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The egg-thief architect: experimental oviraptorosaur nesting physiology, the possibility of adult-mediated incubation, and the feasibility of indirect contact incubation

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Non-technical Summary

Oviraptorosaurs, small, feathered dinosaurs from the Cretaceous, have left an extensive fossil record of egg clutches, including numerous nests preserving adults on top of their eggs. Despite the volume and quality of these finds, the bizarre nest arrangement makes them difficult to interpret. Oviraptorosaur-style nests consist of up to three layers of eggs, organized in concentric rings within the interior walls of a volcano-shaped mound. Such nests are unknown among modern animals, and so this study used actualistic experimentation to investigate the thermodynamics of the clutch. Experiments used 36 infertile emu eggs, which are close in mass to those of medium-sized oviraptorosaurs, arranged in a sand nest as interpreted from the fossil record. A surrogate dinosaur was constructed (warmed by an interior water bath) to represent an adult attending its nest. Energy from the surrogate was monitored as it flowed throughout the nest. Resulting clutch temperatures are significantly above ambient conditions and fall in a range between modern bird and crocodile incubation temperatures. These experiments seem to support the notion that an attending adult oviraptorosaur would have the capacity to raise clutch temperatures above ambient using its body temperature, perhaps representative of crucial innovations on the path from crocodilian-type nesting to modern avian reproductive practices.

Abstract

Numerous, high-quality reproduction-related oviraptorosaur fossils have been described. However, oviraptorosaur-style nests are unknown among extant animals, and their curious construction makes nesting behavior difficult to interpret. Experiments were undertaken to better understand oviraptorosaur nesting strategies. A surrogate was constructed and placed atop mock-oviraptorosaur nests built from sand and 36 infertile emu eggs (as *Macroolithus* approximations) arranged according to the most current nest reconstructions. Thermometers, placed within each egg and throughout the experimental area, recorded energy flow from the surrogate dinosaur into the nesting microenvironment. One experiment examined a basic open nest warmed from above; the second, a fully buried clutch warmed from above; and the third, a nest open like the first but with heating elements (representing hindlimbs) extending down into the nest. It was found that egg temperatures in each scenario surpassed ambient temperatures without requiring excessive energy input. Final clutch temperatures were below most avian values, closer to crocodilian incubation, but are likely conservative, considering experimental parameters. These results may support the idea that an oviraptorosaur could use adult-generated energy to warm a clutch above ambient conditions. Additionally, egg tiers would be warmer and more uniform in temperature if heated by elements within the nest, such as hindlimbs, instead of solely from above. Results from the second experiment indicate that an endothermic adult could possibly warm a clutch fully buried beneath itself despite a barrier. Although not likely a behavior exhibited by oviraptorosaurs, such results suggest an important evolutionary step bridging guarded subterranean eggs and contact-incubated subaerial eggs.

Introduction

Oviraptorosaur dinosaurs have left an extensive record of reproduction-related fossils. More than 50 egg clutches have been described (Tanaka et al. 2018a), as well as numerous examples of embryonic material (Norell et al. 1994, 2001; Weishampel et al. 2008; Wang et al. 2016; Bi et al. 2021) and adult–clutch associations (Norell et al. 1995, 2018; Dong and Currie 1996; Clark et al. 1999; Fanti et al. 2012; Jin et al. 2019; Bi et al. 2021). Oviraptorosaur nests are readily identifiable due to their multi-tiered, highly organized clutches of paired eggs. However, this curious nesting style is unknown among extant animals, and so, despite the remarkable

volume and quality of these fossils, much of oviraptorosaur nesting behavior and physiology remains unclear.

There is ongoing discussion regarding whether such a nest would allow for incubation via adult-generated metabolic energy, a possibility with implications for the evolution of avian nesting strategies. Thermoregulatory contact incubation, the method of incubation employed by most extant birds, has been criticized as infeasible for oviraptorosaurs due to various factors, including physiology, body size, nest architecture, and clutch arrangement (Deeming 2002, 2006; Yang et al. 2019b). Other researchers support the possibility, citing regular adult–clutch contact, preserved adult posture similar to brooding birds, eggshell porosity, phylogenetic positioning, and nest substrate (Norell et al. 1995, 2018; Hopp and Orsen 2004; Tanaka et al. 2015, 2018b; Varricchio and Jackson 2016).

The study herein describes a series of actualistic experiments conducted to further our understanding of oviraptorosaur incubation possibilities. While providing some general insight, these tests were constructed to investigate whether an attending adult of an oviraptorosaur-style nest could use metabolic energy to raise and maintain clutch temperatures above ambient conditions without a prohibitively high caloric investment. The experiments used a mock, medium-sized oviraptorosaur nest created from infertile emu (*Dromaius*) eggs and sand. Because adult animals work in tandem with their nests to incubate a clutch, a surrogate dinosaur (containing a heated water bath) was built to accommodate the "adult" part of the adult–nest unit (Deeming 2002). Thermometers placed within the eggs and the nesting environment tracked energy distribution from the surrogate throughout the system. Experiment 1 consisted of the heated surrogate placed on top of an open nest (arranged according to Yang et al. 2019b). Experiment 2 used the same surrogate and clutch configuration, but with fully buried eggs. Experiment 3 was the same as Experiment 1, but heating elements were extended into the nest center instead of being reserved at the top.

This study was carried out with the following assumptions: at least some adult oviraptorosaurs attended their nests, were endothermic, had an insulative dermal covering, and could reasonably cover their clutches. The clutch component of the experiment was arranged to mimic the most current interpretations of midsized oviraptorosaur nests: three tiers of paired and partially buried eggs (blunt end exposed and pointed toward the empty nest center) angled at 35–40° and emplaced within the interior walls of a volcano-shaped sediment structure in concentric rings whose diameters increase with each level (Yang et al. 2019b).

Literature regarding these experimental parameters is summarized in the following section. As with any paleobiological experiment, these tests are approximations, and the results should be interpreted accordingly.

Summary of Oviraptorosaur Nesting Fossils and Reconstructions

Oviraptorosaur nests have been envisioned in various forms (Fig. 1). An early interpretation (Sabath 1991) depicts oviraptorosaur eggs buried in a mound structure, although at the time, the egg-laying species had not been identified. Norell et al. (1994) uncovered the oviraptorosaur–egg connection through embryonic remains, and the next year, an adult–clutch association was described (Norell et al. 1995). This specimen preserves an adult posed in a manner comparable to a modern, incubating bird—commonly referred to as a brooding posture. Additionally, the well-
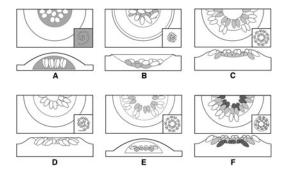

Figure 1. Illustrations of different oviraptorosaur nest interpretations. Upper-level eggs are white; second level, light gray; and the deepest level, dark gray. Dotted lines indicate burial. Inset boxes show egg organization. Not to scale. A, Eggs vertical or subvertical, arranged in a spiral pattern, single level, buried in a chamber of organic material (gray space), and covered with sand (Sabath 1991). B, Disorganized clutch of subhorizontal eggs, multiple layers, and placed in an open pit with a slightly raised rim. Illustrated in both Norell et al. (1995) and Clark et al. (1999), although it does *not* match the in-text description. C, Two ring-like layers of partially buried, paired, and subhorizontal eggs arranged in an open nest that is more likely a mound than a pit. Matches in-text descriptions by Norell et al. (1995, 2018), Clark et al. (1999), and Fanti et al. (2012). D, A single layer of unburied, subhorizontal eggs arranged in a spiral pattern within an open mound nest (Dong and Currie 1996). E, Two stacked rings of subhorizontal eggs sequestered in a fully buried nest (Deeming 2002, 2006). F, A three-tiered open mound nest with partially buried eggs arranged in rings. The eggs sit at 30–40° angles with their blunt ends interior. Described by Yang et al. (2019b) and the most current, general interpretation.

preserved eggs provide details of the clutch arrangement. Norell et al. (1995), and later Clark et al. (1999) for the same specimen, describe the eggs as paired, subhorizontal, and arranged in multi-tiered rings open to the air (Fig. 1C). Dong and Currie (1996) describe another adult–clutch association, interpreting the nest as raised and open with a spiraling clutch (Fig. 1D).

Subsequent publications (Deeming 2002, 2006) again argued for covered mound nesting based on new finds and interpretations. They emphasized the efficacy and popularity of covered mound nests among modern crocodilians and megapodes, suggesting that this was the most likely nesting mode for oviraptorosaurs (Fig. 1E). However, the most recent research seems to support a return to the open nest hypothesis based on further discoveries (Norell et al. 2018; Bi et al. 2021), nesting substrate and geography (Tanaka et al. 2018b), and eggshell pigmentation and porosity (Wiemann et al. 2017; Tanaka et al. 2018a). Wiemann et al. (2017) allow for vegetative nest covering, but despite many described clutches, no geologic evidence of nest-bound vegetation matter has yet been identified. Additionally, several adult–clutch associations (Fanti et al. 2012; Norell et al. 2018; Bi et al. 2021) appear to show direct adult–egg contact, further supporting at least partially exposed eggs.

Yang et al. (2019b) provide an excellent review of oviraptorosaur nesting literature and the most thorough description of midsized oviraptorosaur-type nests—guiding the nest construction of the experiments described herein. Yang et al. (2019b) reconstruct these nests as consisting of up to three tiers of paired and partially buried eggs angled at 35–40° with their blunt ends toward the empty nest center. The eggs are emplaced within the interior walls of a volcano-shaped sediment structure in concentric rings whose diameters increase with each level (Fig. 1F). Like Dong and Currie (1996), Yang et al. (2019b) argue for a raised, open nest (instead of a sunken pit) based on reconstructed egg inclination angles and eggshell porosity. Dong and Currie (1996) use

positional evidence, interpreting the nest as built up from ground level rather than from below. Their described specimen (IVPP V9608) shows portions of the adult pes within the center of the clutch, with unguals at the same level as the eggs, but the right manus rests outside the perimeter of the clutch yet on the same plane as the unguals and eggs (Dong and Currie 1996). The similar relative positioning of skeletal and clutch elements is described by Fanti et al. (2012). This specimen's hindlimbs are also located within the nest center and lie below the eggs and body. The head is preserved outside the clutch but on a lower plane than the body, as with the hindlimbs. A sunken oviraptorosaur nest would likely force a hand or head lying outside the clutch to rest above the eggs at ground level. However, taphonomic interference makes such inferences uncertain. While the current consensus is that more evidence exists for raised rather than sunken nests (and the experiments were designed accordingly), the lack of preserved nest structure (such as the raised sediment rim preserved in a troodontid nest; Varricchio et al. 1997, 1999) makes definitive comment difficult. Trace fossil evidence of nest walls or boundaries would certainly improve future interpretations.

Oviraptorosaur Nest Attendance and Endothermy

A remarkable number of oviraptorosaur adult–clutch associations have been described (Norell et al. 1995, 2018; Dong and Currie 1996; Clark et al. 1999; Fanti et al. 2012; Jin et al. 2019; Bi et al. 2021). While there is disagreement over whether the adults were incubating their clutches, most researchers agree that these oviraptorosaurs were at least attending their nests. An alternative explanation is that perhaps adult–clutch fossil specimens represent individuals trapped in the act of oviposition (Dong and Currie 1996; Yang et al. 2019b), yet the sheer number of associations makes this seem less plausible. Furthermore, the presence of well-developed embryonic material (Bi et al. 2021) in an adult–clutch association casts further doubt on this interpretation. At least for now, it appears most likely that some oviraptorosaurs, like most modern archosaurs, did exhibit nest attendance. As such, for the experiments described herein, the presence of an attending adult was approximated to best simulate a functioning adult–nest unit.

Nest attendance behavior is essential for incubation via adult-derived energy, and it is most frequently coupled with endothermic physiology. While some ectotherms can physically warm their eggs (e.g., Pythonidae; Slip and Shine 1988; Stahlschmidt and Denardo 2009), the vast majority of contact incubators are endothermic. A substantial body of work demonstrates that endothermy was widespread among dinosaurs (Barrick and Showers 1994; Fricke and Rogers 2000; Amiot et al. 2006; Eagle et al. 2011; Grigg et al. 2022; Wiemann et al. 2022). Specific to oviraptorosaurs, Eagle et al. (2015) suggest body temperatures of 31.9 ± 2.9°C. More recent oxygen isotope uptake analysis indicates higher oviraptorosaur temperatures between 35°C and 40°C (Amiot et al. 2017), in line with many extant birds and mammals. Almost all endotherms possess integumental covering, and as pennaraptorans, oviraptorosaurs were most likely feathered (Lefèvre et al. 2020; Hendrickx et al. 2022). Several oviraptorosaur fossils preserve direct evidence of feathers (Qiang et al. 1998; Xu et al. 2010).

Oviraptorosaur Clutch Coverage

Based on the adult–clutch association (MPC-D 107/15) described by Fanti et al. (2012), Yang et al. (2019b) raise concerns about oviraptorosaurs' ability to physically cover their clutches. It has also been suggested that oviraptorosaurs exhibit larger clutch volumes than would be expected for an animal of their size (Varricchio and Jackson 2016). As Yang et al. (2019b) point out, the inability of an attending adult to effectively cover the clutch would make adult-mediated incubation problematic, and the prospect had to be considered before experimentation.

MPC-D 107/15 is one of the more poorly preserved nesting oviraptorosaurs, and comparison to other specimens shows that egg clutches tend to fit more compactly underneath attending adults than MPC-D 107/15 suggests (Norell et al. 1995, 2018; Clark et al. 1999; Bi et al. 2021) (Fig. 2, Table 1). IGM 100/1004 (Norell et al. 2018) has an estimated mass of 79.2–115 kg (Varricchio et al. [2008] calculates the lower end using Anderson et al. [1985]; upper end calculated using Campione et al. [2014]). IGM 100/979 does not have femur circumference available to calculate mass, but the specimen has been estimated to be about 11% smaller than IGM 100/1004 (Norell et al. 2018), resulting in an approximate range of 70.5–102 kg (Norell et al. 1995; Clark et al. 1999). The adult oviraptorosaur from LDNHMF2008 (Bi et al. 2021) has an estimated mass of 72.5–110 kg (calculated using Anderson et al. [1985] and Campione et al. [2014], respectively). In contrast, Fanti et al. (2012) reconstruct the mass (again via Anderson et al. 1985) of MPC-D 107/15 as roughly 40 kg, compared with 58 kg when calculated via Campione et al. (2014).

To interpret relative clutch coverage, approximate clutch areas can be reconstructed by circumscribing circles on concyclic triangles (triangles chosen as all can be circumscribed, unlike shapes with greater than three sides) derived from the furthest three points of egg material in each clutch. These clutch areas are described from an overhead view and do not consider three-dimensionality. Calculated areas are likely larger than actual (see clutch from Bi et al. 2021; Fig. 2C herein), but are consistent for relative comparison between specimens. For example, even though Nemegtomaia (MPC-D 107/15) is just over half the mass of the nesting Citipati, its minimum reconstructed clutch area is substantially larger (Table 1; Fig. 2). On the other hand, adult mass to nest area ratios for IGM 100/979, IGM 100/1004, and LDNHMF2008 are similar, and numerous publications suggest that the adults represented by these specimens could have covered their clutches for incubation (Norell et al. 1995, 2018; Hopp and Orsen 2004; Fanti et al. 2012; Tanaka et al. 2018b; Bi et al. 2021). With this disparity in mind, other specimens seem more suitable than MPC-D 107/15 for predicting adult–clutch coverage.

Given that oviraptorosaurs appear to have exhibited the physiology and behavior required to incubate their clutches, the question then shifts to nest thermodynamics. Would an oviraptorosaur-style nest allow an attending adult to keep clutch temperatures above ambient conditions? Considering the lack of natural, modern analogues, it is useful to turn to experimentation for further insight.

Methods
Experimental Investigation

A suite of actualistic experiments (Figs. 3, 4) was undertaken to investigate the thermodynamics of uniquely structured oviraptorosaur nests and provide a better understanding of whether an attending adult could warm its clutch above ambient temperatures. In each of the three experiments, a surrogate dinosaur
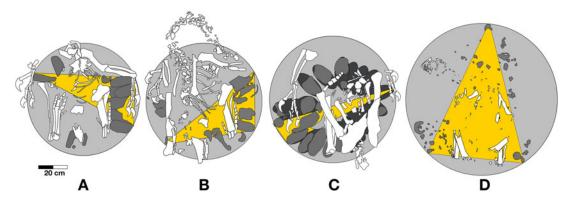
Figure 2. Four nesting oviraptorosaurs, redrawn from Norell et al. (1995) and Clark et al. (1999) (A), Norell et al. (2018) (B), Bi et al. (2021) (C), and Fanti et al. (2012) (D). Shown at the same scale. Gray circles represent approximate clutch areas reconstructed by circumscribing circles on concyclic triangles (yellow) derived from the farthest three points of egg material in each clutch. Estimations are likely larger than actual (see clutch represented by C; Bi et al. 2021), but are useful for specimen comparison. The *Citipati osmolskae* in A has an estimated mass of 102 kg and a clutch area of 4700 cm^2. B, Also *C. osmolskae*, has an estimated mass of 115 kg and clutch area of 5090 cm^2. C, An indeterminate oviraptorosaur has an estimated mass of 110 kg and a clutch area of 6020 cm^2. D, *Nemegtomaia barsboldi*, has an estimated mass of 58 kg (Fanti et al. 2012), but a clutch area of 8730 cm^2. Yang et al. (2019b) suggest that oviraptorosaurs were unable to cover their nests based on *N. barsboldi* (D), but this specimen is poorly preserved and yields vastly different body mass:clutch area ratios than other adult–clutch oviraptorosaur associations.

Table 1. Estimated adult oviraptorid masses, clutch area, and mass:clutch area ratios for specimens of adult–clutch associations.

Authors	Specimen	Species	Adult mass (kg)[a]	Estimated clutch area (cm^2)	Ratio (mass:area)
Norell et al. 1995; Clark et al. 1999	IGM 100/979	*Citipati osmolskae*	102	4700	0.0217
Norell et al. 2018	IGM 100/1004	*C. osmolskae*	115	5090	0.0226
Bi et al. 2021	LDNHMF2008	Undetermined	110	6020	0.0183
Fanti et al. 2012	MPC-D 107/15	*Nemegtomaia barsboldi*	58.0	8730	0.00664

[a]For consistency in comparison, masses are upper-range values recalculated from femur circumference using Campione et al. (2014), excepting IGM 100/979, which lacks suitable material. IGM 100/979 is roughly 11% smaller than IGM 100/1004 (Norell et al. 2018), and its mass is approximated as such.

(with the approximate body mass and temperature of a medium-sized oviraptorosaur) was placed atop a replica oviraptorosaur nest constructed from sand and three tiers of nonviable emu eggs.

Experiment 1 examined the energy flow within a basic, open nest—mimicking a scenario where an attending adult is warming the three-dimensional clutch from atop the nest (Fig. 4B). Once positioned, all electrical energy required to keep the surrogate at body temperature was metered. Experiment 2 differed from the first in that the clutch was completely buried instead of partially exposed. The entire center of the nest cavity was filled in with sand (but each egg was still positioned as in Experiment 1), and the adult again was set atop to warm the clutch from above (Fig. 4C). A fully buried nest model provides a useful point of comparison to the open, partially buried clutches currently hypothesized by most authors (and examined in Experiment 1). The fully buried trials also examine the efficacy of indirect contact incubation (Hogan and Varricchio 2021). Indirect contact incubation is the hypothetical process by which an endothermic adult might transfer metabolically generated energy through a substrate to its buried clutch. However, Experiment 2 does not serve as a direct comparative test of the hypothesis that oviraptorosaur clutches were buried and warmed through decaying plant matter, because the energy entering the experimental systems originated from different parameters with no organics used.

Experiment 3 utilized an open nest, as in Experiment 1, but added a pair of pumps (KEDSUM 800GPH Submersible Water Pump) to circulate water out of the central surrogate bath and down into the nest hollow through a series of tubes, all the way to egg level 1 and the central nest floor before returning the water to the surrogate (Fig. 4D). This test was designed to imitate an incubating adult with its legs and/or body sunk into the center of the clutch, providing observations of whether a clutch could benefit from temperature regulation via hindlimbs or other ventrally located and exposed skin. There is disagreement over whether attending oviraptorosaurs' abdomens were positioned to facilitate incubation (Norell et al. 2018; Yang et al. 2019b). Most modern birds rely on abdominal contact through brood patches to incubate their eggs. However, the novel nature of oviraptorosaur nests makes considering novel incubation practices worthwhile. Medium-sized oviraptorosaur nests have a center devoid of eggs, a space likely used by the adult to brace and position itself (Tanaka et al. 2018a), where their hindlimbs are conspicuously placed (Norell et al. 1995: fig. 1, 2018: fig. 4; Fanti et al. 2012: fig. 3; Bi et al. 2021: fig. 1). Many modern birds use their hindlimbs or other featherless regions to expel heat for their thermoregulation, and the same process applied within the confines of an oviraptorosaur nest might allow for some measure of clutch warming—a scenario approximated through Experiment 3. An experiment combining a subterranean clutch and heating elements extended at depth was not run, as these options seem mutually exclusive.

In each experiment, once the surrogate was placed on the nest, temperature changes in the nest system were monitored by

Figure 3. Photographs of the experimental arrangement. A, Nonviable emu eggs placed in a three-level oviraptorosaur-style clutch before experimentation. B, The blunt end of each egg was carefully tapped open to allow a thermometer to be placed inside before resealing. C, Eggs back into place with thermometers inserted. D, Close-up of experimental eggs. Central column probes are visible attached to a stake in the middle of the clutch (stake top was truncated before tests were run). E, Surrogate dinosaur seen from above. It held ~70 kg of water, heated to approximately 39°C, and had a total mass of ~80 kg. F, Surrogate shown as it looked while resting on the nest in all experiments.
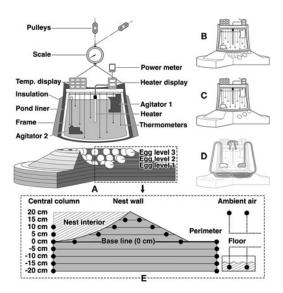

Figure 4. Diagram of the surrogate dinosaur, nest system, and experimental configurations. A, Cross section of the surrogate and nest. B, Experiment 1 setup, a basic open nest, as described by Yang et al. (2019b), heated from above. The surrogate rested on top of the nest structure, with the majority of its weight held by a pulley. C, Experiment 2 setup, identical to Experiment 1, except the internal air pocket of the nest was filled with sediment to create a subterranean nesting system. D, Experiment 3 setup, identical to Experiment 1, except that water was circulated down through pipes and into the nest from the surrogate. Designed to mimic an open nest where an adult might use its hindlimbs or similar to warm the clutch from within instead of above. E, Pullout showing thermometer placement (black dots) within the nest environment.

thermometers (Aquaneat aquarium digital thermometers) distributed throughout. A thermometer was placed inside each emu egg (then resealed), at 5 cm vertical increments in the perimeter of the sediment foundation, in the center of the sediment foundation, in the walls of the nest structure, and in the center of the nest structure. Thermometers also monitored the ambient air outside the nest to verify the room's temperature, and another set of thermometers measured the floor temperature. Finally, a series of thermometers within the surrogate relayed its "body" temperature over time. Each environmental monitoring point had two separate dedicated thermometers. Results from a point were averaged between those thermometers. Egg-level temperatures were averaged across all thermometers at that particular egg level. Temperatures were recorded every 5 minutes for the first hour of experimentation, every hour for the first 8 hours, and every 8 hours for the remaining week.

The nest used in these experiments followed the most current interpretation of oviraptorosaur clutch architecture (Yang et al. 2019b), including three tiers (egg levels) of paired eggs, an egg inclination of approximately 35–40° (blunt ends pointing toward the nest center), egg placement within the inside walls of a volcano-shaped mound, and partial burial (excluding Experiment 2). Each experiment was conducted twice, and the results were averaged between the trials. For considerations of efficacy, an attending adult (represented by the surrogate) unable to raise and maintain egg temperatures notably above ambient would indicate that incubation via adult-generated energy appears impracticable in that scenario. Furthermore, an experiment that keeps clutch temperature beyond ambient yet requires an

unrealistic amount of energy (as monitored through the electrical meter) would likewise be considered impracticable.

Nest System and Foundation

A cylindrical container (height = 20 cm, diameter = 122 cm) was filled with ~500 kg of multipurpose sand. This sediment mostly consisted of sand-sized clasts, although it was well mixed with some included clay and gravel. The sand was kept dry to mirror the well-drained paleosols described around oviraptorosaur clutches (Eberth 1993; Dingus et al. 2008). This container was placed in a temperature-controlled room with a cement foundation. No other rooms or utilities were located below the experimental area. The ambient air temperature was set to ~21.5°C but was independently monitored throughout each experiment, as was the temperature of the cement floor.

The nest structure was built upon the sediment-filled container using only emu eggs and the same sand mix used prior. No geologic evidence of plant debris or other non-sediment infill has been described in oviraptorosaur nests, and the experiment did not examine these possibilities. The first (lowermost) ring of 10 emu eggs was placed in the center of the sediment basin, and then sand was built around the ring to provide the base for the next level. The second (middle) ring of 14 eggs was then laid down, followed by more sediment, and then finally, the third (uppermost) ring of 12 eggs (egg numbers in each level chosen based on averages of nests described in Tanaka et al. [2018a] and Yang et al. [2019b]). The resulting nest structure matched the squat, volcano-shaped nest profile described by Yang et al. (2019b). The eggs were only partially buried, their blunt ends exposed on the interior of the nest (excepting Experiment 2). Some depictions of oviraptorosaur nests (Dong and Currie 1996; Tanaka et al. 2018a) show the uppermost egg ring (level 3) as completely exposed. Fanti et al. (2012) suggest based contact between adult elements and eggs, but also acknowledge that the upper eggs may have been partially buried instead of fully exposed. These experiments invoked the partially buried interpretation, so level 3 eggs were not fully exposed and instead matched the two lower rings. Partial burial aided uppermost egg level stability and helped ensure the level 3 eggs experienced conditions similar to those of eggs in levels 1 and 2. This nest configuration was maintained for Experiments 1 and 3; however, Experiment 2 differed in that all eggs were fully buried, as the center nest cavity was filled up to the maximum nest height (egg level 3 completely buried; Fig. 4C)—a full mound instead of an open mound/volcano. Otherwise, the overall nest shape, egg locations, angles, orientation, and all other parameters remained the same as in Experiments 1 and 3.

Clutch dimensions were based on measurements of clutches from medium-sized oviraptorosaurs. Tanaka et al. (2018a) provide data on the sizes of the inner and outer diameters of oviraptorosaur clutches. The inner diameter is the distance between two opposite eggs in the lowest ring of the nest, whereas the outer diameter refers to the distance between two eggs (far egg ends) in the uppermost ring. Essentially, the inner diameter refers to the circular bottom of the empty nest interior, whereas the outer diameter is the minimum circle that encompasses all eggs in the clutch. Average clutch dimensions from *Macroolithus* eggs close in mass to emu eggs give an inner diameter of 18 cm and an outer diameter of 58 cm (Tanaka et al. 2018a). The nests described by Yang et al. (2019b) have inner diameters between 11 and 28 cm and outer diameters between 51 and

82 cm. Accordingly, the experimental nest was constructed to have an inner diameter of 20 cm and an outer diameter of 60 cm. *Macroolithus* eggs within the range of masses for experimental emu eggs (423–630 g) have approximate lengths of 172.76–188.98 mm, breadths of 66.04–77.7 mm, and breadth to length ratios between 0.365 and 0.430 (Tanaka et al. 2018a: supplementary information). Experimental emu egg breadth:length ratios ranged from 0.670 to 0.708. While clutch dimensions could still be approximated, this wider ratio meant that the experimental eggs could not be arranged as compactly as those in *Macroolithus* clutches and still maintain the parameters detailed in Yang et al. (2019b).

It was necessary to thread the thermometer wires throughout the nest. Each thermometer was powered by a small watch battery in a data display outside the experimental area, but there was initial concern that nonnegligible extraneous energy could enter the nest system as heat from these wires. Given the low energy demands to run each thermometer, all batteries had a lifetime far exceeding the combined experimental timeline. Even if the total capacity of every battery *had* been used during experimentation, it would amount to fewer than 0.236 kcal/day—an insignificant contribution in the scope of these experiments. All this considered, it is highly unlikely that wiring significantly impacted the results.

Eggs

Infertile emu eggs, acquired through the generosity of the Montana Emu Ranch Company, were selected to represent medium-sized oviraptorosaur eggs in the experimental models. Although no modern egg quite equals the elongated forms of oviraptorosaurs, emu eggs are comparable in mass, eggshell thickness, and maybe pigmentation. *Macroolithus* egg mass ranges from 380.5 to 911.0 g, averaging around 588 g (Tanaka et al. 2018a). The emu eggs used in this study weighed 423–630 g, with a mean of 541.5 g. For *Macroolithus* eggshell, thickness ranges between 0.713 and 1.88 mm (Tanaka et al. 2018a). Sampled *Macroolithus* eggshell from nests close in size to the desired model yield thicknesses of 0.71–1.3 mm (Norell et al. 2018), 1.0–1.2 mm (Fanti et al. 2012), and 1.3–1.5 mm (Yang et al. 2019b). Emu eggshell thickness averages between 1.07 and 1.27 mm (Majewska et al. 2008), within the range of many *Macroolithus* samples. Wiemann et al. (2017) argue that some *Macroolithus* eggs appear to have borne pigmentation which would have resulted in a blue-green coloration, a spectrum conveniently matched by modern emu eggs. A hole was drilled into the blunt end of each egg before placing a thermometer inside. The thermometer probe was approximately centrally located within each egg, although due to aggravation/settling, it is possible that some final thermometer locations were above or below the center. The hole was then resealed with a small amount of modeling clay and tape. Two eggs were broken and became unusable during initial testing and exploration, but none of the 36 experimental eggs broke once testing had begun.

Surrogate

A surrogate dinosaur was constructed mirroring the approximate mass and body temperature of a medium-sized oviraptorosaur. This surrogate was used to warm the nest in each suite of experiments. An interior frame for the surrogate was built from an approximately 80 L feed bucket (mouth diameter of about

60 cm). The bottom of the bucket was cut out and then flipped upside down so that the bottom opening was similar in size to the outer clutch diameter. A pond liner (14.5 mm PVC/polyester) was added to the interior bucket frame to hold water and provide a nonrigid bottom boundary. This structure was then placed on top of a larger circle of pond liner. A series of 16 grommets were added to the pond liner circle and then threaded with weight-bearing rope. When the rope was stretched taut, the outer circle of the pond liner pulled up around the interior structure, holding the water bath and providing adjustment points to ensure even weight distribution. The rope perimeter provided attachment points for a series of carabiners that stepped up to a balanced, central point. This surrogate structure was hooked to a hanging scale attached to a 6:1 pulley system centered above the experimental nest. A second, laterally displaced pulley system was added to make vertical and horizontal movement manageable.

The grommet-reinforced pond liner held the necessary water without tearing, leaking, or otherwise failing. The interior bath was filled with enough water to approximate the body mass of a medium-sized oviraptorosaur. Tanaka et al. (2018a) calculate a range of parental masses (85.7–196.4 kg) from clutches of *Macroolithus*, specifically a mass of 128.79 kg for an adult with eggs of a mass comparable to the average emu egg used in this study (560.5 g vs. 541.5 g, respectively). However, this estimate is based on clutch volume, and due to the unusually large clutch sizes seen in oviraptorosaur nests, these masses may be somewhat higher than those derived from anatomical measurements. IGM 100/1004 (Norell et al. 2018) has a mass range of 79.2 kg (Varricchio et al. [2008], calculated via Anderson et al. [1985]) to ~115 kg (calculated via Campione et al. [2014]). Adult oviraptorosaurs described in Norell et al. (1995) and Bi et al. (2021) have similar ranges (Table 1, Fig. 2). For these experiments, it was judged conservative to err on the lower side of the distribution, as higher masses of water might inflate perceived experimental efficiency through greater thermal inertia (greater mass of water would more effectively moderate nest system temperatures). Accordingly, the bath was filled with ~70 kg of water for an approximate total surrogate mass of 80 kg.

The surrogate's water heater (Hygger 500-watt submersible heater) was set to 40°C and monitored by eight separate thermometers distributed throughout the water bath. Early testing indicated the resulting surrogate temperatures would be below the set heater threshold. The most recent investigation of oviraptorosaur body temperatures indicates a range of 35–40°C (Amiot et al. 2017), and setting the heater to strive for 40°C would ensure surrogate temperatures remained within this proposed range. The heater was connected to a power meter (Poniie PN2000) so that all electrical energy used for heating could be monitored. Two pumps were added to the water bath to help agitate and circulate water to reduce temperature stratification within the water column. The outside perimeter of the surrogate was lined with insulation (~9-cm-thick fiberglass loft), and an insulated foam lid was created for the top. No insulation was added to the bottom of the surrogate.

Results

Experiment 1: Open Nest Warmed from Above

For Experiment 1 (Fig. 5A–C), the eggs in level 1 had an initial mean temperature of 21.9°C and an ending mean temperature of 29.5°C. Level 2 egg average temperature was initially 21.5°C, rising to 30.8°C by the end of the experiment. Level 3 eggs also

began at 21.5°C but increased to 32.0°C throughout the experiment. Egg level 3 warmed faster than level 2, which warmed faster than level 1; 3 (the uppermost level) stabilized at the highest temperature, while level 1 stabilized at the lowest. The average ambient air temperature throughout was 21.4°C, fluctuating ±0.8°C. The average floor temperature was 19.5°C, fluctuating between 21.4°C and 18.9°C. Over the full week of the experiment, the surrogate dinosaur had a mean temperature of 39°C, with a high of 39.3°C and a low of 38.7°C. Surrogate energy usage in Experiment 1 averaged 475 kcal/day.

Experiment 2: Subterranean Nest Warmed from Above

In Experiment 2 (Fig. 5D–F), the eggs in level 1 began with a mean temperature of 20.6°C and rose to a final temperature of 26.7°C. Level 2 eggs had an initial temperature of 21.1°C and a final temperature of 29.0°C. Eggs in level 3 started at 21.3°C and ended at 30.9°C. As in Experiment 1, each level of eggs warmed more quickly than the level(s) below. During Experiment 2, the average air temperature was 22.5°C, with fluctuations between 23.4°C and 21.8°C. The average floor temperature was 19.4°C, with fluctuations within ±0.5°C. The surrogate dinosaur averaged 38.5°C, with a high of 39.2°C and a low of 38.3°C. Surrogate energy usage in Experiment 2 averaged 704 kcal/day.

Experiment 3: Open Nest Warmed with Interior Elements

For Experiment 3 (Fig. 5G–I), the mean initial temperature of eggs in level 1 was 21.2°C, warming to 32°C by the end of the experiment. Eggs in level 2 began at 21.4°C and ended at 32.9°C. Level 3 eggs started at 21.0°C and rose to 32.3°C by the end of the experiment. During Experiment 3, the average ambient air temperature was 21.6°C, with fluctuations between 22.3°C and 20.6°C. The average ambient temperature of the floor surface was 18.6°C, with fluctuations of ±0.3°C. The surrogate averaged 39.1°C, with a high of 39.7°C and a low of 37.8°C. Surrogate energy usage in Experiment 3 averaged 434 kcal/day.

Central Nest Column

Temperatures are described from heights/depths relative to the nest base (0 cm). Internal nest air temperature in Experiment 1 varied from 33.4°C at 10 cm above the surface of the sand to 31.0°C at the air–sand interface (0 cm). At −5 cm (5 cm below the nest base), the sand was 27.6°C, and the temperature decreased steadily with depth to 20.7°C at −20 cm. Because the interior of the nest was infilled for Experiment 2, no portion of the central column was aerial. At 10 cm above the nest base level, the sediment temperature was 32.6°C. At the base level (0 cm), the temperature was 27.7°C, gradually decreasing to 20.7°C at −20 cm. The internal nest air temperature in Experiment 3 was 40.2°C at 10 cm above the nest base and 34.4°C at the nest base. At −5 cm the sediment temperature was 30.3°C, gradually dropping until it reached 22.2°C at −20 cm.

Interior Nest Walls

In Experiment 1, the temperature of the interior nest walls was 28.6°C at 15 cm, 29.2°C at 10 cm, 29.3°C at 5 cm, and 31.0°C at 0 cm. In Experiment 2, the temperature of the interior nest walls was 28.5°C at 15 cm, 29.3°C at 10 cm, 28.3°C at 5 cm, and 27.6°C at 0 cm. For Experiment 3, the temperature of the interior
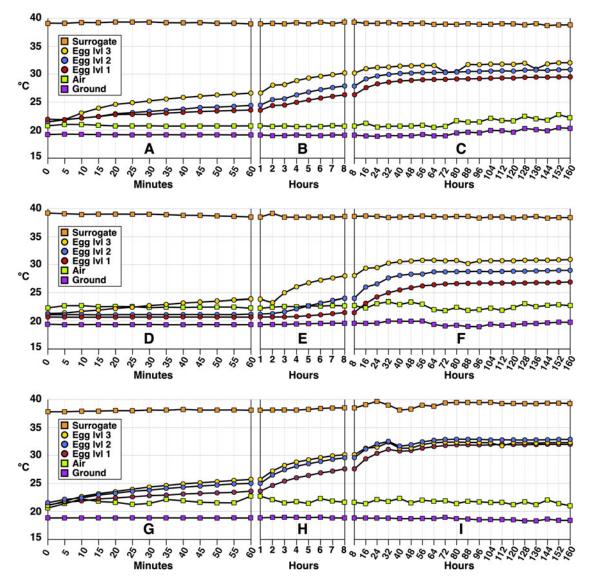
Figure 5. Temperature trends of the three egg levels, surrogate dinosaur, and the ambient air and ground throughout each experiment: A–C, Experiment 1; D–F, Experiment 2; G–I, Experiment 3. Left-side graphs (A, D, G) map the first 60 minutes of energy flow into the nest, center graphs (B, E, H) depict the following 7 hours, and right-side graphs (C, F, I) show the remaining time. All nest scenarios showed warming trends similar to modern bird nests, a quasi-logarithmic curve. Eggs warm more slowly and plateau at lower temperatures in Experiment 2 (D–F). Additionally, there is a greater temperature difference between each egg level. Eggs in levels 2 and 3 of Experiment 3 warmed more quickly than in Experiment 1, and these levels reached higher average temperatures with less segregation.

nest walls steadily increased with depth: 31.7°C at 15 cm, 32.3°C at 10 cm, 34.7°C at 5 cm, and 35.4°C at 0 cm.

Exterior Nest Walls

For Experiments 1 and 2 (listed respectively), the temperature of the exterior nest wall was 29.4°C and 28.5°C at 15 cm, 25.5°C and 24.9°C at 10 cm, 26.6°C and 26.0°C at 5 cm, and 25.7°C versus 24.8°C at the base level. Exterior nest wall temperatures were somewhat higher in Experiment 3: 33.5°C at 15 cm, 27.7°C at 10 cm, 27.9°C at 5 cm, and 26.5°C at 0 cm.

Exterior Perimeter

Final temperatures taken from depths along the perimeter of the experimental area varied little between experiments. Surface-level

(0 cm) temperatures at the perimeter ranged from 23.0°C to 23.2°C, then 22.6–22.8°C at −5 cm, 21.9–22.2°C at −10 cm, 21.4–21.8°C at −15 cm, and 20.7–21.2°C at −20 cm.

Energy Usage

The surrogate used ~475 kcal/day during Experiment 1, 704 kcal/day for Experiment 2, and 434 kcal/day for Experiment 3. Ranges were similar for Experiment 1 (~466–819 kcal/day) and Experiment 2 (~416–992 kcal/day). Experiment 3 had a comparable maximum but a lower minimum (~217–900 kcal/day).

Discussion

Each experimental system succeeded in raising and maintaining egg temperatures above ambient air and sediment temperatures.

Table 2. Averaged egg temperatures from each level at selected intervals.

		Initial	1 hr	8 hr	24 hr	72 hr	160 hr
Experiment 1 (°C)	Level 3	21.5	26.6	30.2	31.2	30.4	32.0
	Level 2	21.5	24.4	27.9	29.7	30.3	30.8
	Level 1	21.9	23.6	26.3	28.3	29.1	29.5
Experiment 2 (°C)	Level 3	21.3	23.9	28.0	29.4	30.6	30.9
	Level 2	21.1	21.2	24.0	26.6	28.7	29.0
	Level 1	20.6	20.6	21.4	24.2	26.5	26.7
Experiment 3 (°C)	Level 3	21.0	25.7	30.1	31.5	32.4	32.3
	Level 2	21.4	25	29.6	32.0	32.8	32.9
	Level 1	21.2	23.6	27.6	30.4	31.8	32.0

Final egg level average temperatures ranges were 29.5–32°C in Experiment 1, 26.7–30.9°C in Experiment 2, and 32.0–32.9°C in Experiment 3 (Table 2, Figs. 6, 7). Surrogate energy usage was comparable in Experiments 1 and 3. The greater sediment–surrogate contact in Experiment 2 likely accounts for the experiment's increased energy consumption (more electricity used to keep the water bath at temperature). It is *not* suggested that these values are equivalent to what an incubating oviraptorosaur might expend. Instead, compared with energy expended by incubating emus, ~645–813 kcal/day (Buttemer and Dawson 1989), it can be said that neither the buried nor the open-style experiments required unrealistically high energy input to keep the clutch warm. In these regards, the experiments were successful. However, several limitations are examined in the following sections, followed by further considerations regarding the unique nature of oviraptorosaur nests. Finally, aspects of the evolution of subaerial nesting strategies are examined in light of these experiments.

Limitations

Experimental Temperatures. The egg temperatures achieved in these experiments were closer to crocodilian than avian norms, suggesting that clutch temperatures in an oviraptorosaur-style nest could not reach those observed in modern birds. It is likely that dinosaur egg incubation times were significantly longer than those predicted for birds with similar-sized eggs (Erickson et al. 2017; Varricchio et al. 2018), and lower incubation temperatures could be a factor.

In a scenario where incubation temperatures were similar to modern crocodilian values, an attending endothermic adult might still provide a benefit by moderating temperature fluctuation. Observations of saltwater crocodile (*Crocodylus porosus*) nests indicate that temperature changes may disproportionally affect egg development (Webb et al. 1983). A nest at 30°C required about 85 days to hatch, whereas a nest at 27°C needed ~136 days (51 day difference). However, a nest at 33°C (3°C higher) would hatch in around 73 days (12 day difference). Because of the asymmetrical effects of temperature fluctuation on egg development (the increase in incubation time from dropping below the average clutch temperature is significantly greater than the decrease in incubation time from raising clutch temperatures an equal amount), Webb et al. (1983) suggest that nests with temperatures that fluctuate a few degrees around a median value likely have longer incubation times than a clutch at constant temperature.

It should be considered that relatively cool ambient conditions likely exacerbated low experimental clutch temperatures. There were high average temperatures globally in the Cretaceous, and the sandstone containing oviraptorosaur clutches has been described as forming in dry, largely eolian sediments from semi-arid to arid climates (Eberth 1993; Dingus et al. 2008). The average experimental ambient temperature (~21.5°C) is likely low compared with what many nesting oviraptorosaurs might have experienced. Future experimentation in warmer ambient conditions would likely show increased experimental clutch temperatures and might make a more appropriate comparison.

The use of infertile eggs could also have played a role in decreasing experimental clutch temperatures. Developing embryos generate their own energy, and eggs containing live ostrich (*Struthio camelus*) embryos can be 2°C warmer than infertile eggs (Swart and Rahn 1988). Metabolic heating from embryos in alligator (*Alligator mississippiensis*) clutches can elevate temperatures by 1.8°C (Ewert and Nelson 2003). Accordingly, an oviraptorosaur-style nest with fertile eggs would likely yield higher egg temperatures than those shown in these experiments.

Temperature gradients within an egg ought to be considered as well (Gill 1995; Turner 2002). Eggs can experience a gradient of 2–6°C, with a rough average in the middle of the egg (Swart et al. 1987; Swart and Rahn 1988), and as Turner (2002) highlights, it is most useful to compare egg temperatures originating from the same locations. In these oviraptorosaur nest experiments, thermometers were placed centrally to best discern average egg temperature and are most appropriately compared against other central egg temperatures. For example, Rahn (1991) calculates an average egg center temperature of 35.85°C (1.8 SD) across a variety of modern birds (Rahn 1991; Turner 2002). Future research employing similar methods may benefit from thermometers adhered to both the inside top and bottom of each egg (especially large ratite eggs), instead of just centrally placed. This distribution would allow for more precise measurements that could be more suitably compared with egg temperatures from noncentral locations.

Additional Incubation Factors. Egg temperature is the strongest predictor of incubation rate and hatching success (Tombre and Erikstad 1996; Szczerbińska et al. 2003; Martin et al. 2007; DuRant et al. 2013). As such, resulting egg temperature was the
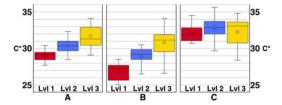
Figure 6. Box and whisker plot of the final (160 hr) egg temperature values from each level (red, level 1; blue, level 2; yellow, level 3) of each experiment. Box encompasses upper and lower quartiles; whiskers, the minimum and maximum values; interior line, the median; and interior circle, the mean. A, Values from Experiment 1, the basic open nest. B, Temperatures from Experiment 2, the fully buried clutch. C, Egg temperatures from Experiment 3, the interiorly warmed clutch. Eggs represented in B are cooler than the other experiments with more significant temperature differences between levels. The eggs shown in C have more temperature overlap than in other scenarios, and overall less temperature differentiation between levels. The temperature spread between each averaged egg level was 2.5°C in Experiment 1, 4.2°C in Experiment 2, and 0.9°C in Experiment 3.

Figure 7. Heat map profiles reconstructed from initial and final temperature readings (rounded to the nearest degree) in each experiment: A, Experiment 1; B, Experiment 2; C, Experiment 3. Starting temperatures of the nest and clutch in each experiment were between 23°C and 19°C. In general, temperature gradients seem compacted in the vertical axis, likely due to contact with the cool cement floor of the experimental area (18–20°C). A, Eggs were kept well above ambient air (22.2°C) and floor (20.3°C) temperatures. Sediments in the nest structure, above the baseline, we also kept above ambient temperatures, with the center of the nest at 31.0°C. B, Overall, eggs did not reach temperatures as high as seen in Experiment 1; however, the upper two levels came close. As seen in the temperature profile, if located more centrally, the eggs may have warmed even more. Energy from the surrogate clearly penetrates the sand, influencing depths even 30 cm below. This might be extended if the sediment profile itself were deepened instead of discontinuing on a cement floor. Current research (Wiemann et al. 2017; Norell et al. 2018; Yang et al. 2019b; Bi et al. 2021) indicates that oviraptorosaur eggs were not fully buried, but data from this experiment suggest that it may nonetheless be possible for buried eggs to be warmed by an attending endothermic adult—perhaps a necessary step in the evolution of subaerial eggs. C, When heating elements were extended into the nest, the entire microenvironment warmed significantly. Such a heating strategy could potentially be implemented through an adult's legs, feet, or other exposed ventral skin.

focus of experimentation. However, the limited scope of the study necessarily required that other important factors remained unexplored.

These experiments did not examine how oviraptorosaur-style nests would aid/hinder clutch cooling; perhaps a crucial part of incubation in the hot environments where many oviraptorosaur specimens have been described. Some birds (*Peltohyas australis*, *Pluvianus aegyptius*) contact incubate their clutches only at night or when ambient temperatures are cool, otherwise covering and leaving their nests unattended (Maclean 1974). In these cases, raising clutch temperatures is not always the prime concern. Beyond clutch temperatures, oviraptorosaurs' novel clutch arrangements likely affected other aspects of incubation. For example, the three-dimensionality, close spatial packing, and large clutch sizes might strain embryonic respiration. These experiments indicated that clutches could have been warmed by attending adults, but perhaps embryo development would instead be limited by oxygen availability in the packed nest confines in these scenarios. Incubation success was likely constrained by factors beyond clutch warmth, and further investigation is needed to understand additional limitations.

Nest Construction. Because sand is often a three-phase medium (solid particles, liquid moisture, and gaseous air pockets), it can be thermodynamically complex (Haigh 2012). For thermal conductivity, two of the most significant properties of sediments are moisture content and grain size (Chen 2008). Neither of these variables was examined in these experiments, but their effects can be surmised from the results of other studies. Higher moisture content leads to a more conductive matrix (Chen 2008; Tarnawski et al. 2009) and thus a less insulative nest microenvironment. For grain size, thermal conductivity tends to increase as porosity decreases. Finer-grained sediment contacts more and contains fewer insulative air pockets (Chen 2008). The sediment used in this experiment was dry, well-mixed sand with some included clay and gravel. It is likely that clutch temperatures would not be warmed as efficiently with moist or finer-grained sediments. Nevertheless, Tanaka et al. (2015) indicate that sediment preference was not a significant factor in oviraptorosaur nesting. Still, further investigation examining efficacy of oviraptorosaur-style nests built with various sediments compositions would be worthwhile.
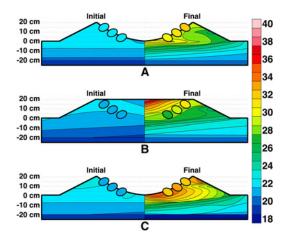
Further Considerations of Oviraptorosaur Nesting

Three-Dimensional Egg Emplacement. Oviraptorosaur clutches are unique in that they are open to the air and distributed three-dimensionally. Discussion of oviraptorosaur clutch arrangement often focuses on interpretating eggs in rising, concentric rings (or occasionally interpreted as a rising spiral). However, this three-dimensionality also affects usable nest surface area. A clutch of rising, concentric rings means that eggs are placed within the interior walls of a conical frustum. At least for the dimensions of oviraptorosaur nests containing *Macroolithus*-type eggs, the interior frustum walls cover more surface area than that of a two-dimensional nest with an equal maximum diameter. A monolayer clutch, placed within a 60 cm circular plane, can be distributed across approximately 2827 cm². In comparison, the walls of a conical frustum with a base diameter of 20 cm, an upper diameter of 60 cm, and a height of 20 cm cover an area of 3554 cm²—a 25.7% increase in surface area (Fig. 8).

If oviraptorosaurs could incubate their eggs via adult-derived energy, then an oviraptorosaur-style nest would allow an adult (of similar proportions discussed here) to incubate more nest surface area than if the nest had instead been distributed over a flat surface. Assuming similar egg spacing, a nest with a greater area could hold more eggs than a nest with less area. Notably, oviraptorosaurs appear to have had larger clutch volumes than are predicted for their body mass (Varricchio and Jackson 2003, 2016), and perhaps their unique nesting mode aided successful incubation of their proportionally large clutches.
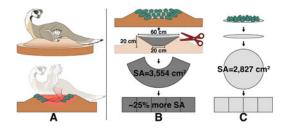
Figure 8. Hypothetical oviraptorosaur nesting depiction and nest surface area comparison. A, It is perhaps possible that an oviraptorosaur could have warmed its nest cavity by radiating energy from exposed skin, perhaps on the hindlimbs or underbelly. Oviraptorosaur adult–clutch associations preserve a brooding posture with their legs centrally placed within the nest, likely allowing the adult to cover the clutch without harming the eggs (see Tanaka et al. 2018a). This leg positioning would also be ideal for warming the nest from within. B, The interior hollow of an oviraptorosaur-style nest approximates the shape of a conical frustum (truncated cone). The eggs are emplaced within the wall of the frustum. If the frustum wall were laid out flat, given similar dimensions to a medium-sized oviraptorosaur nest (upper diameter = 60 cm, lower diameter = 20 cm, height = 20 cm) then it would have roughly 25% more nest surface area than a flat, circular nest of the same upper diameter (C). (Egg number and arrangement shown at the bottom of B and C are relative and do not reflect actual spacing or maximum egg counts.) Given the increased nest surface area, and assuming eggs are spaced similarly, a three-dimensional oviraptorosaur-type nest could hold more eggs than a flat, monolayer nest. If oviraptorosaurs were able to use their own body heat to warm their clutches, then their peculiar, three-dimensional clutch arrangement might play a role in aiding the successful incubation of their notably large clutch volumes.

Hindlimb-mediated Incubation Hypothesis. Given the uniqueness of oviraptorosaur nests, it is useful to consider novel incubation possibilities. Traditional contact incubation may have been problematic to implement, as it seems impractical to maintain skin–egg contact across such a large and three-dimensionally distributed clutch. However, an attending adult covering the clutch could suitably warm the nesting microenvironment without directly contacting each egg at all times. Yang et al. (2019b) emphasized that, in nesting oviraptorosaur specimens, many eggs are not covered by the abdominal region (although Norell et al. [2018] indicated otherwise). They suggest that the abdomen would be the heat generator (where brood patches form in modern birds), and without its coverage the adult oviraptorosaur could not incubate its clutch. In contrast to the abdominal region, oviraptorosaur hindlimbs are near centrally positioned in IGM 100/979 (Norell et al. 1995; Clark et al. 1999), IGM 100/1004 (Norell et al. 2018), and LDNHMF2008 (Bi et al. 2021) (Fig. 2).

Having the hindlimbs anchored to the bottom center of the nest puts them in an ideal location for warming the nesting microenvironment. Perhaps oviraptorosaurs could raise clutch temperatures by dissipating energy through their hindlimbs or other ventrally exposed skin. This would radiate heat into the nest from an interior, central location and not just from above (Experiment 3 vs. Experiment 1). As supported by the results of Experiment 3, internal warming could elevate and equalize clutch temperatures (Figs. 6, 7). Adult hindlimbs may have acted like radiator coils, warming the nest microenvironment from the interior. The top of the nest would be capped and insulated by the adult, and the sand foundation would provide some insulation along the walls and floor. In this hypothetical case, no brood patch is necessary, nor would the adult need to contact the entirety of its clutch. Nevertheless, adult-generated heat would permeate the nest and warm the clutch. It is unlikely that this would be as effective as traditional contact incubation, but perhaps it was sufficient.

Hindlimbs are suggested as a likely heat dissipator, because many modern birds (e.g., wood stork [*Mycteria americana*; Kahl 1963]; turkey vultures [*Cathartes aura*; Arad et al. 1989]; and emu [Maloney and Dawson 1994]) use their legs in a thermoregulatory capacity. Steen and Steen (1965) found that, at high temperatures, herons (*Ardea cinerea*) and gulls (*Larus marinus*) can dissipate 50% of resting heat production through their legs, and Phillips and Sanborn (1994) reported 40% dissipation for ostrich, emu, and double-wattled cassowary (*Casuarius casuarius*). Given the phylogenetic position of Oviraptorosauria within Pennaraptora, coupled with data from several fossils, it is likely that oviraptorosaurs were feathered (Qiang et al. 1998; Xu et al. 2010; Persons et al. 2013; Lefèvre et al. 2020; Hendrickx et al. 2022). Fossil evidence suggests that *Caudipteryx* (Qiang et al. 1998) and *Similicaudipteryx* (Xu et al. 2010), like many modern birds, had unfeathered tarsometatarsi and pedes—although this could be due to imperfect preservation. Given unfeathered portions of the hindlimbs, it seems possible that some non-avian dinosaurs used this anatomy for thermoregulation. Perhaps oviraptorosaurs also used these features to warm their clutches.

Hindlimb-mediated incubation is used by some modern species including white-tailed tropic birds (*Phaethon lepturus*; Hart et al. 2016), Nazca boobies (*Sula granti*; Morgan et al. 2003), and Australasian gannets (*Morus serrator*; Evans 1995). Many of these are Pelecaniformes, whose high surface area webbed feet can effectively conduct energy to an egg without needing a brood patch. Morgan et al. (2003) showed that the feet of incubating Nazca boobies can even exceed abdominal temperatures, indicating that the feet were not solely relegated to redirecting abdominal heat. These examples show that, even among modern birds, hindlimbs have evolved to be used in incubation. However, given significant differences in hindlimb morphology, they are unsuitable for direct comparisons to oviraptorosaur incubation. Additionally, these birds still incubate through direct contact, and as previously mentioned, oviraptorosaur-style nests may not allow an attending adult to contact the entire clutch at once.

Hatching Asynchrony/Synchrony. Hatching asynchrony has been hypothesized for oviraptorosaurs based on clutches containing embryonic material at differing stages of development (Weishampel et al. 2008; Yang et al. 2019a; Bi et al. 2021). Given the unique construction of oviraptorosaur nests, the mechanisms by which hatching asynchrony could arise are unclear. Bi et al. (2021) suggest that adults delayed incubation until clutch completion, with asynchronous hatching emerging due to non-uniform egg conditions, such as temperature stratification between egg levels. The results of Experiment 1 show that such banding may be possible, although temperature overlap between egg levels (Fig. 6) indicates that in this scenario, resulting asynchrony would not be as linear as each egg level hatching in descending order.

Alternatively, in most modern birds, asynchronous hatching results from early-onset incubation and variable oviposition times (Hébert 2002). However, early onset incubation may be difficult to pair with oviraptorosaur clutch size and arrangement. Large clutch sizes mean some eggs could be laid weeks apart, but this concern could be alleviated in a communal nesting scenario (Varricchio and Jackson 2016). Also, all asynchronous hatching options beg the question of nest structure stability. Would the structural integrity of the nest be compromised by eggs hatching at different rates? Significant sediment compaction may occur over the period of incubation, enough that the nest

could maintain its shape regardless of hatching order. However, given the highly organized nature of the nest, the fact that eggs are immured in the nest walls as construction material, the process of hatching, and the effort of the young to escape the nest, it also seems possible that partial nest collapse could occur. Casual observations from the experiments herein indicate that the removal or adjustment of eggs can indeed impair nest structure. However, nest structural integrity was not the focus of these experiments, and further explicit investigation is needed.

Varricchio (2021) cautions that preserving embryos at different stages of development within a single clutch does not necessarily correspond to asynchronous hatching. Diachronous embryonic death can yield the same result, even if the embryos would have hatched synchronously (Jackson et al. 2015; Varricchio 2021). Because of this, hatching synchrony should not be ruled out for oviraptorosaurs. Given a scenario like that modeled in Experiment 3 (i.e., largely uniform egg temperatures), incubation delayed until clutch completion could yield synchronous hatching. Of course, it is also possible that hatching synchrony varied from species to species, given the variety of oviraptorosaurs and their nesting strategies.

Evolution of Subaerial Nesting Strategies

Decades ago, Gauthier (1986) considered a potential oviraptorosaur–bird relationship, and Sabath (1991), in a description of an oviraptorosaur clutch, mused on the "nesting behavior of the primitive birds: how early did they start to use the parents' metabolism as the energy source for the incubating embryo?" (p. 173). Given modern archosaur behavior and current fossil evidence, it is likely that the dominant avian nesting strategy of contact incubating exposed eggs evolved from a prior state of adult guarding and egg burial (Deeming 2002; Varricchio and Jackson 2016). This behavioral transition marks a major shift within the reptilian–avian reproductive continuum; thermoregulatory contact incubation often requires attending behavior, endothermy, and exposed eggs. While nest attendance seems to be fairly conserved among archosaurs (Murray et al. 2020), and there has been robust discussion on the evolution of endothermy (including the possible role of reproductive strategies in driving endothermic innovation: Farmer 2000; Koteja 2000; Bacigalupe et al. 2017; Polymeropoulos et al. 2018), there has been comparatively little conversation regarding the steps necessary to move from a subterranean to subaerial habit.

Because complex behavior often evolves incrementally (Lorenz 1958; Gould 1982; Gomez and Miikkulainen 1997), partial egg burial, as an intermediate between subterranean and subaerial, is perhaps a predictable egg state. Varricchio and Jackson (2016) highlight partial egg burial as an important feature arising between ancestral reptilian and derived avian strategies. While seemingly common behavior in extinct pennaraptorans, partial egg burial is rare among extant archosaurs (Grellet-Tinner et al. 2006)—a factor that has hindered our understanding of the efficacy of partial egg burial and the evolution of subaerial nesting strategies.

It has been argued that the incubation of partially buried eggs via adult-generated heat would be infeasible (Ruben et al. 2003), but several bird species (three-banded courser, *Rhinoptilus cinctus*; Egyptian plover, *Pluvianus aegyptius*; Kentish plover, *Charadrius alexandrinus*) manage it today (Maclean 1974; Howell 1979). Experimentally, Hogan and Varricchio (2021) also demonstrated that partially buried eggs, when contact incubated, can be kept well above ambient temperatures with reasonable energy demands, even in cold climates. Results from the present study seem to corroborate and expand upon those of Hogan and Varricchio (2021), as partially buried eggs reached and maintained temperatures beyond those of the ambient air and sediment and within the lower bands of avian incubation (see Experiments 1 and 3). While such incubation methods may be viable, they are less efficient than contact incubating fully exposed eggs. As such, it seems appropriate to differentiate between "weak" contact incubation (partially buried eggs) and "strong" contact incubation (fully exposed eggs) (Hogan and Varricchio 2021). While a path from weak to strong contact incubation appears to be a straightforward evolutionary trajectory, in what manner did partial egg burial arise in the first place?

Thermoregulatory contact incubation relies on close physical contact between the adult and the egg, and it has been suggested that adult-generated energy transfer to eggs can only be effective if the eggs are exposed (Deeming 2002; Tanaka et al. 2015). The vast majority of modern birds exhibit thermoregulatory contact incubation. However, this behavior must have evolved from prior iterations upon a past suite of behaviors (Fig. 9). Although unseen among today's avifauna, it is perhaps possible that endothermic adults conducted energy to their eggs through a sedimentary medium (Hogan and Varricchio 2021). The possibility of indirect contact incubation is supported by the results of Experiment 2, in which fully buried eggs are kept significantly above ambient temperatures despite being encased in sediments (Figs. 5B, 7C).

For any adult and its buried clutch, there would be a maximum burial distance at which thermal input would become negligible. However, eggs buried above this thermal input threshold would benefit from some measure of warmth. Temperature is the strongest predictor of incubation rate and hatchling success (Tombre and Erikstad 1996; Szczerbińska et al. 2003; Martin et al. 2007; DuRant et al. 2013); even a minor increase could affect the survival rate of the young. In Experiment 2, eggs in the lowest level, 20 cm below the surrogate, were kept at ~5°C above ambient
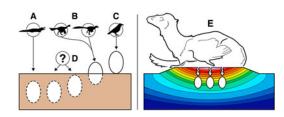

Figure 9. Indirect contact incubation could provide the mechanism needed to move from reptilian subterranean to avian subaerial nesting states. A, Basal ectothermic (blue) archosaurs attend their buried clutches, and the fossil record shows that some maniraptorans, likely endothermic (red), attended their partially buried eggs (B) as well. Contact incubation of fully exposed eggs would be more effective than incubating partially buried eggs, making an evolutionary trajectory between the two appear straightforward. While partial egg burial (B) is a convenient halfway marker between subterranean and subaerial states (C, as seen in modern birds), it is unclear how any measure of egg exposure evolved in the first place. D, Perhaps, before egg exposure, an attending endothermic adult could transmit some measure of metabolic energy through a barrier of sediment to a buried clutch. Over time this could drive clutches toward shallower burial to increase exposure to the adult's metabolic energy. E, Experimental investigation suggests that energy transmission through a sediment barrier is possible, with clutches in such scenarios being warmed significantly beyond ambient temperatures. Eggs closer to the surface experience greater thermal benefits than those buried deeper. Buried eggs experience a measure of protection from predation and the elements that would be lessened as they are laid closer to the surface—but the presence of an attending, endothermic adult would alleviate the effects of these environmental pressures.

temperatures. Through natural selection, buried clutches might gradually be brought closer to the surface and the guarding endotherm, thus benefiting more from the adult's energy. Notably, in the absence of an attending endothermic adult, laying eggs nearer to the surface seems detrimental, as it yields less protection against temperature fluctuations, weather, and predation.

Conclusion

The experiments conducted herein sought to provide metrics with which to better understand oviraptorosaur nesting strategies and the evolution of modern avian nesting behavior. Although dozens of oviraptorosaur clutches and many adult–clutch associations have been discovered, it is still difficult to interpret oviraptorosaur nesting behavior, largely due to the unique clutch arrangement and nest architecture. Results from these experiments support the proposition that an endothermic, attending oviraptorosaur could warm its clutch above ambient air and sediment temperatures without requiring unreasonable metabolic energy input—albeit at temperatures below those seen in modern bird incubation. A temperature gradient may exist across the different tiers of eggs in a multilevel nest, but the inclusion of heat-radiating elements (possibly hindlimbs) in the nest could significantly reduce this stratification by elevating the temperature of eggs in the lower levels.

The distinctive arrangement of oviraptorosaur eggs should not only spark discussions of feasibility, but also considerations of advantages. Although unique within Archosauria, multi-tiered nests are widespread among oviraptorosaurs. Oviraptorosaurs are known for their proportionally large clutch volumes, perhaps enabled or supported by their three-dimensional egg arrangements. The clutch is distributed across the interior walls of the nest crater, a shape approximating a conical frustum, allowing an incubating adult to effectively cover more area than if the nest were laid out flat in a circular plane.

More broadly speaking, the results support the notion that partially buried eggs can benefit from the heat generated by an attending adult and that eggs separated from an attending adult by a layer of sediment could nevertheless benefit from that adult's heat generation as long as they are above the thermal input threshold. These conclusions provide insight into the reptilian–avian reproductive continuum, and although the strategies described earlier appear to be absent among modern archosaurs, they may still have been crucial steps in the evolution of modern avian nesting behavior.

Literature Cited

Amiot, R., C. Lecuyer, E. Buffetaut, G. Escarguel, F. Fluteau, and F. Martineau. 2006. Oxygen isotopes from biogenic apatites suggest widespread endothermy in Cretaceous dinosaurs. *Earth and Planetary Science Letters* 246:41–54.

Amiot, R., X. Wang, S. Wang, C. Lécuyer, J. M. Mazin, J. Mo, J. P. Flandrois, F. Fourel, X. Wang, X. Xu, Z. Zhang, Z. Zhou, and R. Benson. 2017. δ¹⁸O-derived incubation temperatures of oviraptorosaur eggs. *Palaeontology* 60: 633–647.

Anderson, J. F., A. Hall-Martin, and D. A. Russell. 1985. Long-bone circumference and weight in mammals, birds and dinosaurs. *Journal of Zoology* 207:53–61.

Arad, Z., U. Midtgård, and M. H. Bernstein. 1989. Thermoregulation in turkey vultures: vascular anatomy, arteriovenous heat exchange, and behavior. *The Condor* 91:505–514.

Bacigalupe, L. D., A. J. Moore, R. F. Nespolo, E. L. Rezende, and F. Bozinovic. 2017. Quantitative genetic modeling of the parental care hypothesis for the evolution of endothermy. *Frontiers in Physiology* 8:1005.

Barrick, R. E., and W. J. Showers. 1994. Thermophysiology of *Tyrannosaurus rex*: evidence from oxygen isotopes. *Science* 265:222–224.

Bi, S., R. Amiot, C. P. de Fabrègues, M. Pittman, M. C. Lamanna, Y. Yu, C. Yu, T. Yang, S. Zhang, Q. Zhao, and X. Xu. 2021. An oviraptorid preserved atop an embryo-bearing egg clutch sheds light on the reproductive biology of non-avialan theropod dinosaurs. *Science Bulletin* 66:947–954.

Buttemer, W. A., and T. J. Dawson. 1989. Body temperature, water flux and estimated energy expenditure of incubating emus (*Dromaius novaehollandiae*). *Comparative Biochemistry and Physiology A* 94: 21–24.

Campione, N. E., D. C. Evans, C. M. Brown, and M. T. Carrano. 2014. Body mass estimation in non-avian bipeds using a theoretical conversion to quadruped stylopodial proportions. *Methods in Ecology and Evolution* 5:913–923.

Chen, S. X. 2008. Thermal conductivity of sands. *Heat and Mass Transfer* 44:1241–1246.

Clark, J. M., M. Norell, L. M. Chiappe, M. S. U. Akademi, and Mongolian-American Museum Paleontological Project. 1999. An oviraptorid skeleton from the late Cretaceous of Ukhaa Tolgod, Mongolia, preserved in an avianlike brooding position over an oviraptorid nest. *American Museum Novitates* 3265:1–36.

Deeming, D. C. 2002. *Avian incubation: behaviour, environment and evolution.* Oxford University Press, Oxford.

Deeming, D. C. 2006. Ultrastructural and functional morphology of eggshells supports the idea that dinosaur eggs were incubated buried in a substrate. *Palaeontology* 49:171–185.

Dingus, L., D. B. Loope, D. Dashzeveg, C. C. Swisher, C. Minjin, M. J. Novacek, and M. A. Norell. 2008. The geology of Ukhaa Tolgod (Djadokhta Formation, Upper Cretaceous, Nemegt Basin, Mongolia). *American Museum Novitates* 3616:1–40.

Dong, Z. M., and P. J. Currie. 1996. On the discovery of an oviraptorid skeleton on a nest of eggs at Bayan Mandahu, Inner Mongolia, People's Republic of China. *Canadian Journal of Earth Sciences* 33:631–636.

DuRant, S. E., W. A. Hopkins, G. R. Hepp, and J. R. Walters. 2013. Ecological, evolutionary, and conservation implications of incubation temperature-dependent phenotypes in birds. *Biological Reviews* 88:499–509.

Eagle, R. A., T. Tutken, T. S. Martin, A. K. Tripati, H. C. Fricke, M. Connely, R. L. Cifelli, and J. M. Eiler. 2011. Dinosaur body

temperatures determined from isotopic (^{13}C-^{18}O) ordering in fossil biominerals. *Science* 333:443–445.

Eagle, R. A., M. Enriquez, G. Grellet-Tinner, A. Pérez-Huerta, D. Hu, T. Tütken, S. Montanari, S. J. Loyd, P. Ramirez, A. K. Tripati, M. J. Kohn, T. E. Cerling, L. M. Chiappe, and J. M. Eiler. 2015. Isotopic ordering in eggshells reflects body temperatures and suggests differing thermophysiology in two Cretaceous dinosaurs. *Nature Communications* 6:8296.

Eberth, D. A. 1993. Depositional environments and facies transitions of dinosaur-bearing Upper Cretaceous redbeds at Bayan Mandahu (Inner Mongolia, People's Republic of China). *Canadian Journal of Earth Sciences* 30:2196–2213.

Erickson, G. M., D. K. Zelenitsky, D. I. Kay, and M. A. Norell. 2017. Dinosaur incubation periods directly determined from growth-line counts in embryonic teeth show reptilian-grade development. *Proceedings of the National Academy of Sciences USA* 114:540–545.

Evans, R. M. 1995. Incubation temperature in the Australasian gannet *Morus serrator*. *Ibis* 137:340–344.

Ewert, M. A., and C. E. Nelson. 2003. Metabolic heating of embryos and sex determination in the American alligator, *Alligator mississippiensis*. *Journal of Thermal Biology* 28:159–165.

Fanti, F., P. J. Currie, and D. Badamgarav. 2012. New specimens of *Nemegtomaia* from the Baruungoyot and Nemegt formations (Late Cretaceous) of Mongolia. *PLoS ONE* 7:e31330.

Farmer, C. G. 2000. Parental care: the key to understanding endothermy and other convergent features in birds and mammals. *American Naturalist* 155:326–334.

Fricke, H. C., and R. R. Rogers. 2000. Multiple taxon–multiple locality approach to providing oxygen isotope evidence for warm-blooded theropod dinosaurs. *Geology* 28:799–802.

Gauthier, J. 1986. Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Sciences* 8:1–55.

Gill, F. B. 1995. *Ornithology*. Freeman, New York.

Gomez, F., and R. Miikkulainen. 1997. Incremental evolution of complex general behavior. *Adaptive Behavior* 5:317–342.

Gould, J. L. 1982. *Ethology: the mechanisms and evolution of behavior*. Norton, New York.

Grellet-Tinner, G., L. Chiappe, M. Norell, and D. Bottjer. 2006. Dinosaur eggs and nesting behaviors: a paleobiological investigation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 232:294–321.

Grigg, G., J. Nowack, J. E. P. W. Bicudo, N. C. Bal, H. N. Woodward, and R. S. Seymour. 2022. Whole-body endothermy: ancient, homologous and widespread among the ancestors of mammals, birds and crocodylians. *Biological Reviews* 97:766–801.

Haigh, S. K. 2012. Thermal conductivity of sands. *Geotechnique* 62:617–625.

Hart, L. A., C. T. Downs, and M. Brown. 2016. Hot footing eggs: thermal imaging reveals foot mediated incubation in white-tailed tropicbirds, *Phaethon lepturus*. *Journal of Ornithology* 157:635–640.

Hébert, P. N. 2002. Ecological factors affecting initiation of incubation behaviour. *Oxford Ornithology Series* 13:270–279.

Hendrickx, C., P. R. Bell, M. Pittman, A. R. Milner, E. Cuesta, J. O'Connor, M. Loewen, P. J. Currie, O. Mateus, T. G. Kaye, and R. Delcourt. 2022. Morphology and distribution of scales, dermal ossifications, and other non-feather integumentary structures in non-avialan theropod dinosaurs. *Biological Reviews* 97:960–1004.

Hogan, J. D., and D. J. Varricchio. 2021. Do paleontologists dream of electric dinosaurs? Investigating the presumed inefficiency of dinosaurs contact incubating partially buried eggs. *Paleobiology* 47:101–114.

Hopp, T. P., and M. J. Orsen. 2004. Dinosaur brooding behavior and the origin of flight feathers. P. 234 *in* P. J. Currie, E. B. Koppelhus, M. A. Shugar, and J. L. Wright, eds. *Feathered dragons: studies on the transition from dinosaurs to birds*. Indiana University Press, Bloomington.

Howell, T. R. 1979. Breeding biology of the Egyptian plover, *Pluvianus aegyptius*. University of California Press, Oakland.

Jackson, F. J., D. J. Varricchio, R. A. Jackson, A. Walde, and G. Bishop. 2015. Taphonomy of extant desert tortoise and loggerhead sea turtle nesting sites: implications for interpreting the fossil record. *Palaios* 30:207–223.

Jin, X., D. J. Varricchio, A. W. Poust, and T. He. 2019. An oviraptorosaur adult-egg association from the Cretaceous of Jiangxi Province, China. *Journal of Vertebrate Paleontology* 39:e1739060.

Kahl, M. P. 1963. Thermoregulation in the wood stork, with special reference to the role of the legs. *Physiological Zoology* 36:141–151.

Koteja, P. 2000. Energy assimilation, parental care and the evolution of endothermy. *Proceedings of the Royal Society of London B* 267:479–484.

Lefèvre, U., A. Cau, D. Hu, and P. Godefroit. 2020. Feather evolution in Pennaraptora. Pp. 103–111 *in* C. Foth and O. W. M. Rauhut, eds. *The evolution of feathers*. Springer, Cham, Switzerland.

Lorenz, K. Z. 1958. The evolution of behavior. *Scientific American*. 199:67–82.

Maclean, G. L. 1974. Egg-covering in the Charadrii. *Ostrich* 45:167–174.

Magnusson, W. E. 1979. Maintenance of temperature of crocodile nests (Reptilia, Crocodilidae). *Journal of Herpetology* 13:439–443.

Majewska, D., D. Szczerbinska, Z. Tarasewicz, M. Ligocki, A. Danczak, L. S. Nedzusiak, and A. Sammel. 2008. Age-related changes in the quality of emu (*Dromaius novaehollandiae*) eggs. *Archiv für Geflügelkunde/European Poultry Science* 72:168.

Maloney, S. K., and T. J. Dawson. 1994. Thermoregulation in a large bird, the emu (*Dromaius novaehollandiae*). *Journal of Comparative Physiology B* 164:464–472.

Martin, T. E., S. K. Auer, R. D. Bassar, A. M. Niklison, and P. Lloyd. 2007. Geographic variation in avian incubation periods and parental influences on embryonic temperature. *Evolution* 61:2558–2569.

Morgan, S. M., M. A. Ashley-Ross, and D. J. Anderson. 2003. Foot-mediated incubation: Nazca booby (*Sula granti*) feet as surrogate brood patches. *Physiological and Biochemical Zoology* 76:360–366.

Murray, C. M., B. I. Crother, and J. S. Doody. 2020. The evolution of crocodilian nesting ecology and behavior. *Ecology and Evolution* 10:131–149.

Norell, M. A., J. M. Clark, D. Demberelyin, B. Rhinchen, L. M. Chiappe, A. R. Davidson, and M. J. Novacek. 1994. A theropod dinosaur embryo and the affinities of the Flaming Cliffs dinosaur eggs. *Science* 266:779–782.

Norell, M. A., J. M. Clark, L. M. Chiappe, and D. Dashzeveg. 1995. A nesting dinosaur. *Nature* 378:774–776.

Norell, M. A., J. M. Clark, and L. M. Chiappe. 2001. An embryonic oviraptorid (Dinosauria: Theropoda) from the Upper Cretaceous of Mongolia. *American Museum Novitates* 2001:1–20.

Norell, M. A., A. M. Balanoff, D. E. Barta, and G. M. Erickson. 2018. A second specimen of Citipati osmolskae associated with a nest of eggs from Ukhaa Tolgod, Omnogov Aimag, Mongolia. *American Museum Novitates* 3899:1–44.

Persons, W. S., P. J. Currie, and M. A. Norell. 2013. Oviraptorosaur tail forms and functions. *Acta Palaeontologica Polonica* 59:553–567.

Phillips, P. K., and A. F. Sanborn. 1994. An infrared, thermographic study of surface temperature in three ratites: ostrich, emu and double-wattled cassowary. *Journal of Thermal Biology* 19:423–430.

Polymeropoulos, E. T., R. Oelkrug, and M. Jastroch. 2018. The evolution of endothermy—from patterns to mechanisms. *Frontiers in Physiology* 9:891.

Qiang, J., P. J. Currie, M. A. Norell, and J. Shu-An. 1998. Two feathered dinosaurs from northeastern China. *Nature* 393:753–761.

Rahn, H. 1991. Why birds lay eggs. Pp. 345–360 *in* D. C. Deeming and M. W. J. Ferguson, eds. *Egg incubation: its effects on embryonic development in birds and reptiles*. Cambridge University Press, Cambridge.

Ruben, J., T. Jones, and N. Geist. 2003. Respiratory and reproductive paleophysiology of dinosaurs and early birds. *Physiological and Biochemical Zoology* 76:141–164.

Sabath, K. 1991. Upper Cretaceous amniotic eggs from Gobi Desert. *Acta Palaeontologica Polonica* 36:51–192.

Slip, D. J., and R. Shine. 1988. Reptilian endothermy: a field study of thermoregulation by brooding diamond pythons. *Journal of Zoology* 216:367–378.

Stahlschmidt, Z. R., and D. F. Denardo. 2009. Effect of nest temperature on egg-brooding dynamics in Children's pythons. *Physiology and Behavior* 98:302–306.

Steen, I., and J. B. Steen. 1965. The importance of the legs in the thermoregulation of birds. *Acta Physiologica Scandinavica* 63:285–291.

Swart, D., and H. Rahn. 1988. Microclimate of ostrich nests: measurements of egg temperature and nest humidity using egg hygrometers. *Journal of Comparative Physiology B* 157:845–853.

Swart, D., H. Rahn, and J. de Kock. 1987. Nest microclimate and incubation water loss of eggs of the African ostrich (Struthio camelus var. domesticus). Supplement published under auspices of the American Society of Zoologists and the Division of Comparative Physiology and Biochemistry, *Journal of Experimental Zoology* **1**:239–246.

Szczerbińska, D., D. Majewska, Z. Tarasewicz, A. Danczak, and L. Ligocki. 2003. Hatchability of emu (*Dromaius novaehollandiae*) eggs in relation to incubation temperature. *Electronic Journal of Polish Agricultural Universities, Animal Husbandry* **6**.

Tanaka, K., D. K. Zelenitsky, and F. Therrien. 2015. Eggshell porosity provides insight on evolution of nesting in dinosaurs. *PLoS ONE* **10**:e0142829.

Tanaka, K., D. K. Zelenitsky, J. Lü, C. L. DeBuhr, L. Yi, S. Jia, F. Ding, M. Xia, D. Liu, C. Shen, and R. Chen. 2018a. Incubation behaviours of oviraptorosaur dinosaurs in relation to body size. *Biology Letters* **14**:20180135.

Tanaka, K., D. K. Zelenitsky, F. Therrien, and Y. Kobayashi. 2018b. Nest substrate reflects incubation style in extant archosaurs with implications for dinosaur nesting habits. *Scientific Reports* **8**:1–10

Tarnawski, V. R., T. Momose, W. H. Leong, G. Bovesecchi, and P. Coppa. 2009. Thermal conductivity of standard sands. Part I. Dry-state conditions. *International Journal of Thermophysics,* **30**:949–968.

Tombre, I. M., and K. E. Erikstad. 1996. An experimental study of incubation effort in high-Arctic barnacle geese. *Journal of Animal Ecology* **65**:325–331

Turner, J. S. 2002. Maintenance of egg temperature. Pp. 119–142 *in* D. C. Deeming, ed. *Avian incubation: behaviour, environment, and evolution.* Oxford University Press, Oxford.

Varricchio, D. J. 2021. An exceptional adult-clutch-embryo association and its implications for dinosaur reproduction. *Science Bulletin* **66**:868–870.

Varricchio, D. J., and F. D. Jackson. 2003. Origins of avian reproduction: answers and questions from dinosaurs. *Palaeovertebrata* **32**:149–169.

Varricchio, D. J., and F. D. Jackson. 2016. Reproduction in Mesozoic birds and evolution of the modern avian reproductive mode. *The Auk* **133**:654–684.

Varricchio, D. J., F. Jackson, J. J. Borkowski, and J. R. Horner. 1997. Nest and egg clutches of the dinosaur *Troodon formosus* and the evolution of avian reproductive traits. *Nature* **385**:247–250.

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

Varricchio, D. J., J. R. Moore, G. M. Erickson, M. A. Norell, F. D. Jackson, and J. J. Borkowski. 2008. Avian paternal care had dinosaur origin. *Science* **322**:1826–1828.

Varricchio, D. J., M. Kundrat, and J. Hogan. 2018. An intermediate incubation period and primitive brooding in a theropod dinosaur. *Scientific Reports* **8**:1–6.

Wang, S., S. Zhang, C. Sullivan, and X. Xu. 2016. Elongatoolithid eggs containing oviraptorid (Theropoda, Oviraptorosauria) embryos from the Upper Cretaceous of southern China. *BMC Evolutionary Biology* **16**:1–21.

Webb, G. J. W., S. C. Manolis, R. Buckworth, G. C. Sack. 1983. An examination of Crocodylus porosus nests in two northern Australian freshwater swamps, with an analysis of embryo mortality. *Wildlife Research* **10**:571–605.

Weishampel, D. B., D. E. Fastovsky, M. Watabe, D. J. Varricchio, F. Jackson, K. Tsogtbaatar, and R. Barsbold. 2008. New oviraptorid embryos from Bugin-Tsav, Nemegt Formation (Upper Cretaceous), Mongolia, with insights into their habitat and growth. *Journal of Vertebrate Paleontology* **28**:1110–1119.

Wiemann, J., T. R. Yang, P. N. Sander, M. Schneider, M. Engeser, S. Kath-Schorr, C. E. Müller, and P. M. Sander. 2017. Dinosaur origin of egg color: oviraptors laid blue-green eggs. *PeerJ* **5**:e3706

Wiemann, J., I. Menéndez, J. M. Crawford, M. Fabbri, J. A. Gauthier, P. M. Hull, M. A. Norell, and D. E. Briggs. 2022. Fossil biomolecules reveal an avian metabolism in the ancestral dinosaur. *Nature* **606**:522–526.

Xu, X., X. Zheng, and H. You. 2010. Exceptional dinosaur fossils show ontogenetic development of early feathers. *Nature* **464**:1338–1341.

Yang, T. R., T. Engler, J. N. Lallensack, A. Samathi, M. Makowska, and B. Schillinger. 2019a. Hatching asynchrony in oviraptorid dinosaurs sheds light on their unique nesting biology. *Integrative Organismal Biology* **1**:obz030.

Yang, T. R., J. Wiemann, L. Xu, Y.-N. Cheng, X. Wu, and M. Sander. 2019b. Reconstruction of oviraptorid clutches illuminates their unique nesting biology. *Acta Palaeontologica Polonica* **64**. https://doi.org/10.4202/app.00497.2018.