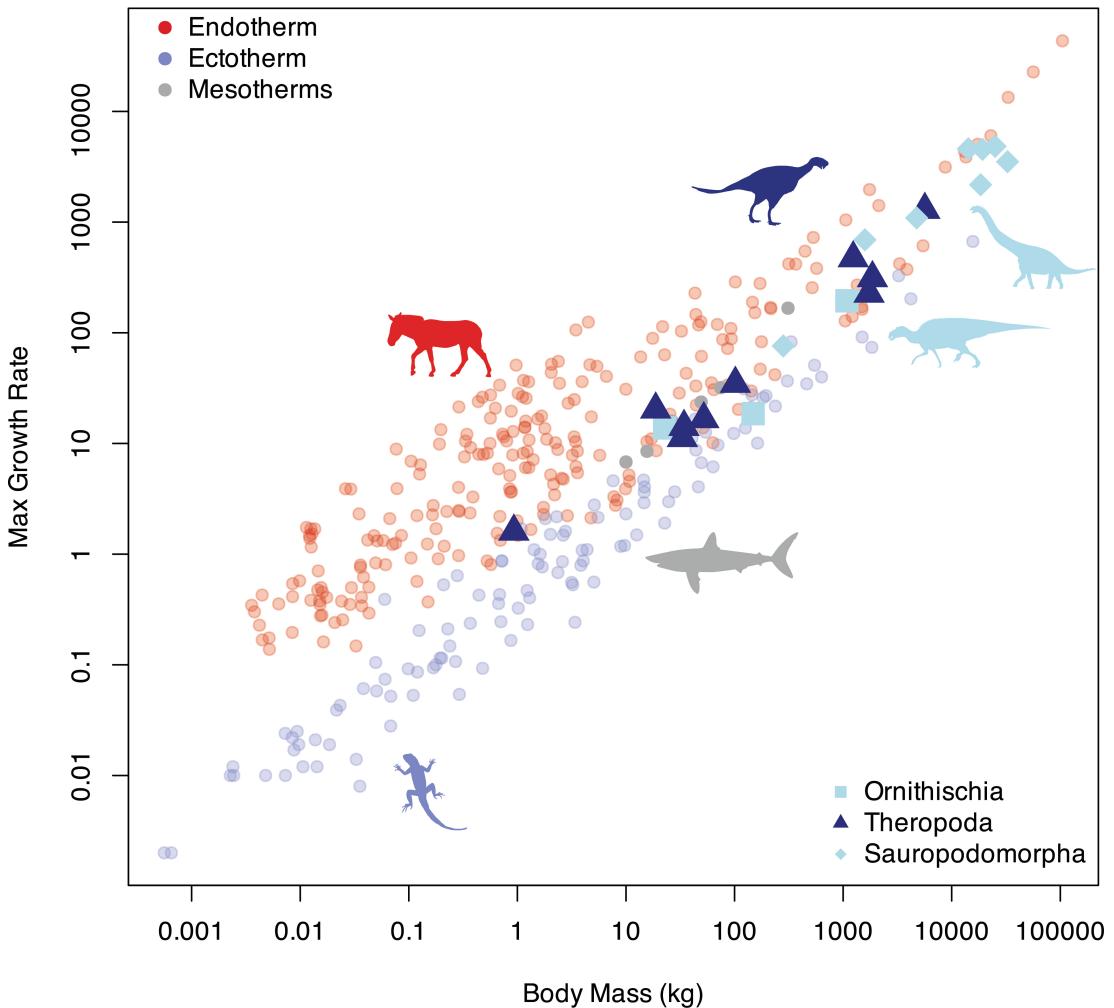


Figure 2. Plot of extant vertebrates and non-avian dinosaur maximum growth rate from Grady *et al.* [56] against body mass, with extant vertebrates and non-avian dinosaurs in dark blue, endotherms in red, ectotherms in light blue and mesotherms in grey. The data in this plot are informative rather than interpretive and are intended to highlight the intermediate nature of hypothesized non-avian dinosaur brain size relative to extant groups. This does not impact analyses, results or macroevolutionary interpretations, and so we present the data in its original publication form without regression lines. Silhouettes highlight *Euhelopus zdanskyi* (T. Michael Keesey; CC BY-SA 3.0) and *Isurus* (Fidji Berio; CC0 1.0).

expensive brain hypothesis within birds and mammals, and that evolutionary increases in brain size may require evolutionary increases in energetic investment per individual offspring.

A developmental version of this hypothesis specifically predicts the coevolution of extended parental provisioning (parental care) and increased brain size [68,69]. Increased parental care evolves to compensate for the increased energetic investment needed for the offspring to develop a relatively larger brain. This pattern is present within birds [68] and has been proposed to explain the brain size gap between endothermic groups and ectothermic groups [69]. For example, a recent comparative study across vertebrates showed that increases in brain size and relative offspring size were prevalent in endotherms (birds, mammals and chondrichthyans), but weak or non-significant in ectotherms [70]. This suggests that the evolution of large brain sizes requires both greater parental investment and stable body temperatures. Also consistent with parts of this hypothesis, Song *et al.* [71] showed that lizards sourced with free energy (e.g. basking lizards) have relatively larger brain sizes than lizards with unfavourable energy budgets (e.g. nocturnal lizards). Here, we examine these hypotheses further, considering a wider range of reproductive output traits and with quantitative data for dinosaurs on the bird-stem lineage.

Non-avian dinosaur brain sizes are often estimated from endocranial cavity volumes. The proportion of endocast volume occupied by the brain varies among extant amniotes, with mammal and

bird brains filling approximately the entire endocranial cavity [64], and most reptile brains filling approximately 66–33% of the endocranial cavity [54,72]. The relative volume of the endocranial cavity has been used to estimate relative brain size in non-avian dinosaurs [51,54,73]. Non-avian dinosaurs (excluding sauropodomorphs) possessed relative brain sizes larger than that of extant reptiles and smaller than that of extant birds and mammals [55], and brain sizes varied by group, with ornithomimids and maniraptoran theropods possessing relatively larger brains for their body size [73,74]. A deeper understanding of these energetic trade-offs present among living reptiles may indicate an ancestral condition of reproductive output scaling and brain size, and potentially the degree of parental provisioning, present within non-avian dinosaurs (figure 1).

1.1.2. Metabolic rate

BMR [75] is thought to affect reproductive output through the partitioning of energy between maintenance, growth and reproduction [48]. The increased-intake hypothesis suggests that a relatively high BMR, linked with high rates of assimilation of energy from the environment, is correlated with greater reproductive success [48,49]. Experimental studies of the Marsh Tit (*Parus palustris*) show that as brood size was artificially increased, adult BMR also increased [49]. In contrast, the compensation hypothesis (or allocation hypothesis) predicts that BMR should be negatively correlated with reproductive output [48,49,76]. A higher BMR would require greater energetic investment into maintenance costs and reduce energetic investment into reproduction. This hypothesis has found mixed support, with a low BMR being correlated with higher reproductive output at the individual level in Leach's storm-petrels (*Oceanodroma leucorhoa*) [48], while small mammals show no relationship between BMR and reproductive output traits [77]. Physiological hypotheses such as this predict how a taxon's total reproductive output (e.g. total clutch mass) may vary in response to metabolic rate. It does not specify whether the relative change in reproductive output occurs through a shift in the size and/or number of offspring. These broader predictions contrast with those of brain size-related hypotheses, which more specifically predict greater investment in individual offspring, and potentially egg/neonate size with increasing brain size. The present study aims to test whether metabolic rate broadly influences total reproductive output across amniotes and, importantly, the mechanism by which this total output is varied.

Hypotheses regarding the metabolic rates of non-avian dinosaurs vary, from true endothermy, similar to that of extant mammals or birds, in theropod dinosaurs (often insulated with feathers) [57,78], to intermediate BMRs, lower than those of extant mammals and birds, in some other dinosaurs [57]. Non-avian dinosaur growth rates are intermediate between those of living endotherms and ectotherms, higher than extant reptiles but lower than birds and mammals [56,79], and are used as evidence of intermediate metabolic rates in non-avian dinosaurs (figure 2; but see [80] for issues with growth rate as a metabolism proxy). Similar to the potential implications of testing the expensive brain hypothesis in extant reptiles, understanding the relationship between metabolism and reproductive output within reptiles may clarify existing hypotheses regarding non-avian dinosaur metabolism (figure 2).

Here, we investigate the scaling of three reproductive output traits: clutch (or litter) mass, egg (or neonate) mass and clutch (or litter) size across living and extinct amniotes, including birds, crocodylians, squamates, turtles, mammals and non-avian dinosaurs. We use phylogenetic generalized linear regressions of reproductive output traits against brain size and metabolic rate, controlling for variation in adult body mass, to evaluate drivers of trade-offs between clutch/litter size and individual egg/neonate mass within these groups. We then characterize the scaling relationships of these traits in non-avian dinosaurs to document patterns of change in reproductive output along the bird-stem lineage. These analyses place constraints on the primitive condition for amniotes, the prevailing mode of reproduction in dinosaur-dominated terrestrial ecosystems of the Mesozoic and potential explanations of the evolution of large egg sizes in birds.

2. Methods

2.1. Taxon selection

2.1.1. Extant amniotes

We collected data on reproductive output traits, metabolic rates and brain size across 2857 extant amniote species, including 541 birds, 23 crocodylians, 1187 squamates, 56 turtles and 851 mammals (table 1). All measurements were log₁₀-transformed prior to analysis.

2.1.2. Non-avian dinosaurs

We included data for non-avian dinosaur eggs and egg clutches for which the egg-laying species (referring to the body fossil species, not the ootaxon) of the group was known, allowing an estimate of adult body mass. This allowed egg mass data for 35 non-avian dinosaurs, including five ornithischians, 12 theropods and 17 sauropods [31,43,44,81], and clutch mass or clutch size data for three ornithischians, seven theropods and three sauropods [31,43,44,81]. These three reproductive output traits, together with adult body mass estimates, were available for *Protoceratops andrewsi* [44], *Troodon formosus* [34], *Massospondylus carinatus* [44], *Maiasaura peeblesorum* [30], *Citipati osmolskae* [29], an unspecified lambeosaurine and two sauropods [44]. We also estimated group-level body mass range (e.g. for adult body size in indeterminate sauropod eggs for which the egg-laying species is not known).

Phylogenies for use in phylogenetic generalized least squares (PGLS) regressions were derived from pruned versions of the bird tree distribution from McTavish *et al.* [82] (9239 species), squamate tree distribution from Tonini *et al.* [83] (9574 species), mammal tree distribution from Upham *et al.* [84] (5911 species), crocodilian phylogeny from Kumar *et al.* [85] (62 species) and turtle phylogeny from Thomson *et al.* [86] (279 species). We performed each of our analyses on the consensus tree. Polytomies present in the squamate tree were randomly resolved. Phylogenies were read in and generated using the R package 'ape' [87] in R v. 4.1.2.

2.2. Data

We gathered data from the literature on the reproductive output traits of clutch mass, egg mass and clutch size in birds and reptiles, with all masses in kilograms (see electronic supplementary material). Some squamate egg sizes [88] were given in volume (mm³) and were converted to mass assuming a density of 1.03 cc g⁻¹ [89]. For squamate taxa for which no egg masses were available, hatchling or neonate mass was used instead [90]. Within placental mammals, we collected reproductive output traits of litter mass, neonate mass, weaning mass and litter size. In marsupial mammals, we used the mass at pouch vacation as our proxy neonate mass [91], as this may reflect a degree of parental investment similar to that involved in the *in utero* growth of placental mammal offspring. Within non-avian dinosaurs, egg masses were derived from both egg volumes or linear measurements using equations depending on the shape (ellipsoidal or spherical) of the egg [92]. Reproductive output traits of living species were primarily sourced from Werner & Griebeler [43,44] (precocial birds, mammals and crocodylians), Ernest [93] (mammals) and Meiri *et al.* [23] (squamates), in addition to various other sources (see electronic supplementary material).

Our analyses primarily used species body mass values (in kg) as a dependent variable for the scaling of reproductive output traits. For this, we compiled data on female body masses where possible and alternatively used non-sex-specific body masses to maximize sample size (see electronic supplementary material for data). Intraspecific female body masses can significantly differ from male body masses (sexual dimorphism [94,95]) and therefore may influence intraspecific analyses of body size scaling. However, the large range of body sizes within our regression models (approx. 70 000 000-fold variation in mammals, approx. 17 000-fold variation in birds and approx. 500 000-fold variation in squamates) decreases the potential bias caused by dimorphism of adult body masses within species. When possible, adult body masses from the same datasets as the neonatal body masses were used, and in all other instances, body masses were taken from other references. For non-avian dinosaurs, body masses were estimated using scaling equations that estimate tetrapod body mass using the shaft circumferences of the humerus and femur, in quadrupeds, or only the femur, in bipeds [96]. Comparisons with extant reptiles and mammals, utilizing femoral and humeral circumferences, have

Table 1. Number of species (*n*) per group included in each regression model set.

group	regression model set	<i>n</i>
birds	reproductive output	458
	metabolic rate	100
	brain size	65
	brain size and metabolic rate	22
crocodylians	reproductive output	18
	metabolic rate	NA
	brain size	2
	brain size and metabolic rate	NA
squamates	reproductive output	1338
	metabolic rate	82
	brain size	114
	brain size and metabolic rate	21
turtles	reproductive output	21
	metabolic rate	NA
	brain size	NA
	brain size and metabolic rate	NA
mammals	reproductive output	818
	metabolic rate	350
	brain size	583
	brain size and metabolic rate	251
non-avian dinosaurs	reproductive output	13
	metabolic rate	NA
	brain size	NA
	brain size and metabolic rate	NA

been shown to be independent of phylogenetic history, gait and limb posture [97,98]. These estimations are highly congruent with volumetric models [96].

We also gathered data on the BMRs of birds and mammals and standard metabolic rates (SMRs) of squamates (see electronic supplementary material). Metabolic rates were sourced from Clarke *et al.* [99] (mammals), McNab [100] (birds) and White & Seymour [101] (reptiles). Metabolic rates were converted to Watts using the conversion factor of $0.278 \text{ W} = 1 \text{ kJ h}^{-1}$ [102]. SMR in reptiles is often measured in ml of O_2 respired per hour at a specific temperature representing the possible ambient range (1–45°C). In this study, we used the temperature-normalized (38°C) Q10 SMR (see [103,104] for method) value for our reptiles and the conversion factor of $1 \text{ ml h}^{-1} = 0.0056 \text{ W}$.

We gathered data on the general developmental state of offspring (altricial | precocial) to test for its potential effects on reproductive scaling across birds and mammals [44,105,106]. We also tested for the presence of a relationship between quantitative, continuous proxies of developmental state of offspring in birds [107] and reproductive output traits (results reported in electronic supplementary material, table S5).

We gathered data on brain size (in kg) within birds, squamates and mammals (see electronic supplementary material). Brain mass was sourced from Stark & Pincheira-Donoso [108] (squamates), Ksepka *et al.* [55] (birds) and Smaers *et al.* [109] (mammals).

2.3. Developing allometric relationships for reproduction, metabolism and encephalization in birds, reptiles, mammals and dinosaurs

All statistical analyses were run in R v. 4.5.2 (R Foundation for Statistical Computing). PGLS analysis was run using the ‘comparative.data’ and ‘pgls’ functions of caper v. 1.0.1 [110]. We compared regression models using Akaike’s information criterion for finite sample sizes (AICc) [111], and calculated AICc weights [112] using the ‘akaike.weights’ function of qpcR v. 1.4.1 [113]. Levene’s test for variance homogeneity was run using the ‘leveneTest’ function of car v. 3.1.3 [114].

We estimated phylogenetic signal in the relationships between traits during the fitting of PGLS regression models using Pagel’s λ [115], for which a λ of zero indicates an absence of phylogenetic signal in the regression residuals, while a λ of 1.0 indicates that residuals conform to expectations under Brownian motion [116]. We allowed λ to vary freely, and we fit the value of λ using maximum likelihood while fitting our PGLS models. Pagel’s lambda was chosen over Blomberg’s K due to its robust nature when dealing with incomplete phylogenies, the presence of soft polytomies and incomplete branch length information [117]. Pagel’s lambda was computed using the ‘lambda’ argument in the ‘pgls’ function of caper v. 1.0.1 [110].

To estimate reproductive scaling relationships across birds, non-avian reptiles, mammals and dinosaurs, we ran the following regression equations for each group: (i) clutch/litter mass $\sim$ body mass, (ii) egg/neonate mass $\sim$ body mass and (iii) clutch/litter size $\sim$ body mass. To compare the reproductive scaling of non-avian dinosaurs to living groups of amniotes, we evaluated the fit of dinosaur reproductive output data to models derived for each major extant group (mammals, birds, squamates, crocodylians and turtles) both visually and through model parameter comparisons (e.g. slope and intercept).

To analyse the partial effects of the developmental state of offspring (altricial versus precocial) on the scaling relationships between reproductive output traits and adult body mass, we ran the following regressions in birds and mammals: (iv) clutch/litter mass $\sim$ body mass * developmental mode, (v) egg/neonate mass $\sim$ body mass * developmental mode, (vi) clutch/litter size $\sim$ body mass * developmental mode. The significance of differences in slope between altricial and precocial species was evaluated using the significance of the interaction term, and we used AICc weights to compare these to simpler models, e.g. (for [iv]) clutch/litter mass $\sim$ body mass + developmental mode, clutch/litter mass $\sim$ body mass and an intercept-only null model clutch/litter mass $\sim$ 1.

We then developed regressions to analyse the effects of body mass, brain size and metabolic rate on reproductive output traits within birds, squamates and mammals. We ran regressions of the following general form to determine the partial effects of brain mass and metabolic rate on reproductive output traits after accounting for variation in body mass (e.g. clutch/litter mass $\sim$ brain mass + body mass), also comparing to simpler models using AICc weights, as above. For visualization of the relationships between traits corrected for variation in adult body mass, we plotted PGLS residuals (on body mass) of reproductive output traits, brain size and metabolic rates on body mass.

These regressions were carried out separately for birds, squamates and mammals. Interaction terms were also used to test for variation in reproductive scaling within groups (e.g. placental | marsupials; varanid lizard | snake | non-varanid lizards). Varanid lizards were grouped separately from non-varanid lizards, given that varanid lizards have previously been used in comparative analysis to assess metabolism and thermoregulation in non-avian dinosaurs [60,100,118–120]. Previous works on dinosaur biology utilizing modern comparisons have also differentiated between varanid lizards and other lizards and reptiles [120]. Placentals and marsupials were separated on the basis of their differing reproductive strategies.

2.4. Dinosaur phylogeny and ancestral character estimation

To visualize the potential shifts in reproductive output scaling across dinosaur evolution, we generated a tree for Dinosauria, including living birds, using the pruned versions of the bird tree distribution from Jetz *et al.* [121] (9993 species; based on the Hackett *et al.* backbone [122]) and the time-calibrated non-avian dinosaur tree from Benson *et al.* (624 taxa) [123]. Ancestral character estimation for our continuous reproductive output trait (clutch mass/egg mass/clutch size) was done using the ‘contMap’ function of phytools v. 1.2 [124]. This package estimates internal node character states using maximum likelihood with the ‘fastAnc’ function, which reroots the tree at all internal nodes and calculates the contrast state at the root each time [125,126]. This results in values that equal the maximum likelihood

estimates under a Brownian evolutionary process [116]. We chose to use a Brownian model as it makes the fewest assumptions and accounts for uncertainty across major evolutionary transitions (e.g. dinosaur–bird). There are alternative models for estimating ancestral states of reproductive output traits, such as Ornstein–Uhlenbeck(OU) and early burst (EB). Future studies could investigate these models to determine if they fit reproductive scaling traits and are consistent with our findings.

3. Results

3.1. Allometry of reproductive output traits

3.1.1. Clutch/litter mass

A significant, positive relationship between clutch/litter mass and body mass is present in all living groups, with slopes <1.0 , indicating negative allometry. Isometry (slope = 1.0) is outside two standard errors (s.e.) of the slope estimate in all groups (slope ± 2 s.e.: birds = 0.575–0.675, squamates = 0.818–0.878 (non-snake squamates), mammals = 0.705–0.761, crocodylians = 0.475–0.959), except in turtles (slope ± 2 s.e. = 0.834–1.06) and snakes (0.951–1.01; based on significant interaction term; [figure 3](#); [table 2](#); electronic supplementary material, table S1). Non-avian dinosaurs also exhibit non-significant, negative allometry between clutch mass and body mass that is closer in slope (0.141–0.733) to those of birds and crocodylians than to those of squamates or mammals ([figure 3](#); [table 2](#); electronic supplementary material, table S1). Non-avian dinosaurs also show greater variation around the relationship between clutch mass and body mass than other groups ($R^2 = 0.29$ in dinosaurs; $R^2 = 0.6$ in birds; $R^2 = 0.76$ in squamates; $R^2 = 0.79$ in mammals; differences $p > 0.001$; Levene's test; electronic supplementary material, table S7) with theropods generally showing higher relative clutch mass than other dinosaurs ([figure 3](#); see also [39]).

3.1.2. Egg/neonate mass

A significant, positive relationship between egg/neonate mass and body mass is present in all living groups, with slopes that indicate negative allometry ([figure 4](#); [table 2](#); electronic supplementary material, table S1; slope ± 2 s.e. birds = 0.669–0.741 (altricial) or 0.672–0.744 (precocial, based on significant interaction term), squamates = 0.607–0.655, mammals = 0.677–0.757 (altricial) or 0.592–0.664 (precocial, based on significant interaction term), crocodylians = 0.206–0.414, and turtles (slope = 0.164–0.404). Dinosaurs show a significant, negative allometry between egg mass and body mass (slope ± 2 s.e. = 0.185–0.633) that is more similar in slope to crocodylians than to other groups ([figure 4](#); [table 2](#); electronic supplementary material, table S1). Variation around the relationship between egg mass and body mass in dinosaurs is similar to that of extant groups ($R^2 = 0.59$ in dinosaurs; $R^2 = 0.83$ in birds; $R^2 = 0.67$ in squamates; $R^2 = 0.79$ in mammals), although a statistically significant difference in variance is present ($p < 0.001$; Levene's test; electronic supplementary material, table S7).

3.1.3. Clutch size

A significant, positive relationship between clutch size and body mass is present in living non-avian reptiles, with a slope that indicates negative allometry in squamates (slope ± 2 s.e. = 0.189–0.237 (non-snake squamates) or 0.278–0.326 (snakes, based on significant interaction term)), crocodylians (slope ± 2 s.e. = 0.226–0.606) and turtles (slope ± 2 s.e. = 0.461–0.673; [figure 5](#); [table 2](#); electronic supplementary material, table S1). In contrast, a significant inverse scaling relationship (i.e. reverse allometry) of clutch/litter size with body mass is present in altricial birds (slope ± 2 s.e. = –0.138 to –0.010) and marsupials (slope ± 2 s.e. = –0.181 to –0.061), whereas the slope is not significantly different from zero in precocial birds (slope ± 2 s.e. = –0.037 to 0.092) and placental mammals (slope ± 2 s.e. = –0.087 to 0.033; [figure 5](#); [table 2](#); electronic supplementary material, table S1). Dinosaurs exhibit a non-significant relationship between clutch size and body mass (slope ± 2 s.e. = –0.111 to 0.169). All groups exhibit statistically significant differences in variance ($p < 0.001$; Levene's test; electronic supplementary material, table S7).

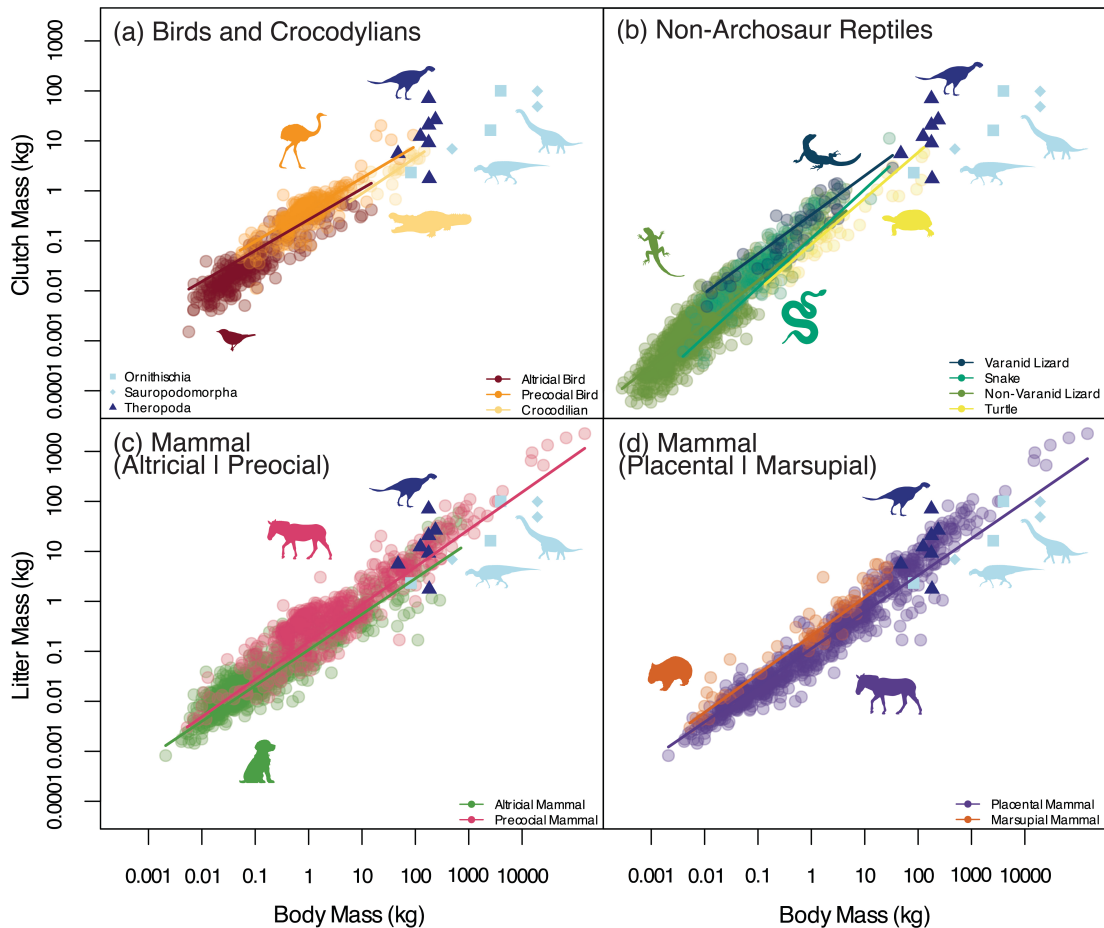


Figure 3. (a) Plot of clutch mass in archosaurs (altricial birds/precocial birds/crocodylians). (b) Plot of clutch mass in squamates (non-varanid lizards/varanid lizards/snakes) and turtles. (c) Plot of litter mass in altricial and precocial mammals. (d) Plot of litter mass in placental and marsupial mammals. Non-avian dinosaurs are plotted in light and dark blue in each plot. Silhouettes highlight *Crocodylinae anthropophagus* (Nobu Tamura, vectorized by Zimices; CC BY-SA 3.0), *Crotalus viridis* (Blair Perry; CCO 1.0), *Gopherus agassizii* (Andrew A. Farke; CC BY 3.0), *Rhea americana* (Ferran Sayol; CCO 1.0), *Varanus komodoensis* (Steven Traver; CCO 1.0) and *Vombatus ursinus* (Sarah Werning; CC BY 3.0).

3.2. The effect of developmental state on reproductive output

After controlling for body mass in extant amniotes, we found that developmental state (precociality versus altriciality) has significant effects on some reproductive output traits (table 2; electronic supplementary material, table S1), primarily that precocial birds and mammals have larger clutches/litter masses than altricial species. In birds, precociality has a positive relationship with clutch mass (coefficient = 0.193, $p < 0.05$) and clutch size (coefficient = 0.188, $p < 0.05$) but none with egg mass (coefficient = 0.003; $p = 0.9549$). Interaction terms with developmental state are included in the best models (based on AICc weight; electronic supplementary material, table S1) of the relationships of egg mass and clutch size with body mass, indicating precocial species have a shallower slope of egg mass on body mass than altricial species (interaction term = -0.078 ; $p = 0.011$), and a steeper slope of clutch size and body mass (interaction term = 0.101 ; $p = 0.05$), described above (see table 2).

In mammals, precociality has a significant positive relationship with litter mass (coefficient = 1.737; $p \leq 0.05$) and neonate mass (coefficient = 0.298; $p = 0.002$) and a significant negative relationship with litter size ($n = 818$; coefficient = -0.182 ; $p = 0.0081$; although a model instead including marsupial | placental is better supported by AICc; electronic supplementary material, table S1). An interaction term with developmental state is included in the best models of the relationships of neonate mass, indicating a steeper slope of the relationship between neonate mass and body mass in precocial mammals (interaction term: 0.069 ; $p = 0.015$). The best model for the relationship of litter size to body mass includes a significant interaction term with placental | marsupial, indicating a less negative relationship between litter size and body mass in placentals than in marsupials (interaction term =

Table 2. Regression results from bird, squamate, and mammal clutch/litter mass, egg/neonate mass, and clutch/litter size scaling with developmental state (altricial | precocial: birds and mammals) and group (non-varanid lizard | varanid lizard | snake and placental | marsupial) (asterisk indicates statistically significant p -value). All continuous variables were log10-transformed. Altriciality is the default state of altricial | precocial, marsupial is the default state of placental | marsupial for mammals, and non-varanid lizards are default state of non-varanid lizard | varanid | snake for squamates. Regression models with an AICc weight greater than 0.125 were reported, for full results and detailed coefficients see electronic supplementary material, table S1.

group	model	R^2	term	estimate	s.e.	p	weight	n
birds	clutch mass ~ body mass + altricial precocial	0.599	intercept	-0.5668	0.145	0*	0.676	458
			body mass	0.6251	0.025	0*		
squamates	clutch mass ~ body mass * non-varanid lizard varanid snake	0.7639	precocial	0.193	0.074	0*		
			intercept	-0.9485	0.1	0*	0.997	1338
			body mass	0.8476	0.015	0*		
			snake	0.0022	0.13	0.9862		
mammals	litter mass ~ body mass + altricial precocial	0.788	varanid	0.4721	0.181	0*		
			body mass: snake	0.1336	0.038	0*		
			body mass: varanid	-0.0653	0.046	0.1607		
			intercept	-0.9747	0.269	0*	0.421	818
			body mass	0.7326	0.014	0*		
crocodylians	clutch mass ~ body mass	0.688	precocial	0.1737	0.086	0*		
			intercept	-0.771	0.255	0*	NA	18
turtles	clutch mass ~ body mass	0.962	body mass	0.717	0.121	0*		
			intercept	-1.067	0.04	0*	NA	21
non-avian dinosaurs	clutch mass ~ body mass	0.443	body mass	0.92	0.043	0*		
			intercept	0.022	0.421	0.958	NA	13
birds	egg mass ~ body mass * altricial precocial	0.828	body mass	0.437	0.148	0.013*		
			intercept	-1.164	0.082	0*	0.741	458
			body mass	0.7051	0.018	0*		
	precocial			0.0025	0.043	0.9549		

(Continued.)

Table 2. (Continued.)

group	model	R ²	term	estimate	s.e.	p	weight	n
squamates	egg mass ~ body mass + non-varanid lizard varanid snake	0.6667	body mass: precocial	−0.0775	0.03	0*		
			intercept	−1.9163	0.102	0*	0.944	1338
			body mass	0.6307	0.012	0*		
			snake	−0.0645	0.117	0.582		
mammals	neonate mass ~ body mass * altricial precocial	0.789	varanid	0.5554	0.182	0*		
			intercept	−1.3973	0.314	0*	0.945	818
			body mass	0.7165	0.02	0*		
			precocial	0.2982	0.097	0*		
crocodylians	egg mass ~ body mass	0.685	body mass: precocial	0.0687	0.028	0*		
			intercept	−1.554	0.107	0*	NA	18
			body mass	0.31	0.052	0*		
turtles	egg mass ~ body mass	0.552	intercept	−2.045	0.131	0*	NA	21
			body mass	0.284	0.06	0*		
non-avian dinosaurs	egg mass ~ body mass	0.587	intercept	−1.228	0.318	0.003*	NA	13
			body mass	0.409	0.112	0.004*		
birds	clutch size ~ body mass * altricial precocial	0.019	intercept	0.5882	0.171	0*	0.429	458
			body mass	−0.0737	0.032	0*		
			precocial	0.1884	0.085	0*		
squamates	clutch size ~ body mass * non-varanid lizard varanid snake	0.2615	body mass: altricial precocial	0.1012	0.052	0.0504*		
			intercept	0.96	0.09	0*	0.924	1338
			body mass	0.213	0.012	0*		
			snake	0.005	0.107	0.961		
	varanid			−0.053	0.16	0.738		

(Continued.)

Table 2. (Continued.)

group	model	R^2	term	estimate	s.e.	p	weight	n
mammals	litter size ~ body mass * placental marsupial	0.027	body mass: snake	0.089	0.03	0.003		
			body mass: varanid	0.004	0.037	0.924		
			intercept	0.3958	0.318	0.2129	0.572	818
			body mass	-0.121	0.03	0*		
			placental	-0.1715	0.42	0.6835		
crocodylians	clutch size ~ body mass	0.544	body mass: placental	0.0943	0.032	0*		
			intercept	0.784	0.155	0*	NA	18
			body mass	0.416	0.095	0*		
turtles	clutch size ~ body mass	0.864	intercept	0.983	0.048	0*	NA	21
			body mass	0.567	0.053	0*		
non-avian dinosaurs	clutch size ~ body mass	0.015	intercept	1.25	0.198	0*	NA	13
			body mass	0.029	0.07	0.689		

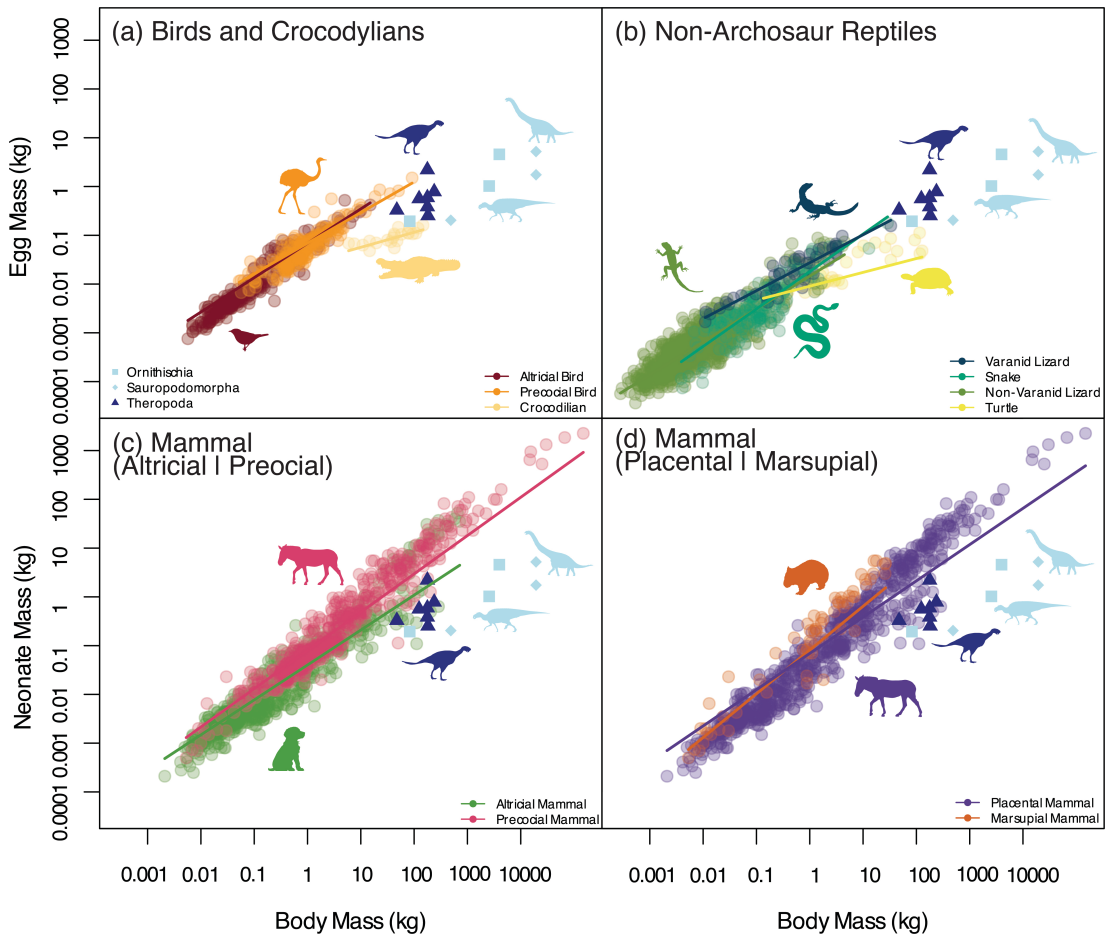


Figure 4. (a) Plot of egg mass in archosaurs (altricial birds/precocial birds/crocodylians). (b) Plot of egg mass in squamates (non-varanid lizards/varanid lizards/snakes) and turtles. (c) Plot of neonate mass in altricial and precocial mammals. (d) Plot of neonate mass in placental and marsupial mammals. Non-avian dinosaurs are plotted in light and dark blue in each plot.

0.0943, $p < 0.05$), described above (see [table 2](#)). Results for quantitative proxies of developmental state of offspring in birds can be found in the electronic supplementary material (electronic supplementary material, table S5).

3.3. The effect of metabolism (basal metabolic rate and standard metabolic rate) on reproductive output

We found mixed support for relationships between metabolic rates and reproductive output traits among groups ([table 3](#); electronic supplementary material, table S2; all results for partial effects of metabolic rates after accounting for adult body mass variation). There were no significant relationships in birds. Within squamates, SMR shows a significant negative relationship with egg mass (slope = -0.302 , $p \leq 0.05$) and no significant relationship with clutch mass or clutch size ([table 3](#)). Within mammals, BMR shows a significant positive relationship with litter mass (slope = 0.95 , $p \leq 0.05$) and neonate mass (slope = 0.102 , $p \leq 0.05$; [table 3](#)). The interaction with developmental state of offspring (altricial | precocial) is not included in any form among the best models of these relationships (based on AICc weights) and has no effect on the relationship between BMR and reproductive output traits (electronic supplementary material, table S2).

3.4. The effect of brain size on reproductive output

We found significant relationships between relative brain mass and several reproductive output traits ([table 4](#); electronic supplementary material, table S3; all results for partial effects of brain mass after accounting for adult body mass variation). Within birds, brain size shows a significant positive

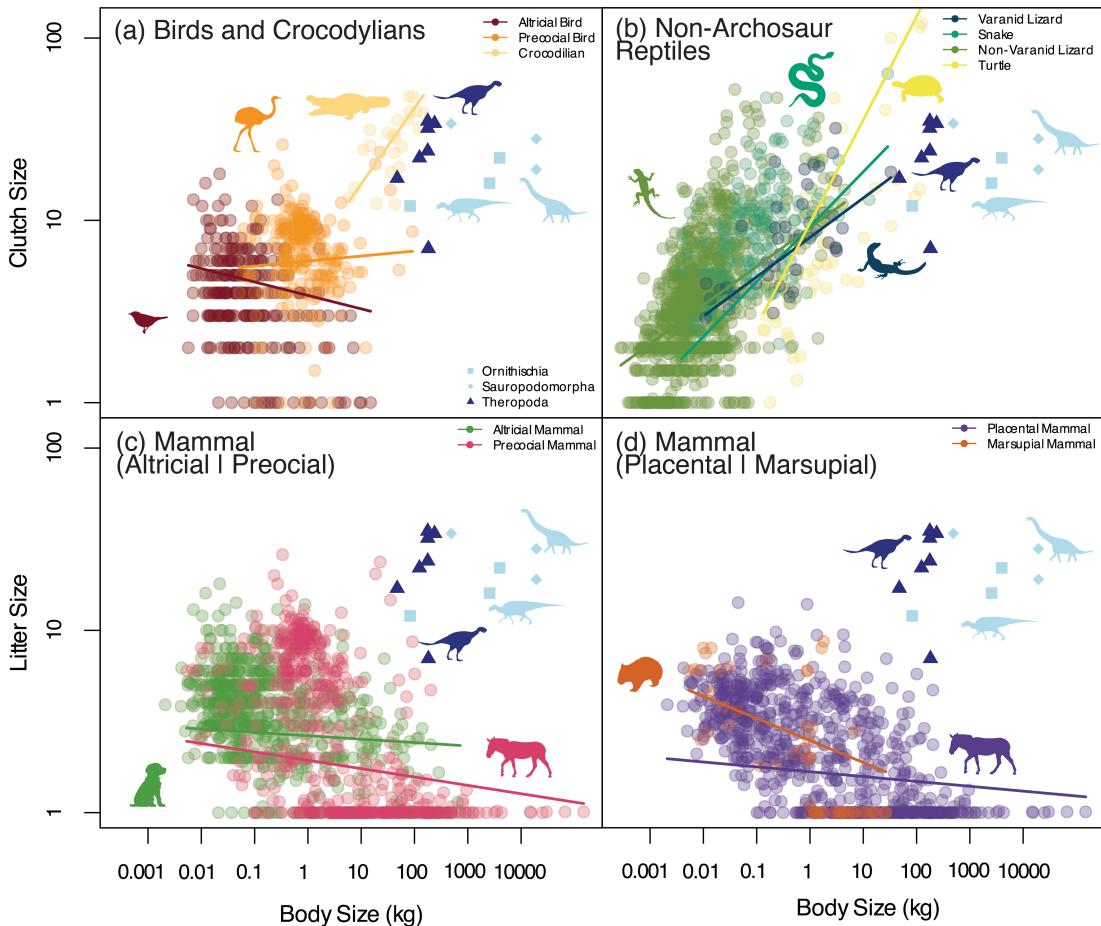


Figure 5. Plot of clutch/litter size against body mass. (a) Plot of clutch size in archosaurs (altricial birds/precocial birds/crocodylians). (b) Plot of clutch size in squamates (non-varanid lizards/varanid lizards/snakes) and turtles. (c) Plot of litter size in altricial and precocial mammals. (d) Plot of litter size in placental and marsupial mammals. Non-avian dinosaurs are plotted in light and dark blue in each plot.

relationship with egg mass (slope = 0.449, $p \leq 0.05$), but no statistically significant relationship with clutch mass or clutch size (table 4). Within squamates, brain size shows no significant relationship with any reproductive output traits. Within mammals, brain size has a significant positive relationship with litter mass (slope = 0.182; $p \leq 0.05$) and neonate mass (slope = 0.307; $p \leq 0.05$) and a significant negative relationship with litter size (slope = -0.12, $p \leq 0.05$; table 4). The interaction with developmental state of offspring (altricial | precocial) had no effect on the relationship between brain size and reproductive output traits (electronic supplementary material, table S3). In mammals, marsupial | placental had no significant effect on the scaling relationship between brain size and reproductive output traits.

4. Discussion

We examined the scaling of reproductive output traits with adult body mass across major groups of extant amniotes (birds, reptiles and mammals) and in dinosaurs. All groups show increasing clutch/litter mass and egg/neonate mass with increasing adult body size, albeit with negative allometry (figures 3 and 6). The scaling relationships of clutch/litter mass show relatively little variation among groups (figure 6), whereas the scaling relationships of egg/neonate mass vary more (figure 6), and the scaling relationships of clutch/litter size show considerably greater variation, including both positive relationships (in crocodylians, squamates and turtles), inverse relationships (in birds and mammals) and relationships that cannot be distinguished from zero (non-significant) (in dinosaurs) (figure 6). These results show that variation in the scaling relationship of the number of individual offspring produced (i.e. clutch/litter size) is the largest source of variation in reproductive output among major amniote groups. Turtles possess the smallest egg/neonate mass for their body size, whereas placental

Table 3. Regression results from bird and squamate clutch mass, egg mass and clutch size, and mammal litter mass, neonate mass and litter size scaling with metabolic rate models (asterisk indicates statistically significant p -value). All continuous variables were log10-transformed. Altriciality is the default state of altricial | precocial, marsupial is the default state of placental | marsupial for mammals, and non-varanid lizards are default state of non-varanid lizard | varanid | snake for squamates. Regression models with an AICc weight greater than 0.125 were reported, for full results and detailed coefficients see electronic supplementary material, table S2.

group	model	R^2	term	estimate	s.e.	p	AICc weight	n
birds	clutch mass ~ metabolic rate + body mass	0.683	intercept	-0.403	0.165	0.017	0.605	100
			metabolic rate	-0.197	0.112	0.083		
birds	clutch mass ~ body mass	0.678	body mass	0.767	0.091	0		
			intercept	-0.512	0.148	0.001	0.395	100
birds	egg mass ~ body mass	0.819	body mass	0.631	0.044	0		
			intercept	-1.153	0.101	0	0.725	100
birds	egg mass ~ metabolic rate + body mass	0.819	body mass	0.664	0.032	0		
			intercept	-1.133	0.112	0	0.275	100
birds	clutch size ~ altricial precocial	0.0372	metabolic rate	-0.036	0.084	0.669		
			body mass	0.689	0.067	0		
birds	clutch size ~ metabolic rate + altricial precocial	0.0437	intercept	0.496	0.21	0.02	0.39	100
			precocial	0.313	0.161	0.054		
birds	clutch size ~ 1	0	intercept	0.519	0.211	0.015	0.182	100
			body mass	-0.037	0.05	0.46		
birds	clutch size ~ metabolic rate * altricial precocial	0.0347	metabolic rate	-0.047	0.06	0.438		
			precocial	0.325	0.161	0.046		
birds	clutch mass ~ metabolic rate + body mass	0.8172	intercept	0.719	0.18	0	0.169	100
			body mass	-0.037	0.05	0.46		
birds	clutch mass ~ metabolic rate + body mass	0.8172	intercept	0.493	0.209	0.02	0.154	100
			body mass	-0.037	0.05	0.46		
squamates	clutch mass ~ metabolic rate + body mass	0.8172	metabolic rate	-0.114	0.078	0.146		
			precocial	0.271	0.164	0.102		
squamates	clutch mass ~ metabolic rate + body mass	0.8172	metabolic rate: precocial	0.164	0.123	0.185		
			intercept	-1.108	0.282	0	0.631	82

(Continued.)

Table 3. (Continued.)

group	model	R ²	term	estimate	s.e.	p	AICc weight	n
squamates	clutch mass ~ body mass	0.8098	metabolic rate	−0.271	0.152	0.079		
			body mass	1.123	0.13	0		
			intercept	−0.639	0.103	0	0.369	82
squamates	egg mass ~ metabolic rate + body mass	0.6607	body mass	0.909	0.049	0		
			intercept	−2.38	0.264	0	0.827	82
			metabolic rate	−0.302	0.132	0.024		
squamates	egg mass ~ body mass	0.6309	body mass	0.853	0.119	0		
			intercept	−1.871	0.143	0	0.173	82
			body mass	0.598	0.051	0		
squamates	clutch size ~ body mass	0.275	intercept	1.082	0.109	0	0.629	82
			body mass	0.228	0.042	0		
			intercept	1.075	0.225	0	0.214	82
mammals	litter mass ~ metabolic rate + placental marsupial monotreme	0.7917	metabolic rate	−0.004	0.114	0.974		
			body mass	0.231	0.102	0.026		
			intercept	−1.097	0.338	0.001	0.749	350
mammals	litter mass ~ metabolic rate * placental marsupial monotreme	0.7908	metabolic rate	0.95	0.027	0		
			monotreme	−2.48	0.478	0		
			placental	−0.22	0.385	0.568		
mammals	litter mass ~ metabolic rate + placental marsupial monotreme	0.7908	intercept	−1.112	0.345	0.001	0.25	350
			metabolic rate	1.022	0.063	0		
			monotreme	−2.405	0.505	0		
mammals	litter mass ~ metabolic rate + placental marsupial monotreme	0.7908	placental	−0.195	0.393	0.619		
			metabolic rate: monotreme	−0.482	0.898	0.592		

(Continued.)

Table 3. (Continued.)

group	model	R^2	term	estimate	s.e.	p	AICc weight	n
mammals	neonate mass ~ metabolic rate + body mass	0.9972	metabolic rate: placental	−0.091	0.069	0.191		
			intercept	−1.15	0.455	0.012	0.815	350
			metabolic rate	0.102	0.046	0.026		
			body mass	0.603	0.051	0		
mammals	neonate mass ~ body mass	0.9972	intercept	−0.935	0.447	0.037	0.185	350
			body mass	0.718	0.002	0		
mammals	litter size ~ body mass	0.0767	intercept	0.098	0.196	0.619	0.577	350
			body mass	−0.083	0.015	0		
mammals	litter size ~ metabolic rate + body mass	0.078	intercept	0.033	0.217	0.88	0.268	350
			metabolic rate	0.044	0.062	0.48		
			body mass	−0.114	0.047	0.015		

Table 4. Regression results from bird and squamate clutch mass, egg mass, and clutch size, and mammal litter mass, neonate mass, and litter size scaling with brain size models (asterisk indicates statistically significant p -value). All continuous variables were log10-transformed. Altriciality is the default state of altricial | precocial, marsupial is the default state of placental | marsupial for mammals, and non-varanid lizards are default state of non-varanid lizard | varanid | snake for squamates. Regression models with an AICc weight greater than 0.125 were reported, for full results and detailed coefficients see electronic supplementary material, table S3.

group	model	R^2	term	estimate	s.e.	p	weight	n
birds	clutch mass ~ body mass	0.7904	intercept	-0.525	0.126	0	0.722	65
			body mass	0.706	0.046	0		
birds	clutch mass ~ brain size + body mass	0.7894	intercept	-0.243	0.532	0.65	0.276	65
			brain size	0.119	0.22	0.589		
birds	egg mass ~ brain size + body mass	0.9162	body mass	0.635	0.137	0		
			intercept	-0.113	0.295	0.703	0.996	65
birds	clutch size ~ altricial precocial	0.077	brain size	0.449	0.12	0		
			body mass	0.423	0.076	0	0.316	65
birds	clutch size ~ brain size + altricial precocial	0.113	intercept	0.576	0.169	0.001		
			precocial	0.29	0.127	0.025	0.306	65
birds	clutch size ~ brain size * altricial precocial	0.132	intercept	0.271	0.259	0.299		
			brain size	-0.127	0.086	0.145	0.201	65
squamates	clutch mass ~ body mass	0.752	precocial	0.334	0.125	0.01		
			intercept	0.089	0.303	0.769	0.73	114
squamates	clutch mass ~ brain size + body mass	0.756	brain size	-0.185	0.099	0.068		
			precocial	0.863	0.472	0.072		
squamates	clutch mass ~ brain size + body mass	0.756	brain size: precocial	0.227	0.195	0.249		
			intercept	-0.835	0.14	0	0.27	114
squamates	clutch mass ~ brain size + body mass	0.756	body mass	0.874	0.047	0		
			intercept	-1.087	0.721	0.135	0.27	114
squamates	clutch mass ~ brain size + body mass	0.756	brain size	-0.084	0.228	0.713		
			body mass	0.927	0.138	0		

(Continued.)

Table 4. (Continued.)

group	model	R ²	term	estimate	s.e.	p	weight	n
squamates	egg mass ~ body mass	0.753	intercept	-1.757	0.108	0	0.683	114
			body mass	0.701	0.038	0		
squamates	egg mass ~ brain size + body mass	0.748	intercept	-1.328	0.584	0.025	0.317	114
			brain size	0.142	0.185	0.442		
squamates	clutch size ~ body mass	0.213	body mass	0.613	0.112	0		
			intercept	0.936	0.095	0	0.449	114
squamates	clutch size ~ brain size + body mass	0.24	body mass	0.181	0.033	0		
			intercept	0.205	0.491	0.677	0.53	114
			brain size	-0.238	0.156	0.129		
			body mass	0.32	0.094	0.001		
mammals	litter mass ~ brain size + body mass	0.803	intercept	-2.612	0.291	0	1	583
			brain size	0.182	0.03	0		
			body mass	0.207	0.018	0		
			intercept	-2.843	0.33	0	1	583
	neonate mass ~ brain size + body mass	0.819	brain size	0.307	0.029	0		
			body mass	0.152	0.017	0		
mammals	litter size ~ brain size + body mass	0.09	intercept	0.277	0.207	0.181	0.94	583
			brain size	-0.12	0.021	0		
			body mass	0.047	0.013	0		

mammals possess the largest egg/neonate mass for their body size (figures 4 and 6). Clutch/litter size shows the opposite pattern, where turtles produce the largest numbers of eggs for their body size, while birds produce the fewest number of eggs for their body size (figures 5 and 6).

4.1. Reproductive output scaling explanations: developmental state

We find that variation in developmental state at birth is related to variation in reproductive output traits, both within and among groups (see also [121,127–130]). Both birds and mammals have high parental investment in each individual offspring compared to non-avian reptiles. This can be partitioned between prenatal investment (indexed by egg/neonate mass here) and postnatal investment, with altricial species by definition showing a higher degree of postnatal investment to care for developmentally immature offspring. Within mammals, precocial species have slightly larger litter masses, neonate masses and smaller litter sizes than altricial species (figures 3–5). In mammals, this suggests the presence of an inverse relationship between prenatal investment (i.e. investing energy in producing larger litters of heavier individual offspring) and postnatal investment (i.e. investing energy in the care and growth of offspring after birth). This relationship is also present but less pronounced in birds; precocial birds have slightly larger clutch masses and clutch sizes than altricial birds on average, as in mammals (see also [127]), but similar egg masses, unlike in mammals. There are also finer categorizations of developmental state within birds and mammals, e.g. super precociality and altriciality and intermediate stages [106], and using a more subdivided measure of developmental state may also influence patterns of reproductive scaling within groups (see electronic supplementary material for example bird regression models). However, we found little change in the interpretations using this more subdivided scale.

A comparison of the reproductive output traits of non-avian reptiles to those of birds and mammals is consistent with a model in which variation in postnatal investment is related to the trade-off between producing larger counts of smaller offspring or smaller counts of larger offspring. Most non-avian reptiles produce high counts of small offspring (figures 3–6) and also show very limited parental care; some crocodylians engage in nest-guarding behaviour, and some snakes were found to exhibit egg/neonate attending behaviours [131], but this is limited compared to the extensive parental care seen in birds and mammals. Reptiles therefore exhibit a strategy in which parental investment per individual offspring is low overall, including both prenatal investment (small egg sizes) and postnatal investment (lack of extensive parental care). Therefore, in addition to structural (e.g. nest structure) and biological evidence, high counts of small offspring may be taken as support for low postnatal parental care when seen in extinct groups (e.g. non-theropod dinosaurs [37–39] and non-mammalian synapsids [24]).

4.2. Reproductive output scaling explanations: basal (standard) metabolic rate and brain size

We found that variation in metabolic rates does not provide a useful explanation of variation in scaling relationships of reproductive output traits in amniotes (table 3). In contrast, brain size was found to explain the scaling relationships of reproductive output traits across birds and mammals (table 4) and may partially explain the transition from relatively smaller offspring in non-avian dinosaurs to relatively larger offspring in birds, along the bird-stem lineage.

4.2.1. Reproductive output scaling explanations: metabolic rate

Metabolic rate has no significant effect on reproductive output traits across amniotes, after controlling for variation in body mass. A general pattern across amniotes is not present, as most relationships are non-significant, although we do find a statistically significant relationship between BMR and litter mass and neonate mass in mammals (table 3). Outside of mammals, therefore, we find no support for either the compensation hypothesis [48,49] or the increased-intake hypothesis [48] as possible explanations for the scaling relationships of reproductive output traits in most amniotes.

The absence of a widespread relationship between metabolic rate and reproductive output traits across amniotes is also suggested by the similarity of the total clutch/litter masses of non-avian reptiles to those of birds and mammals, despite the fact that non-avian reptiles have much lower metabolic rates than birds or mammals. Therefore, although variation in the BMRs of individuals within a species may have an indirect effect on reproductive output (bats [132]; marsh tits [49]; sparrows [133]; Leach's storm-petrels [48]; rodents [134]), there are no broad-scale interspecific relationships between relative metabolic rate and reproductive output traits.

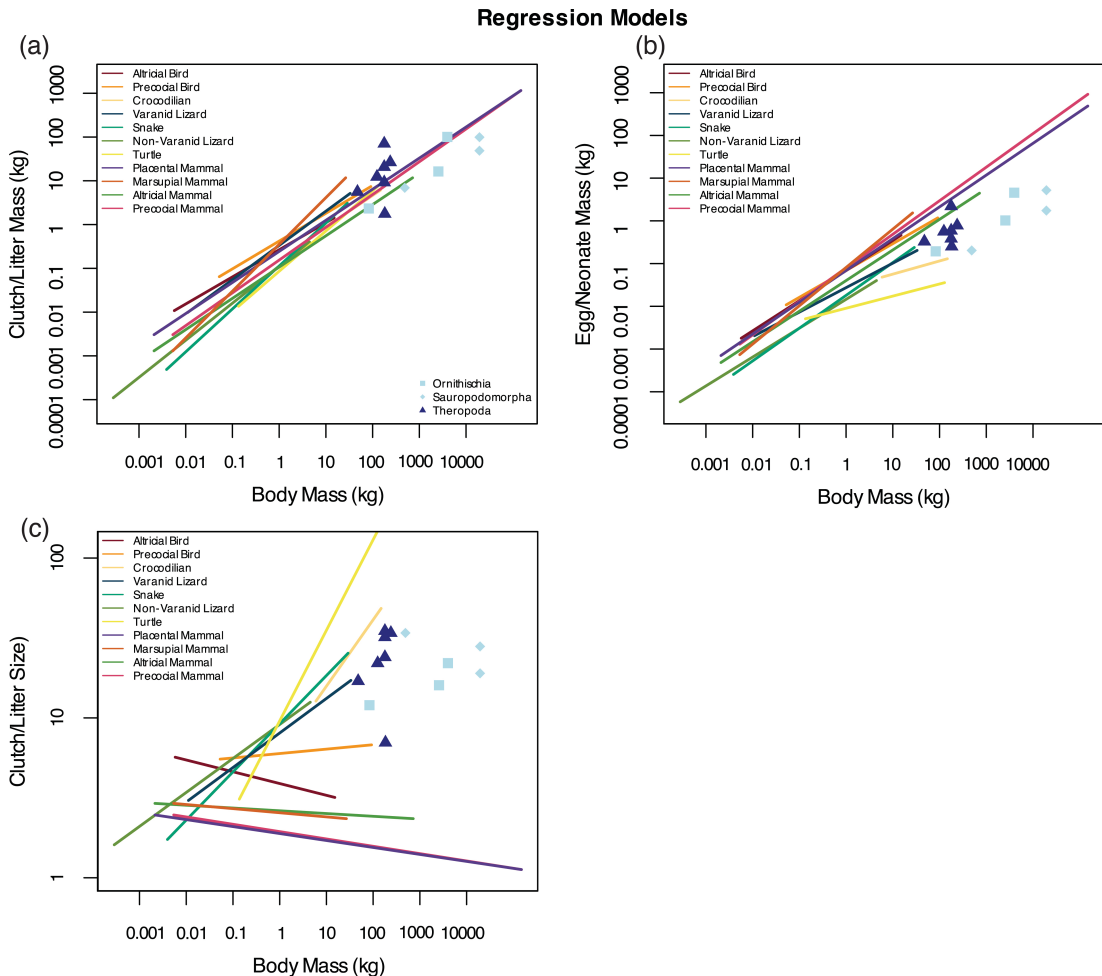


Figure 6. Plot of reproductive output regression lines. (a) Plot of extant clutch/litter mass regression models. (b) Plot of extant egg/neonate mass regression models. (c) Plot of extant clutch/litter size regression models. Non-avian dinosaurs are plotted in light and dark blue in each plot.

Our results are similar to those of other broad-scale studies that showed no correlation between BMR and aspects of reproductive output (in mammals [77,135]). White & Seymour [103] found litter size to be positively correlated with residual BMR in mammals but found most placental group-level relationships to be non-significant (except for carnivorous marsupials, *Dasyuromorphia*). Similarly, age at first birth is uncorrelated with BMR [136]. The correlation of other life-history traits with BMR has also been tested only in placentals with mixed results [63,136]. Gestation time was found to be negatively correlated with BMR [63], suggesting the presence of an energetic trade-off.

4.2.2. Reproductive output scaling explanations: brain mass

We found that brain size has a significant relationship with some reproductive output traits in birds and mammals after controlling for variation in adult body mass. Positive scaling relationships are present between brain size and egg/neonate mass in birds and mammals (and see [70]). A negative scaling relationship between brain size and clutch/litter size is present in mammals. These results are consistent with previous works on birds [62], mammals [46] and subsets of mammals (e.g. altricial | precocial [62]; carnivores [137]).

Our results suggest that growing a relatively larger brain requires greater prenatal investment per individual offspring and that this effect is important in endotherms (birds and mammals; see also [70]). Among endotherms, species with larger relative brain sizes produce fewer, but larger, individual offspring (table 4). The hypothesis that brain size, and not metabolic rate, influences reproductive output traits is also supported by observations of non-avian dinosaurs. Non-avian dinosaurs had elevated metabolic rates, more similar to those of birds and mammals than to those of non-avian reptiles [56,58,60] but relatively smaller brains, mostly similar to reptiles (especially in non-theropod

dinosaurs [38,55,73,138,139]; figures 1 and 2). The co-occurrence of both reproductive output traits and relative brain sizes similar to those of other non-avian reptiles, in most dinosaurs (figures 1 and 4), is consistent with the hypothesis that small relative brain size explains the occurrence of more numerous, but smaller offspring in more (i.e. non-theropod) dinosaurs. We find only limited evidence for a hypothesized trade-off between total reproductive output per clutch and brain size [47,61]. Despite this, squamates show a trade-off between brain size and longevity [108], suggesting that there is a high energetic cost of increasing brain size in squamates. This trade-off is absent in endotherms, which show increasing longevity with larger brain size (mammals [62,66,140]; birds [141–143]). It should be noted that these scaling relationships concern output from a single reproductive attempt and do not include information on the number of clutches per year, which may also be important.

4.3. The evolution of modern bird reproductive output

The reproductive output traits of non-avian dinosaurs are more similar to those of living non-avian reptiles than to birds (figures 3–6), especially among non-theropod dinosaurs (figure 6) [43,44,144]. Dinosaurs had proportionally small eggs, with relative egg masses below (in non-theropod dinosaurs) or at the lower end (in those theropods that have been studied, e.g. [42]) of the distribution of living bird egg sizes (figures 6–8). Moreover, the relatively large clutch sizes of non-avian dinosaurs lie at the upper limit of bird clutch sizes but are similar to those of crocodylians and some squamates (figures 6–8). The distribution of clutch mass among non-theropod dinosaurs is similar to that of birds (figure 7) but is also similar to all other amniote groups (figure 3). Varricchio *et al.* [39] showed that at least some theropods (oviraptorosaurs and troodontids) had larger clutch masses, similar to those of living birds with paternal care.

The larger residual egg sizes of birds are distinct from those of non-avian theropods and other dinosaurs (figure 7). Ancestral character estimation shows that some increases in relative egg size occurred among dinosaurs along the bird-stem lineage. Non-theropod dinosaurs have large clutches of very small eggs compared to their adult body mass, and while theropods such as oviraptorosaurs and troodontids have proportionally larger eggs than non-theropods, they still have proportionally smaller eggs than those of living birds of equivalent body mass (figure 7) [42,145,146]. Relative egg size therefore shows a gradational pattern of increase along the bird-stem lineage, from small egg sizes in non-theropod dinosaurs to larger sizes in at least some theropods, to the largest relative sizes by the origin of the bird crown group (figure 7).

4.3.1. Implications for parental care in non-avian dinosaurs

Parental investment among living amniotes falls along a spectrum from non-avian reptiles, which have high counts of small offspring with zero parental provisioning, to birds and mammals, which have smaller counts of larger offspring with generally substantial parental provisioning, especially in altricial taxa. Most birds invest parental energy in offspring after oviposition, in the form of brooding, uniparental care, cooperative breeding or post-hatching care of fledglings [147–149]. In contrast, crocodylians, the living sister taxon of birds and other dinosaurs, show a much lower degree of energetic investment in parental care, consisting of nest and neonate guarding [150,151].

Some degree of parental care has been hypothesized to occur in both hadrosaurs and non-avian theropods [30,39]. This is primarily supported by indirect evidence, e.g. proportional size of offspring, nest structure and aggregation [30,39]. Nevertheless, the occurrence of large counts of small offspring and lower relative clutch mass in non-avian dinosaurs, especially in non-theropod dinosaurs, suggests that they had limited postnatal parental care, more similar to living reptiles such as crocodylians than to birds. There are most likely differences between non-avian dinosaur groups, given that relative egg size in theropods is much larger than in other dinosaurs, suggesting a higher degree of parental care in theropods than in other dinosaurs.

The relatively large clutch masses of non-avian theropod dinosaurs may suggest both the presence of precocial offspring [152] and the presence of at least some parental care [39] (see also [152]). Juvenile aggregation and the co-occurrence of similarly aged offspring have also been used to suggest evidence of nest-attending in theropod and ornithischian dinosaurs and other extinct groups [153–157]. However, nest-attending and brooding also occur in living non-avian reptiles, including crocodylians [150,151] and squamates [158–161], as well as amphibians [162–164], and so these inferred behaviours of non-avian dinosaurs may differ from the substantive parental care seen in birds

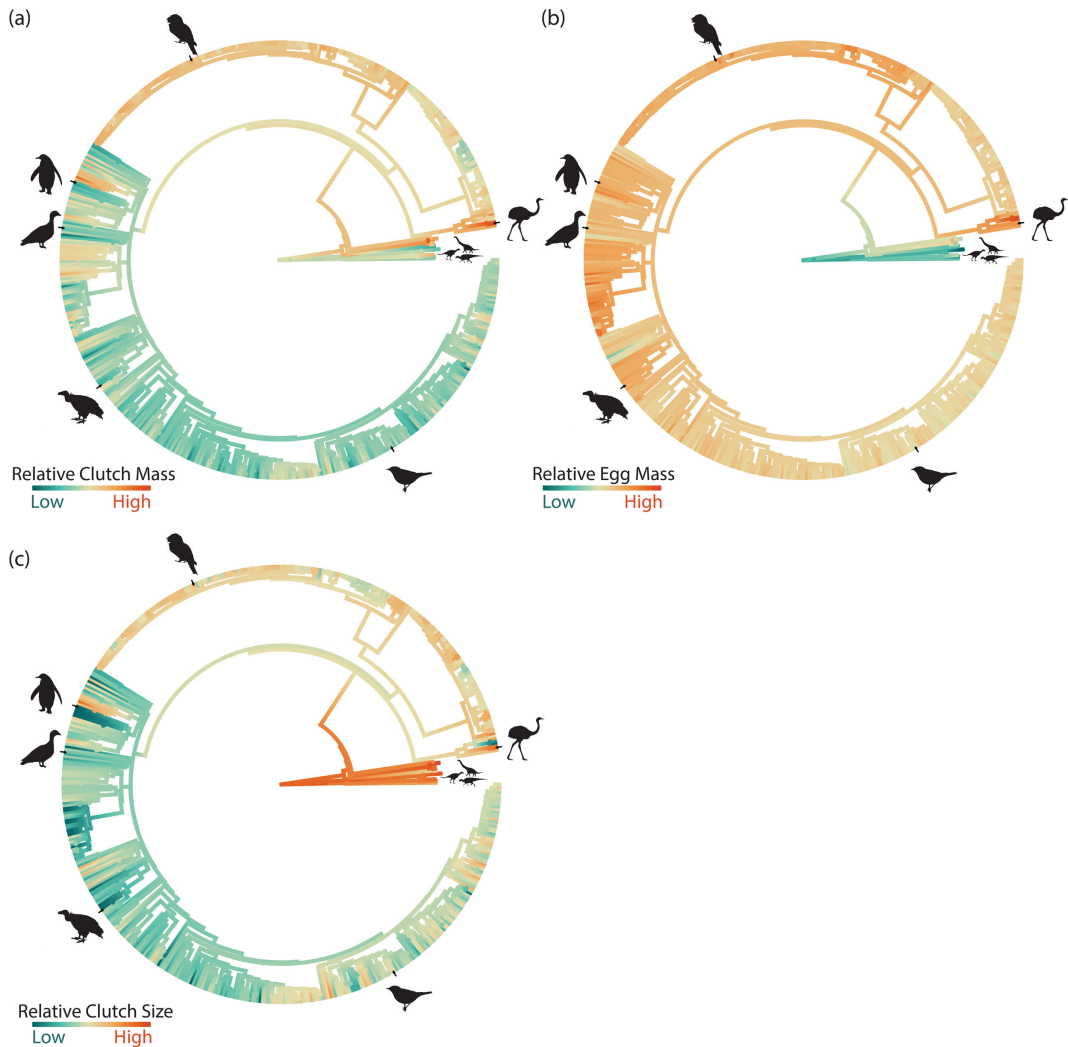


Figure 7. Phylogeny of non-avian dinosaurs and birds with their residual reproductive output traits. (a) Phylogeny with residual clutch mass. (b) Phylogeny with residual egg mass. (c) Phylogeny with residual clutch size. Residual values for all groups, including non-avian dinosaurs, are derived from dinosaur reproductive output trait scaling relationships. Silhouettes highlight *Apterodytes patagonicus* (Steven Traver; CC0 1.0), *Chenonetta jubata* (Michael Scroggie; CC0 1.0), *Gyps fulvus* (Kaija Gahm; CC BY 4.0) and *Podargus strigoides* (Matt Wilkins; CC0 1.0).

and mammals. Additionally, osteohistological and morphological evidence suggesting precociality in sauropodomorphs supports a lack of intense parental care [165,166]. The relatively small egg sizes of sauropodomorph and ornithischian dinosaurs provide additional support that these dinosaurs most likely did not show levels of postnatal parental investment comparable to those of extant birds and mammals.

4.3.2. The evolution of larger brains is correlated with the evolution of increased offspring size and increased parental care

We find that a characteristically bird-like reproductive output, comprising lower counts of larger offspring, evolved late in the bird-stem lineage (figure 7). The results of our comparative analyses suggest these changes are not due to differences in metabolic rates. Instead, we propose that birds evolved to lay fewer, larger eggs and increased parental care to support a larger relative brain size. This shift in reproductive output scaling is also similar to that observed on the mammal-stem lineage [24]. Both dinosaurs and synapsids therefore show an evolutionary shift from laying typically large clutches of relatively small offspring to having small clutches/litters of relatively large offspring, and these shifts co-occurred with a shift from being relatively smaller brained to relatively larger brained.

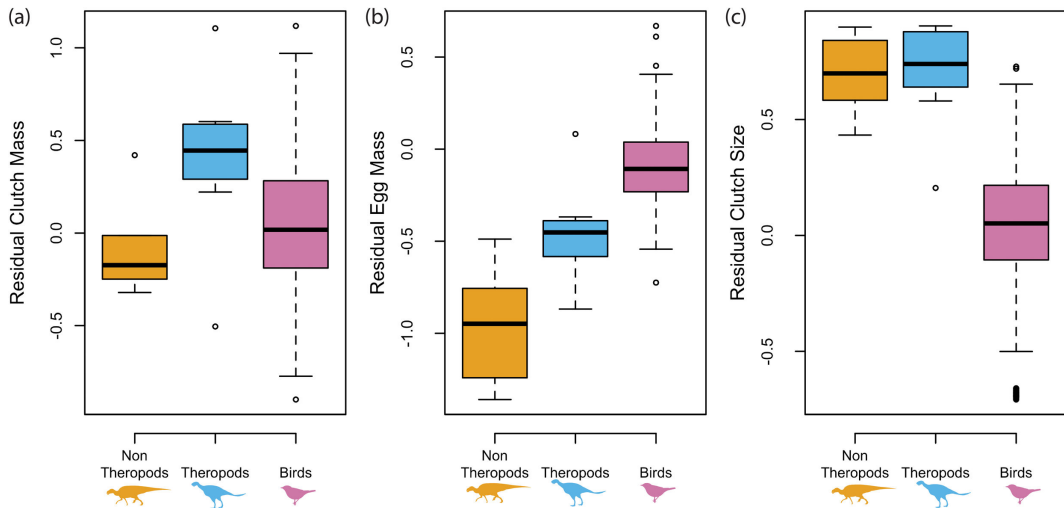


Figure 8. Boxplot of reproductive output traits in non-avian dinosaurs and birds. (a) Boxplot of residual clutch mass in non-theropods (orange), theropods (blue), and birds (pink). (b) Boxplot of residual egg mass in non-theropods (orange), theropods (blue), and birds (pink). (c) Boxplot of residual clutch size in non-theropods (orange), theropods (blue), and birds (pink). Residual values for all groups, including non-avian dinosaurs, are derived from the Dinosauria reproductive output trait scaling relationships.

The relative brain sizes of non-avian dinosaurs varied, with sauropodomorphs exhibiting brain sizes most similar to that of extant reptiles [73], while theropod dinosaurs exhibited more variation, from tyrannosaurids, carcharodontosaurids and oviraptorosaurs having reptile-like brain sizes well below the ranges of modern birds to some small maniraptoriformes exhibiting relative brain sizes at the lower end of the distribution of relative brain size in living birds [52,167]. The origin of the bird crown group is also marked by an increase in relative brain and cerebellum size [55,109]. This pattern is similar to that on the mammalian stem lineage, with origins of Mammaliaformes and Mammalia exhibiting increased brain size and complexity [168].

4.3.3. Potential consequences of increasing egg size on the bird-stem lineage

Increasing relative egg size on the bird-stem lineage may explain changes in nest structure and reproductive anatomy in non-avian dinosaurs. The ancestral archosaur reproductive system, as found in extant crocodylians, is characterized by two functional ovaries, a prolonged maturation of ovarian follicles, and a single oviposition event. In contrast, a derived condition is present in birds, which have one functional ovary and oviduct, rapid maturation of ovarian follicles and daily monoautochronic oviposition [169]. This transition occurred along the bird-stem lineage, with oviraptorosaurs and troodontids showing an intermediate state with two functioning ovaries but having daily monoautochronic oviposition [170,171]. Therefore, the initial origin of monoautochronic oviposition, in non-avian theropods, may be related to evolutionary increases in relative egg size, as the laying of a single egg at a time in regular intervals signifies periods of energetic investment in singular offspring as opposed to multiple offspring at a time. Birds then later underwent further increases in relative egg size and the loss of the right ovary [172,173], among other urogenital adaptations such as the absence of a urethra and urinary tract [174], and reduced, functional gonads only during the breeding period [175,176]. It has been suggested that the loss of the right ovary is an adaptation to reduce weight for flight [177,178]. However, it may also be related to increasing egg mass, necessitating obligate monoautochronic oviposition due to passage space constraints. Increasing egg size on the bird-stem lineage may have been further facilitated by increases in the opening of the pubic symphysis [179] and other skeletal constraints [180], allowing for increases in both relative egg sizes and variety of egg shapes [181].

Changes in the nesting structure of dinosaurs also occurred along the bird-stem lineage, with sauropodomorphs exhibiting more extant crocodylian-like nesting patterns, i.e. buried nests using the substrate for incubation [182] (contra [183]), and theropods exhibiting an intermediate nesting behaviour, with the partial burial of nests and contact incubation [33]. Fully open-air nests were most likely first built by crown birds and their closest extinct relatives [184]. This transition may be attributed to the gas exchange consequences of increasing egg size in theropod dinosaurs and birds,

which is thought to be a limiting factor of clutch mass of eggs buried under substrate [185]. Due to the scaling of surface area to volume, larger eggs are less efficient at gas exchange than smaller eggs, despite pore density increasing with absolute egg mass. The relatively larger size of theropod eggs as compared to sauropod eggs suggests differences in nest type between the two groups. Eggshell pore density supports this, with sauropod eggs possessing a higher eggshell porosity suggestive of incubation in a low oxygen environment (i.e. burial or incubation mounds) and oviraptorosaur eggs having a lower eggshell porosity suggesting they were partially exposed to open air [182,186]. Evolutionary increases in relative egg mass may have decreased the partial pressure of oxygen in buried nests and, hence, the survivability of offspring. This may have caused the transition from buried nests in sauropods to partially buried nests in theropods to fully open-air nests in crown birds [187–193].

5. Conclusions

- (1) We estimated reproductive scaling relationships across amniotes and analysed the partial effects of the developmental state of offspring, relative brain size and relative metabolic rate on reproductive output. Across amniotes, clutch mass is highly conserved, whereas egg mass and especially clutch size show greater variability.
- (2) Non-avian dinosaurs have reproductive output scaling more similar to that of living non-avian reptiles than to birds, especially among non-theropod dinosaurs—with residual egg masses below or at the lower end of the distribution of living bird egg sizes and residual clutch sizes lying on the upper limit of avian relative clutch sizes. This likely reflects an ancestral pattern for amniotes.
- (3) We find that growing a relatively larger brain requires greater prenatal investment per individual offspring. Bird and mammal species with larger relative brain sizes produce fewer, larger individual offspring.
- (4) The evolution of larger brains on the line leading to birds is correlated with the evolution of increased offspring size and increased parental care—and is a potential driver of changes in nesting structure and reproductive anatomy during the dinosaur–bird transition.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Data, code and full results tables supporting this study are deposited in the supplementary material, in the Figshare repository [194].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. S.C.L.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; R.B.J.B.: conceptualization, investigation, methodology, project administration, supervision, visualization, writing—review and editing.

Both authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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References

1. Cody ML. 1966 A general theory of clutch size. *Evolution* **20**, 174–184. (doi:10.1111/j.1558-5646.1966.tb03353.x)
2. Godfray HCJ, Partridge L, Harvey PH. 1991 Clutch size. *Annu. Rev. Ecol. Syst.* **22**, 409–429. (doi:10.1146/annurev.es.22.110191.002205)
3. Grafen A. 2006 A theory of fisher's reproductive value. *J. Math. Biol.* **53**, 15–60. (doi:10.1007/s00285-006-0376-4)
4. Lack D. 1954 *The natural regulation of animal numbers*. Oxford, UK: Clarendon Press.
5. Pianka ER. 1976 Natural selection of optimal reproductive tactics. *Am. Zool.* **16**, 775–784. (doi:10.1093/icb/16.4.775)
6. Stearns SC. 1992 *The evolution of life histories*. Oxford, UK: Oxford University Press.
7. Western D. 1979 Size, life history and ecology in mammals. *Afr. J. Ecol.* **17**, 185–204. (doi:10.1111/j.1365-2028.1979.tb00256.x)

8. Bjorndal KA, Carr A. 1989 Variation in clutch size and egg size in the green turtle nesting population at Tortuguero, Costa Rica. *Herpetologica* **45**, 181–189.
9. Zuffi MAL, Odetti F, Meozzi P. 1999 Body size and clutch size in the European pond turtle (*Emys orbicularis*) from central Italy. *J. Zool.* **247**, 139–143. (doi:10.1017/S0952836999002010)
10. Roff D. 1993 *Evolution of life histories: theory and analysis*. Berlin, Germany: Springer Science & Business Media.
11. Andersen KH *et al.* 2016 Characteristic sizes of life in the oceans, from bacteria to whales. *Ann. Rev. Mar. Sci.* **8**, 217–241. (doi:10.1146/annurev-marine-122414-034144)
12. Bjorndal KA, Carr A, Meylan AB, Mortimer JA. 1985 Reproductive biology of the hawksbill *Eretmochelys imbricata* at Tortuguero, Costa Rica, with notes on the ecology of the species in the caribbean. *Biol. Conserv.* **34**, 353–368. (doi:10.1016/0006-3207(85)90040-0)
13. Santos AJB, Freire EMX, Bellini C, Corso G. 2010 Body mass and the energy budget of gravid hawksbill turtles (*Eretmochelys imbricata*) during the nesting season. *J. Herpetol.* **44**, 352–359. (doi:10.1670/08-287.1)
14. Millar JS. 1977 Adaptive features of mammalian reproduction. *Evolution* **31**, 370–386. (doi:10.1111/j.1558-5646.1977.tb01019.x)
15. Tuomi J. 1980 Mammalian reproductive strategies: a generalized relation of litter size to body size. *Oecologia* **45**, 39–44. (doi:10.1007/BF00346705)
16. Blackburn TM. 1991 An interspecific relationship between egg size and clutch size in birds. *Auk* **108**, 973–977.
17. Lack D. 1967 The significance of clutch-size in waterfowl. *Wildfowl* **18**, 125–128.
18. Congdon JD, Gibbons JW. 1985 Egg components and reproductive characteristics of turtles: relationships to body size. *Herpetologica* **41**, 194–205.
19. Elgar MA, Heaphy LJ. 1989 Covariation between clutch size, egg weight and egg shape: comparative evidence for chelonians. *J. Zool.* **219**, 137–152. (doi:10.1111/j.1469-7998.1989.tb02572.x)
20. Greer AE. 1975 Clutch size in crocodilians. *J. Herpetol.* **9**, 319. (doi:10.2307/1563198)
21. Thorbjarnarson JB. 1996 Reproductive characteristics of the order crocodylia. *Herpetologica* **52**, 8–24.
22. King RB. 2000 Analyzing the relationship between clutch size and female body size in reptiles. *J. Herpetol.* **34**, 148. (doi:10.2307/1565253)
23. Meiri S *et al.* 2020 The global diversity and distribution of lizard clutch sizes. *Glob. Ecol. Biogeogr.* **29**, 1515–1530. (doi:10.1111/geb.13124)
24. Hoffman EA, Rowe TB. 2018 Jurassic stem-mammal perinates and the origin of mammalian reproduction and growth. *Nature* **561**, 104–108. (doi:10.1038/s41586-018-0441-3)
25. Balanoff AM, Rowe T. 2007 Osteological description of an embryonic skeleton of the extinct elephant bird, *Aepyornis* (Palaeognathae: Ratitae). *J. Vertebr. Paleontol.* **27**, 1–53. (doi:10.1671/0272-4634(2007)27[1:ODOAES]2.0.CO;2)
26. Deeming D *et al.* 2015 The fossil record and evolution of avian egg nesting and incubation. In *Nests, eggs, and incubation* (ed. DC Deeming), pp. 8–15. Oxford, UK: Oxford University Press. (doi:10.1093/acprof:oso/9780198718666.003.0002)
27. Grellet-Tinner G, Norell M. 2002 An avian egg from the Campanian of Bayn Dzak, Mongolia. *J. Vertebr. Paleontol.* **22**, 719–721. (doi:10.1671/0272-4634(2002)022[0719:AAEFTC]2.0.CO;2)
28. Jackson FD, Varricchio DJ, Corsini JA. 2013 Avian eggs from the Eocene Willwood and Chadron formations of Wyoming and Nebraska. *J. Vertebr. Paleontol.* **33**, 1190–1201. (doi:10.1080/02724634.2013.769445)
29. Clark JM, Norell M, Chiappe LM, Project M, Akademi MSU. 1999 *An oviraptorid skeleton from the late Cretaceous of Ukhaa Tolgod, Mongolia, preserved in an avianlike brooding position over an oviraptorid nest*. American Museum novitates ; no. 3265. See <https://digitallibrary.amnh.org/handle/2246/3102>.
30. Horner JR. 1999 Egg clutches and embryos of two hadrosaurian dinosaurs. *J. Vertebr. Paleontol.* **19**, 607–611. (doi:10.1080/02724634.1999.10011174)
31. Kundrát M, Cruickshank ARI, Manning TW, Nudds J. 2008 Embryos of therizinosauroid theropods from the Upper Cretaceous of China: diagnosis and analysis of ossification patterns. *Acta Zool.* **89**, 231–251. (doi:10.1111/j.1463-6395.2007.00311.x)
32. Pol D, Mancuso AC, Smith RMH, Marsicano CA, Ramezani J, Cerda IA, Otero A, Fernandez V. 2021 Earliest evidence of herd-living and age segregation amongst dinosaurs. *Sci. Rep.* **11**, 20023. (doi:10.1038/s41598-021-99176-1)
33. Varricchio DJ, Jackson F, Borkowski JJ, Horner JR. 1997 Nest and egg clutches of the dinosaur Troodon formosus and the evolution of avian reproductive traits. *Nature* **385**, 247–250. (doi:10.1038/385247a0)
34. Varricchio DJ, Horner JR, Jackson FD. 2002 Embryos and eggs for the cretaceous theropod dinosaur *Troodon formosus*. *J. Vertebr. Paleontol.* **22**, 564–576. (doi:10.1671/0272-4634(2002)022%5B0564:EAETFC%5D2.0.CO;2)
35. Dhiman H, Verma V, Singh LR, Miglani V, Jha DK, Sanyal P, Tandon SK, Prasad GVR. 2023 New Late Cretaceous titanosaur sauropod dinosaur egg clutches from lower Narmada valley, India: palaeobiology and taphonomy. *PLoS One* **18**, e0278242. (doi:10.1371/journal.pone.0278242)
36. Jackson FD, Garrido A, Schmitt JG, Chiappe LM, Dingus L, Loope DB. 2004 Abnormal, multilayered titanosaur (Dinosauria: Sauropoda) eggs from in situ clutches at the Auca Mahuevo locality, Neuquen Province, Argentina. *J. Vertebr. Paleontol.* **24**, 913–922. (doi:10.1671/0272-4634(2004)024[0913:AMTDSE]2.0.CO;2)
37. Sander PM, Peitz C, Jackson FD, Chiappe LM. 2008 Upper Cretaceous titanosaur nesting sites and their implications for sauropod dinosaur reproductive biology. *Pala.* **284**, 69–107. (doi:10.1127/pala/284/2008/69)
38. Sander PM *et al.* 2011 Biology of the sauropod dinosaurs: the evolution of gigantism. *Biol. Rev.* **86**, 117–155. (doi:10.1111/j.1469-185X.2010.00137.x)
39. Varricchio DJ, Moore JR, Erickson GM, Norell MA, Jackson FD, Borkowski JJ. 2008 Avian paternal care had dinosaur origin. *Science* **322**, 1826–1828. (doi:10.1126/science.1163245)

40. Ruxton GD, Birchard GF, Deeming DC. 2014 Incubation time as an important influence on egg production and distribution into clutches for sauropod dinosaurs. *Paleobiology* **40**, 323–330. (doi:10.1666/13028)
41. Hogan JD, Varricchio DJ. 2021 Do paleontologists dream of electric dinosaurs? Investigating the presumed inefficiency of dinosaurs contact incubating partially buried eggs. *Paleobiology* **47**, 101–114. (doi:10.1017/pab.2020.49)
42. Varricchio DJ, Hogan JD, Freimuth WJ. 2021 Revisiting Russell's troodontid: autecology, physiology, and speculative tool use. *Can. J. Earth Sci.* **58**, 796–811. (doi:10.1139/cjes-2020-0184)
43. Werner J, Griebeler EM. 2011 Reproductive biology and its impact on body size: comparative analysis of mammalian, avian and dinosaurian reproduction. *PLoS One* **6**, e28442. (doi:10.1371/journal.pone.0028442)
44. Werner J, Griebeler EM. New insights into non-avian dinosaur reproduction and their evolutionary and ecological implications: linking fossil evidence to allometries of extant close relatives. *PLoS One* **8**, e72862. (doi:10.1371/journal.pone.0072862)
45. Isler K, van Schaik C. 2006 Costs of encephalization: the energy trade-off hypothesis tested on birds. *J. Hum. Evol.* **51**, 228–243. (doi:10.1016/j.jhevool.2006.03.006)
46. Pagel MD, Harvey PH. 1988 How mammals produce large-brained offspring. *Evolution* **42**, 948–957. (doi:10.1111/j.1558-5646.1988.tb02513.x)
47. Pitnick S, Jones KE, Wilkinson GS. 2006 Mating system and brain size in bats. *Proc. R. Soc. B* **273**, 719–724. (doi:10.1098/rspb.2005.3367)
48. Blackmer AL, Mauck RA, Ackerman JT, Huntington CE, Nevitt GA, Williams JB. 2005 Exploring individual quality: basal metabolic rate and reproductive performance in storm-petrels. *Behav. Ecol.* **16**, 906–913. (doi:10.1093/beheco/ari069)
49. Nilsson J. 2002 Metabolic consequences of hard work. *Proc. R. Soc. Lond. B* **269**, 1735–1739. (doi:10.1098/rspb.2002.2071)
50. White CR, Alton LA, Bywater CL, Lombardi EJ, Marshall DJ. 2022 Metabolic scaling is the product of life-history optimization. *Science* **377**, 834–839. (doi:10.1126/science.abm7649)
51. Hopson JA. 1977 Relative brain size and behavior in Archosaurian reptiles. *Annu. Rev. Ecol. Syst.* **8**, 429–448. (doi:10.1146/annurev.es.08.110177.002241)
52. Hurlburt GR, Ridgely RC, Witmer LM. 2013 Relative size of brain and cerebrum in tyrannosaurid dinosaurs: an analysis using brain-endocast quantitative relationships in extant alligators. In *Tyrannosaurid paleobiology* (eds JM Parrish, RE Molnar, PJ Currie, EB Koppelhus), pp. 134–154. Bloomington: Indiana University Press.
53. Hurlburt GR. 1996 *Relative brain size in recent and fossil amniotes: determination and interpretation*. Toronto: University of Toronto.
54. Jerison HJ. 1969 Brain evolution and dinosaur brains. *Am. Nat.* **103**, 575–588. (doi:10.1086/282627)
55. Ksepka DT *et al.* 2020 Tempo and pattern of avian brain size evolution. *Curr. Biol.* **30**, 2026–2036. (doi:10.1016/j.cub.2020.03.060)
56. Grady JM, Enquist BJ, Dettweiler-Robinson E, Wright NA, Smith FA. 2014 Evidence for mesothermy in dinosaurs. *Science* **344**, 1268–1272. (doi:10.1126/science.1253143)
57. Clarke A. 2013 Dinosaur energetics: setting the bounds on feasible physiologies and ecologies. *Am. Nat.* **182**, 283–297. (doi:10.1086/671259)
58. Erickson GM. 2014 On dinosaur growth. *Annu. Rev. Earth Planet. Sci.* **42**, 675–697. (doi:10.1146/annurev-earth-060313-054858)
59. Seymour RS. 2013 Maximal aerobic and anaerobic power generation in large crocodiles versus mammals: implications for dinosaur gigantothermy. *PLoS One* **8**, e69361. (doi:10.1371/journal.pone.0069361)
60. Wiemann J, Menéndez I, Crawford JM, Fabbri M, Gauthier JA, Hull PM, Norell MA, Briggs DEG. 2022 Fossil biomolecules reveal an avian metabolism in the ancestral dinosaur. *Nature* **606**, 522–526. (doi:10.1038/s41586-022-04770-6)
61. Aiello LC, Wheeler P. 1995 The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. *Curr. Anthropol.* **36**, 199–221. (doi:10.1086/204350)
62. Isler K, van Schaik CP. 2009 The expensive brain: a framework for explaining evolutionary changes in brain size. *J. Hum. Evol.* **57**, 392–400. (doi:10.1016/j.jhevool.2009.04.009)
63. Weisbecker V, Goswami A. 2010 Brain size, life history, and metabolism at the marsupial/placental dichotomy. *Proc. Natl Acad. Sci. USA* **107**, 16216–16221. (doi:10.1073/pnas.0906486107)
64. Iwaniuk AN, Nelson JE. 2003 Developmental differences are correlated with relative brain size in birds: a comparative analysis. *Can. J. Zool.* **81**, 1913–1928. (doi:10.1139/z03-190)
65. Western D, Ssemakula J. 1982 Life history patterns in birds and mammals and their evolutionary interpretation. *Oecologia* **54**, 281–290. (doi:10.1007/BF00379994)
66. Barton RA, Capellini I. 2011 Maternal investment, life histories, and the costs of brain growth in mammals. *Proc. Natl Acad. Sci. USA* **108**, 6169–6174. (doi:10.1073/pnas.1019140108)
67. Ebner C, Pick JL, Tschirren B. 2016 A trade-off between reproductive investment and maternal cerebellum size in a precocial bird. *Biol. Lett.* **12**, 20160659. (doi:10.1098/rsbl.2016.0659)
68. Griesser M, Drobniak SM, Graber SM, van Schaik CP. 2023 Parental provisioning drives brain size in birds. *Proc. Natl Acad. Sci. USA* **120**, e2121467120. (doi:10.1073/pnas.2121467120)
69. van Schaik CP, Song Z, Schuppli C, Drobniak SM, Heldstab SA, Griesser M. 2023 Extended parental provisioning and variation in vertebrate brain sizes. *PLoS Biol.* **21**, e3002016. (doi:10.1371/journal.pbio.3002016)
70. Song Z, Griesser M, van Schaik CP. 2025 Parental investment and body temperature explain encephalization in vertebrates. *Proc. Natl Acad. Sci. USA* **122**, e2506145122. (doi:10.1073/pnas.2506145122)
71. Song Z, Griesser M, Schuppli C, van Schaik CP. 2023 Does the expensive brain hypothesis apply to amphibians and reptiles? *BMC Ecol. Evol.* **23**, 77. (doi:10.1186/s12862-023-02188-w)
72. Hurlburt G. 2002 Endocast volume and brain mass in a size series of alligators. *J. Vertebr. Paleontol.* **23**, 69A.

73. Hopson J, Thomas R, Olson E. 1980 Relative brain size in dinosaurs. In *A cold look at the warm blooded dinosaurs* (eds RDK Thomas, EC Olson), pp. 287–310. Washington, DC: American Association for the Advancement of Science.
74. Larsson HCE, Sereno PC, Wilson JA. 2000 Forebrain enlargement among nonavian theropod dinosaurs. *J. Vertebr. Paleontol.* **20**, 615–618. (doi:10.1671/0272-4634(2000)020%5B0615:FEANTD%5D2.0.CO;2)
75. Bligh J, Johnson KG. 2003 Glossary of terms for thermal physiology. *J. Therm. Biol.* **35**, 941–961. (doi:10.1152/jappl.1973.35.6.941)
76. Gadgil M, Bossert WH. 1970 Life historical consequences of natural selection. *Am. Nat.* **104**, 1–24. (doi:10.1086/282637)
77. Johnson MS, Thomson SC, Speakman JR. 2001 Limits to sustained energy intake. II. Inter-relationships between resting metabolic rate, life-history traits and morphology in *Mus musculus*. *J. Exp. Biol.* **204**, 1937–1946. (doi:10.1242/jeb.204.11.1937)
78. Legendre LJ, Guénard G, Botha-Brink J, Cubo J. 2016 Palaeohistological evidence for ancestral high metabolic rate in Archosaurs. *Syst. Biol.* **65**, 989–996. (doi:10.1093/sysbio/syw033)
79. Erickson GM, Rauhut OWM, Zhou Z, Turner AH, Inouye BD, Hu D, Norell MA. 2009 Was dinosaurian physiology inherited by birds? Reconciling slow growth in archaeopteryx. *PLoS One* **4**, e7390. (doi:10.1371/journal.pone.0007390)
80. Myhrvold NP. 2014 Problems in Erickson et al. 2009. *Anat. Rec. (Hoboken)*. **298**, 489. (doi:10.1002/ar.23101)
81. Legendre LJ, Rubilar-Rogers D, Musser GM, Davis SN, Otero RA, Vargas AO, Clarke JA. 2020 A giant soft-shelled egg from the late cretaceous of Antarctica. *Nature* **583**, 411–414. (doi:10.1038/s41586-020-2377-7)
82. McTavish EJ et al. 2025 A complete and dynamic tree of birds. *Proc. Natl Acad. Sci.* **122**, e2409658122.
83. Tonini JFR, Beard KH, Ferreira RB, Jetz W, Pyron RA. 2016 Fully-sampled phylogenies of squamates reveal evolutionary patterns in threat status. *Biol. Conserv.* **204**, 23–31. (doi:10.1016/j.biocon.2016.03.039)
84. Upham NS, Esselstyn JA, Jetz W. 2019 Inferring the mammal tree: species-level sets of phylogenies for questions in ecology, evolution, and conservation. *PLoS Biol.* **17**, e3000494. (doi:10.1371/journal.pbio.3000494)
85. Kumar S, Suleski M, Craig JM, Kasprzowicz AE, Sanderford M, Li M, Stecher G, Hedges SB. 2022 Timetree 5: an expanded resource for species divergence times. *Mol. Biol. Evol.* **39**, msac174. (doi:10.1093/molbev/msac174)
86. Thomson RC, Spinks PQ, Shaffer HB. 2021 A global phylogeny of turtles reveals a burst of climate-associated diversification on continental margins. *Proc. Natl Acad. Sci. USA* **118**, e2012215118. (doi:10.1073/pnas.2012215118)
87. Paradis E, Schliep K. 2019 ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* **35**, 526–528.
88. Schwarz R, Meiri S. 2017 The fast-slow life-history continuum in insular lizards: a comparison between species with invariant and variable clutch sizes. *J. Biogeogr.* **44**, 2808–2815. (doi:10.1111/jbi.13067)
89. Narushin VG, Romanov MN, Avni-Magen N, Griffin DK. 2024 Accurate calculation of the content volume, density and original weight of museum curated eggs. *Sci. Rep.* **14**, 31594. (doi:10.1038/s41598-024-75397-y)
90. Meiri S, Brown JH, Sibly RM. 2012 The ecology of lizard reproductive output. *Glob. Ecol. Biogeogr.* **21**, 592–602. (doi:10.1111/j.1466-8238.2011.00700.x)
91. Fisher DO, Owens IPF, Johnson CN. 2001 The ecological basis of life history variation in marsupials. *Ecology* **82**, 3531–3540. (doi:10.1890/0012-9658(2001)082%5B3531:TEBOLH%5D2.0.CO;2)
92. Rahn H, Parisi P, Paganelli CV. 1982 Estimating the initial density of birds' eggs. *Condor* **84**, 339. (doi:10.2307/1367380)
93. Ernest SM. 2003 Life history characteristics of placental nonvolant mammals: ecological archives E084–093. *Ecology* **84**, 3402–3402. (doi:10.1890/02-9002)
94. Frayer DW, Wolpoff MH. 1985 Sexual dimorphism. *Annu. Rev. Anthropol.* **14**, 429–473. (doi:10.1146/annurev.an.14.100185.002241)
95. Shine R. 1989 Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Q. Rev. Biol.* **64**, 419–461. (doi:10.1086/416458)
96. Benson RBJ, Hunt G, Carrano MT, Campione N. 2018 Cope's rule and the adaptive landscape of dinosaur body size evolution. *Palaeontology* **61**, 13–48. (doi:10.1111/pala.12329)
97. Campione NE, Evans DC, Brown CM, Carrano MT. 2014 Body mass estimation in non-avian bipeds using a theoretical conversion to quadruped stylopodial proportions. *Methods Ecol. Evol.* **5**, 913–923. (doi:10.1111/2041-210X.12226)
98. Campione NE, Evans DC. 2012 A universal scaling relationship between body mass and proximal limb bone dimensions in quadrupedal terrestrial tetrapods. *BMC Biol.* **10**, 1–22. (doi:10.1186/1741-7007-10-60)
99. Clarke A, Rothery P, Isaac NJB. 2010 Scaling of basal metabolic rate with body mass and temperature in mammals. *J. Anim. Ecol.* **79**, 610–619. (doi:10.1111/j.1365-2656.2010.01672.x)
100. McNab BK. 2009 Resources and energetics determined dinosaur maximal size. *Proc. Natl Acad. Sci. USA* **106**, 12184–12188. (doi:10.1073/pnas.0904000106)
101. White CR, Seymour RS. 2005 Allometric scaling of mammalian metabolism. *J. Exp. Biol.* **208**, 1611–1619. (doi:10.1242/jeb.01501)
102. NIST. 2020 2019 Annual Report. Gaithersburg, MD: US Department of Commerce.
103. White CR, Seymour RS. 2004 Does basal metabolic rate contain a useful signal? Mammalian BMR allometry and correlations with a selection of physiological, ecological, and life-history variables. *Physiol. Biochem. Zool.* **77**, 929–941. (doi:10.1086/425186)
104. Taylor CR, Heglund NC, Maloiy GM. 1982 Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *J. Exp. Biol.* **97**, 1–21. (doi:10.1242/jeb.97.1.1)
105. Derrickson EM. 1992 Comparative reproductive strategies of altricial and precocial eutherian mammals. *Funct. Ecol.* **6**, 57. (doi:10.2307/2389771)

106. Scheiber IBR, Weiß BM, Kingma SA, Komdeur J. 2017 The importance of the altricial - precocial spectrum for social complexity in mammals and birds - a review. *Front. Zool.* **14**, 3. (doi:10.1186/s12983-016-0185-6)
107. Ducatez S, Field DJ. 2021 Disentangling the avian altricial-precocial spectrum: quantitative assessment of developmental mode, phylogenetic signal, and dimensionality. *Evolution* **75**, 2717–2735. (doi:10.1111/evo.14365)
108. Stark G, Pincheira-Donoso D. 2022 The evolution of brain size in ectothermic tetrapods: large brain mass trades-off with lifespan in reptiles. *Evol. Biol.* **49**, 180–188. (doi:10.1007/s11692-022-09562-4)
109. Smaers JB et al. 2021 The evolution of mammalian brain size. *Sci. Adv.* **7**, eabe2101. (doi:10.1126/sciadv.abe2101)
110. Orme D et al. 2013 The caper package: comparative analysis of phylogenetics and evolution in R. See <https://cran.r-universe.dev/caper/doc/caper.pdf>.
111. Hurvich CM, Tsai CL. 1989 Regression and time series model selection in small samples. *Biometrika* **76**, 297–307. (doi:10.1093/biomet/76.2.297)
112. Burnham KP, Anderson DR. 2004 Multimodel inference: understanding AIC and BIC in model selection. *Sociol. Methods Res.* **33**, 261–304. (doi:10.1177/0049124104268644)
113. Spiess AN. 2018 Package qpcR: modelling and analysis of real-time PCR data. See <https://cran.rstudio.com/web/packages/qpcR/qpcR.pdf>.
114. Fox J, Weisberg S. 2018 An R companion to applied regression. Thousand Oaks, CA: Sage Publications.
115. Pagel M. 1999 The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies. *Syst. Biol.* **48**, 612–622. (doi:10.1080/106351599260184)
116. Felsenstein J. 1985 Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15. (doi:10.1086/284325)
117. Molina-Venegas R, Rodríguez M. 2017 Revisiting phylogenetic signal; strong or negligible impacts of polytomies and branch length information? *BMC Evol. Biol.* **17**, 53. (doi:10.1186/s12862-017-0898-y)
118. Barrick RE, Showers WJ, Fischer AG. 1996 Comparison of thermoregulation of four ornithischian dinosaurs and a varanid lizard from the cretaceous two medicine formation: evidence from oxygen isotopes. *Palaios* **11**, 295. (doi:10.2307/3515240)
119. Knaus PL, van Heteren AH, Lungmus JK, Sander PM. 2021 High blood flow into the femur indicates elevated aerobic capacity in synapsids since the synapsida-sauropsida split. *Front. Ecol. Evol.* **9**, 751238. (doi:10.3389/fevo.2021.751238)
120. Seymour RS, Smith SL, White CR, Henderson DM, Schwarz-Wings D. 2012 Blood flow to long bones indicates activity metabolism in mammals, reptiles and dinosaurs. *Proc. R. Soc. B.* **279**, 451–456. (doi:10.1098/rspb.2011.0968)
121. Sibly RM, Witt CC, Wright NA, Venditti C, Jetz W, Brown JH. 2012 Energetics, lifestyle, and reproduction in birds. *Proc. Natl Acad. Sci. USA* **109**, 10937–10941. (doi:10.1073/pnas.1206512109)
122. Hackett SJ et al. 2008 A phylogenomic study of birds reveals their evolutionary history. *Science* **320**, 1763–1768.
123. Benson RB, Campione NE, Carrano MT, Mannion PD, Sullivan C, Upchurch P, Evans DC. 2014 Rates of dinosaur body mass evolution indicate 170 million years of sustained ecological innovation on the avian stem lineage. *PLoS Biol.* **12**, e1001853.
124. Revell L. 2024 phytools 2.0: an updated R ecosystem for phylogenetic comparative methods (and other things). *PeerJ* **12**, e16505. (doi:10.7717/peerj.16505)
125. Revell LJ, Harmon LJ. 2022 *Phylogenetic comparative methods in R*. Princeton, NJ: Princeton University Press.
126. Schluter D, Price T, Mooers AØ, Ludwig D. 1997 Likelihood of ancestor states in adaptive radiation. *Evolution (N Y)* **51**, 1699–1711.
127. Birchard G, Deeming D, Reynolds S. 2015 Egg allometry: influences of phylogeny and the altricial-precocial continuum. In *Nests, eggs, and incubation* (eds DC Deeming, SJ Reynolds), pp. 97–112. Oxford, UK: Oxford University Press. (doi:10.1093/acprof:oso/9780198718666.003.0009)
128. Hennemann WW. 1984 Intrinsic rates of natural increase of altricial and precocial eutherian mammals: the potential price of precociality. *Oikos* **43**, 363. (doi:10.2307/3544154)
129. Martin R. 1984 Scaling effects and adaptive strategies in mammalian lactation. *Symposia of the Zoological Society London* **51**, 87–117.
130. Sibly RM, Brown JH. 2009 Mammal reproductive strategies driven by offspring mortality-size relationships. *Am. Nat.* **173**, E185–99. (doi:10.1086/598680)
131. Gans C. 1996 An overview of parental care among the Reptilia. *Adv. Study Behav.* **25**, 145–157. (doi:10.1016/S0065-3454(08)60332-0)
132. Mclean JA, Speakman JR. 1999 Energy budgets of lactating and non-reproductive brown long-eared bats (*Plecotus auritus*) suggest females use compensation in lactation. *Funct. Ecol.* **13**, 360–372. (doi:10.1046/j.1365-2435.1999.00321.x)
133. Chastel O, Lacroix A, Kersten M. 2003 Pre-breeding energy requirements: thyroid hormone, metabolism and the timing of reproduction in house sparrows *Passer domesticus*. *J. Avian Biol.* **34**, 298–306. (doi:10.1034/j.1600-048X.2003.02528.x)
134. Kalcounis-Rüppell MC, Ribble DO. 2007 A phylogenetic analysis of the breeding systems of Neotomine-Peromyscine rodents. In *Rodent societies: an ecological and evolutionary perspective* (eds JO Wolff, PW Sherman), pp. 68–85. Chicago, Illinois: University of Chicago Press.
135. Johnston SL, Souter DM, Erwin SS, Tolkamp BJ, Yearsley JM, Gordon IJ, Illius AW, Kyriazakis I, Speakman JR. 2007 Associations between basal metabolic rate and reproductive performance in C57BL/6J mice. *J. Exp. Biol.* **210**, 65–74. (doi:10.1242/jeb.02625)
136. Lovegrove BG. 2009 Age at first reproduction and growth rate are independent of basal metabolic rate in mammals. *J. Comp. Physiol. B* **179**, 391–401. (doi:10.1007/s00360-008-0322-4)
137. Weisbecker V, Goswami A. 2014 Reassessing the relationship between brain size, life history, and metabolism at the marsupial/placental dichotomy. *Zool. Sci.* **31**, 608. (doi:10.2108/zs140022)
138. Evans DC, Ridgely R, Witmer LM. 2009 Endocranial Anatomy of Lambeosaurine Hadrosaurids (Dinosauria: Ornithischia): a sensorineural perspective on cranial crest function. *Anat. Rec. Adv. Integr. Anat. Evol. Biol.* **292**, 1315–1337. (doi:10.1002/ar.20984)

139. Müller RT, Ferreira JD, Pretto FA, Bronzati M, Kerber L. 2021 The endocranial anatomy of *Buriolestes schultzi* (Dinosauria: Saurischia) and the early evolution of brain tissues in sauropodomorph dinosaurs. *J. Anat.* **238**, 809–827. (doi:10.1111/joa.13350)
140. Allman JM, McLaughlin T, Hakeem A. 1993 Brain structures and life-span in primate species. *Proc. Natl Acad. Sci. USA* **90**, 3559–3563. (doi:10.1073/pnas.90.8.3559)
141. Jiménez-Ortega D, Kolm N, Immler S, Maklakov AA, Gonzalez-Voyer A. 2020 Long life evolves in large-brained bird lineages. *Evolution* **74**, 2617–2628. (doi:10.1111/evo.14087)
142. Minias P, Podlaszczuk P. 2017 Longevity is associated with relative brain size in birds. *Ecol. Evol.* **7**, 3558–3566. (doi:10.1002/ece3.2961)
143. Sol D, Székely T, Liker A, Lefebvre L. 2007 Big-brained birds survive better in nature. *Proc. R. Soc. B* **274**, 763–769. (doi:10.1098/rspb.2006.3765)
144. Janis CM, Carrano M. 1991 Scaling of reproductive turnover in archosaurs and mammals: why are large terrestrial mammals so rare? *Ann. Zool. Fenn.* **28**, 201–216.
145. Case TJ. 1978 On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. *Q. Rev. Biol.* **53**, 243–282. (doi:10.1086/410622)
146. Varricchio DJ, Jackson FD. 2004 A phylogenetic assessment of prismatic dinosaur eggs from the cretaceous two medicine formation of montana. *J. Vertebr. Paleontol.* **24**, 931–937. (doi:10.1671/0272-4634(2004)024[0931:APAOPD]2.0.CO;2)
147. Cockburn A. 2006 Prevalence of different modes of parental care in birds. *Proc. R. Soc. B* **273**, 1375–1383. (doi:10.1098/rspb.2005.3458)
148. Kendeigh SC. 1952 Parental care and its evolution in birds. III. *Biol. Monogr.* **22**, 1–3.
149. Wesolowski T. 2004 The origin of parental care in birds: a reassessment. *Behav. Ecol.* **15**, 520–523. (doi:10.1093/beheco/arl039)
150. Combrink X, Warner JK, Downs CT. 2017 Nest-site selection, nesting behaviour and spatial ecology of female Nile crocodiles (*Crocodylus niloticus*) in South Africa. *Behav. Processes* **135**, 101–112. (doi:10.1016/j.beproc.2016.12.006)
151. Dugan BA, Rand AS, Burghardt GM, Bock BC. 1981 Interactions between Nesting Crocodiles and Iguanas. *J. Herpetol.* **15**, 409. (doi:10.2307/1563530)
152. Birchard GF, Ruta M, Deeming DC. 2013 Evolution of parental incubation behaviour in dinosaurs cannot be inferred from clutch mass in birds. *Biol. Lett.* **9**, 20130036. (doi:10.1098/rsbl.2013.0036)
153. Botha-Brink J, Modesto SP. 2007 A mixed-age classed ‘pelycosaur’ aggregation from South Africa: earliest evidence of parental care in amniotes? *Proc. R. Soc. B* **274**, 2829–2834. (doi:10.1098/rspb.2007.0803)
154. Forster CA. 1990 Evidence for juvenile groups in the ornithomimid dinosaur *Tenontosaurus tilletti* Ostrom. *J. Paleontol.* **64**, 164–165. (doi:10.1017/S0022336000042402)
155. Horner JR, Makela R. 1979 Nest of juveniles provides evidence of family structure among dinosaurs. *Nature* **282**, 296–298. (doi:10.1038/282296a0)
156. Jasinowski SC, Abdala F. 2017 Aggregations and parental care in the Early Triassic basal cynodonts *Galesaurus planiceps* and *Thrinaxodon liorhinus*. *PeerJ* **5**, e2875. (doi:10.7717/peerj.2875)
157. Krumenacker LJ, Varricchio DJ, Wilson JP, Martin A, Ferguson A. 2019 Taphonomy of and new burrows from *Oryctodromeus cubicularis*, a burrowing neornithischian dinosaur, from the mid-Cretaceous (Albian-Cenomanian) of Idaho and Montana, U.S.A. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **530**, 300–311. (doi:10.1016/j.palaeo.2019.05.047)
158. de Fraipont M, Clobert J, Barbault R. 1996 The evolution of oviparity with egg guarding and viviparity in lizards and snakes: a phylogenetic analysis. *Evolution* **50**, 391–400. (doi:10.1111/j.1558-5646.1996.tb04501.x)
159. Greene HW, May PG, Hardy SR DL, Scituro JM, Farrell TM. 2002 Parental behavior by vipers. In *Biology of the vipers* (eds GW Schuett, M Hoggren, ME Douglas), pp. 179–205. Eagle Mountain, UT: Eagle Mountain Publishing.
160. Sherbrooke WC. 2017 Antipredator nest guarding by female horned lizards (*Phrynosoma*): iguanian parental care. *Herpetologica* **73**, 331–337. (doi:10.1655/Herpetologica-D-17-00028.1)
161. While GM, Halliwell B, Uller T. 2014 The evolutionary ecology of parental care in lizards. In *Reproductive biology and phylogeny of lizards and tuatara* (eds JL Rheubert, DS Siegel, SE Trauth), pp. 588–619. Boca Raton, FL: CRC Press.
162. Bei Y, Meng S, Li G, Xie W, Li J, Zhang L. 2012 First record of nest site and egg guarding in the caecilian *Ichthyophis bannanicus* (Amphibia: Gymnophiona: Ichthyophiidae). *J. Nat. Hist.* **46**, 859–865. (doi:10.1080/00222933.2011.652985)
163. Schulte LM, Ringler E, Rojas B, Stynoski JL. 2020 Developments in amphibian parental care research: history, present advances, and future perspectives. *Herpetol. Monogr.* **34**, 71–97. (doi:10.1655/HERPMONOGRAPHS-D-19-00002.1)
164. Tornick JK. 2010 Factors affecting aggression during nest guarding in the eastern red-backed salamander (*Plethodon cinereus*). *Herpetologica* **66**, 385–392. (doi:10.1655/09-037a.1)
165. Curry Rogers K, Whitney M, D’Emic M, Bagley B. 2016 Precocity in a tiny titanosaur from the Cretaceous of Madagascar. *Science* **352**, 450–453. (doi:10.1126/science.aaf1509)
166. Geist NR, Jones TD. 1996 Juvenile skeletal structure and the reproductive habits of dinosaurs. *Science* **272**, 712–714. (doi:10.1126/science.272.5262.712)
167. Balanoff AM, Bever GS, Norell MA. 2014 Reconsidering the avian nature of the oviraptorosaur brain (Dinosauria: Theropoda). *PLoS One* **9**, e113559. (doi:10.1371/journal.pone.0113559)
168. Rowe TB, Macrini TE, Luo ZX. 2011 Fossil evidence on origin of the mammalian brain. *Science* **332**, 955–957. (doi:10.1126/science.1203117)

169. Palmer BD, Guillelte LJ. 1992 Alligators provide evidence for the evolution of an archosaurian mode of oviparity. *Biol. Reprod.* **46**, 39–47. (doi:10.1095/biolreprod46.1.39)
170. Dong ZM, Currie PJ. 1996 On the discovery of an oviraptorid skeleton on a nest of eggs at Bayan Mandahu, Inner Mongolia, People's Republic of China. *Can. J. Earth Sci.* **33**, 631–636. (doi:10.1139/e96-046)
171. Zelenitsky DK. 2006 Reproductive traits of non-avian theropods. *고생물학회지* **22**, 209–216.
172. Guioli S, Nandi S, Zhao D, Burgess-Shannon J, Lovell-Badge R, Clinton M. 2014 Gonadal asymmetry and sex determination in birds. *Sex. Dev.* **8**, 227–242. (doi:10.1159/000358406)
173. Kinsky FC. 1971 The consistent presence of paired ovaries in the Kiwi (*Apteryx*) with some discussion of this condition in other birds. *J. Ornithol.* **112**, 334–357. (doi:10.1007/BF01640692)
174. Braun EJ. 2015 Osmoregulatory systems of birds. In *Sturkie's avian physiology* (ed. CG Scanes), pp. 285–300, Sixth edition. Cambridge, MA: Academic Press. (doi:10.1016/B978-0-12-407160-5.00012-9)
175. Briskie JV, Montgomerie R. 1997 Sexual selection and the intromittent organ of birds. *J. Avian Biol.* **28**, 73. (doi:10.2307/3677097)
176. Wingfield JC, Hahn TP, Levin R, Honey P. 1992 Environmental predictability and control of gonadal cycles in birds. *J. Exp. Zool.* **261**, 214–231. (doi:10.1002/jez.1402610212)
177. Guillemette M, Ouellet JF. 2005 Temporary flightlessness as a potential cost of reproduction in pre-laying Common Eiders *Somateria mollissima*. *Ibis* **147**, 301–306. (doi:10.1111/j.1474-919x.2005.00402.x)
178. Johnson A. 2011 Organization and functional dynamics of the avian ovary. In *Hormones and reproduction of vertebrates* (eds DO Norris, KH Lopez), pp. 71–90. Cambridge, MA: Academic Press. (doi:10.1016/B978-0-12-374929-1.10003-4)
179. Charles Deeming D, Mayr G. 2018 Pelvis morphology suggests that early Mesozoic birds were too heavy to contact incubate their eggs. *J. Evol. Biol.* **31**, 701–709. (doi:10.1111/jeb.13256)
180. Dyke GJ, Kaiser GW. 2010 Cracking a developmental constraint: egg size and bird evolution. *Records of the Australian Museum* **62**, 207–216. (doi:10.3853/j.0067-1975.62.2010.1547)
181. Deeming DC, Ruta M. 2014 Egg shape changes at the theropod-bird transition, and a morphometric study of amniote eggs. *R. Soc. Open Sci.* **1**, 140311. (doi:10.1098/rsos.140311)
182. Tanaka K et al. 2019 Exceptional preservation of a Late Cretaceous dinosaur nesting site from Mongolia reveals colonial nesting behavior in a non-avian theropod. *Geology* **47**, 843–847. (doi:10.1130/G46328.1)
183. Chiappe LM, Schmitt JG, Jackson FD, Garrido A, Dingus L, Grellet-tinner G. 2004 Nest structure for sauropods: sedimentary criteria for recognition of dinosaur nesting traces. *Palaios* **19**, 89–95. (doi:10.1669/0883-1351(2004)019<0089:NSFSSC>2.0.CO;2)
184. Mainwaring MC, Medina I, Tobalske BW, Hartley IR, Varricchio DJ, Hauber ME. 2023 The evolution of nest site use and nest architecture in modern birds and their ancestors. *Phil. Trans. R. Soc. B* **378**, 20220143. (doi:10.1098/rstb.2022.0143)
185. Ackerman RA. 1980 Physiological and ecological aspects of gas exchange by sea turtle eggs. *Am. Zool.* **20**, 575–583. (doi:10.1093/icb/20.3.575)
186. Varricchio DJ, Jackson FD, Jackson RA, Zelenitsky DK. 2013 Porosity and water vapor conductance of two *Troodon formosus* eggs: an assessment of incubation strategy in a maniraptoran dinosaur. *Paleobiology* **39**, 278–296. (doi:10.1666/11042)
187. Deeming DC. 2006 Ultrastructural and functional morphology of eggshells supports the idea that dinosaur eggs were incubated buried in a substrate. *Palaeontology* **49**, 171–185. (doi:10.1111/j.1475-4983.2005.00536.x)
188. Hechenleitner EM, Grellet-Tinner G, Fiorelli LE. 2015 What do giant titanosaur dinosaurs and modern Australasian megapodes have in common? *PeerJ* **3**, e1341. (doi:10.7717/peerj.1341)
189. Hogan JD, Varricchio DJ. 2023 Chthonic severance: dinosaur eggs of the Mesozoic, the significance of partially buried eggs and contact incubation precursors. *Phil. Trans. R. Soc. B* **378**, 378. (doi:10.1098/rstb.2022.0144)
190. Seymour RS. 1979 Dinosaur eggs: gas conductance through the shell, water loss during incubation and clutch size. *Paleobiology* **5**, 1–11. (doi:10.1017/S0094837300006242)
191. Seymour RS, Ackerman RA. 1980 Adaptations to underground nesting in birds and reptiles. *Am. Zool.* **20**, 437–447. (doi:10.1093/icb/20.2.437)
192. Tanaka K, Zelenitsky DK, Therrien F. 2015 Eggshell porosity provides insight on evolution of nesting in dinosaurs. *PLoS One* **10**, e0142829. (doi:10.1371/journal.pone.0142829)
193. Tanaka K et al. 2018 Incubation behaviours of oviraptorosaur dinosaurs in relation to body size. *Biol. Lett.* **14**, 20180135. (doi:10.1098/rsbl.2018.0135)
194. Lechki SC, Benson RBJ. 2026 Supplementary material from: Evolutionary drivers of reproductive output variation among amniotes, and origins of large offspring in birds. *Figshare*. (doi:10.6084/m9.figshare.c.8526205)