

ORIGINS OF AVIAN REPRODUCTION: ANSWERS AND QUESTIONS FROM DINOSAURS

by

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ABSTRACT

The reproductive biology of living birds differs dramatically from that of other extant vertebrates. Distinctive features common to most birds include a single ovary and oviduct, production of one egg at daily or greater intervals, incubation by brooding and extensive parental care. The prevalence of male parental care is most exceptional among living amniotes. A variety of hypotheses exist to explain the origin of avian reproduction. Central to these models are proposed transitions from a condition of no care to maternal, paternal or biparental care systems. These evolutionary models incorporate a number of features potentially preservable or inferable from the fossil record (integument, skeletal adaptations for flight, egg and clutch size, nest form, hatchling developmental stage, the number and function of oviducts, and the mode of egg incubation). Increasing availability of data on dinosaur reproduction provides a means of assessing these hypotheses with fossil evidence. We compare dinosaur data to a selection of models that emphasize maternal, paternal or biparental care. Despite some congruence with dinosaur features, no single model on the evolution of avian reproduction conforms fully to the fossil record, and the ancestral parental care system of birds remains ambiguous. Further investigation into dinosaur parental care, nest structures, clutch geometry, egg-pairing, eggshell porosity, and embryo identification may eventually resolve these issues.

RESUME

La biologie de la reproduction des oiseaux vivants diffère terriblement de celle des autres vertébrés actuels. Des traits distinctifs communs à la plupart des oiseaux incluent un seul ovaire et un seul oviducte, la production d'un oeuf quotidiennement ou à de plus grands intervalles, une incubation par couvain et un soin parental extensif. La prévalence du soin parental mâle est très exceptionnel parmi les amniotes actuels. Il existe une variété d'hypothèses l'origine de la reproduction avienne. Au centre de ces modèles sont proposées des transitions d'une condition sans soins vers des systèmes de soins maternels, paternels ou biparentaux. Ces modèles évolutifs incorporent un nombre de critères potentiellement conservables ou déductibles du registre fossile (téguments, adaptations squelettiques au vol, taille des oeufs et des pontes, forme du nid, stade de développement à la naissance, nombre et fonction de oviductes and le mode d'incubation des oeufs). La disponibilité croissante de données sur la reproduction des dinosaures fournit un moyen d'assoir ces hypothèses avec l'évidence des fossiles. Nous comparons les données sur les dinosaures à une sélection de modèles qui mettent l'accent sur le soin maternel, paternel ou biparental. Malgré quelques congruences avec des caractéristiques dinosauriennes, aucun modèle unique sur l'évolution de la reproduction des oiseaux n'est pleinement conforme au registre fossile et le système de soin parental ancestral des oiseaux reste ambigu. Des investigations complémentaires sur le soin parental chez les dinosaures, sur la structure des nids, la géométrie des pontes, les paires d'oeufs, la porosité des coquilles d'oeufs et l'identification de l'embryon peuvent éventuellement résoudre ces questions.

"The time has come for our discipline to realize that ornithology is extant dinosaur biology." R. O. Prum (2002)

INTRODUCTION

The reproductive biology of living birds differs dramatically from that of other extant vertebrates. Those birds of spring nesting in the backyard or nearby park may appear commonplace, but in the producing and raising of young they exhibit unique anatomical, physiological, and behavioral adaptations. Distinctive features common to most bird species include a single functional ovary and oviduct, production of one egg at daily or greater intervals, incubation by brooding, and the extensive participation of males in the care of eggs and young. Male parental care either exclusively or within a biparental-care system occurs in over 90% of living avian species but in less than 5% of mammals (Clutton-Brock, 1991). How this avian style of reproduction evolved has been the subject of much discourse over the last twenty years. In particular, controversy has arisen concerning the origins and subsequent transitions in parental care among birds and their ancestors (Reynolds *et al.*, 2002). A variety of hypotheses exist that propose a transition from a condition of no care to maternal (Burley & Johnson, 2002), paternal (Van Rhijn, 1984; Elzanowski, 1985; Wesolowski, 1994; Ligon, 1999) or biparental care (Kavanau, 1987). These hypotheses generally link the origin of avian-style reproduction with the occurrence of other features associated with modern birds, e.g. feathers, flight, and endothermy.

The last twenty years have also witnessed the proliferation of research on dinosaur reproduction. Since the provocative work on *Maiasaura* suggesting parental care (Horner & Makela, 1979; Horner, 1984), paleontologists have discovered rich egg localities throughout the world, and a fantastic diversity of eggs and eggshell now exists (Carpenter *et al.*, 1994; Carpenter, 1999). Important recent additions in understanding reproductive biology include dinosaur nests (Varricchio *et al.*, 1999; Chiappe *et al.*, 2003), brooding dinosaurs (Norell *et al.*, 1995; Dong & Currie, 1996; Varricchio *et al.*, 1997), and critically important embryos (Horner & Currie, 1994; Norell *et al.*, 1994; Mateus *et al.*, 1997; Horner, 1999; Varricchio *et al.*, 2002;), some with truly exceptional preservation (Chiappe *et al.*, 1998). After foundational work on the nature of fossil eggshell (Hirsch & Packard, 1987; Sabbath, 1991; Mikhailov, 1997), documentation continues with ever increasing detail and new technologies (Kohring, 1999; Garcia & Vainey-Liaud, 2001; Zelenitsky & Modesto, 2003; Grellet-Tinner, in press). The knowledge base regarding dinosaur reproduction has grown significantly as demonstrated by recent volumes dedicated to the subject (Carpenter *et al.*, 1994; Carpenter, 1999) and the 1999 and 2003 International Symposia on Dinosaur Eggs and Babies.

Previously, neontologists based evolutionary hypotheses for the origin of avian-style reproduction largely on attributes observable in living birds. This is understandable, for the fossil record until recently provided little evidence in this area. Dinosaur reproductive research, however, has developed to the point where it can now contribute to answering these evolutionary questions (Prum, 2002). The extensive phylogenetic work demonstrating the dinosaur ancestry of birds (Gauthier, 1986; Padian & Chiappe, 1998; Norell *et al.*, 1999; Sereno, 1999; Holtz, 2000) further substantiates the role of paleontology in understanding modern birds. This paper attempts to facilitate blending of neontologic and paleontologic data by 1) briefly outlining the characteristic

features of avian reproduction, 2) reviewing evolutionary theories on the origin of avian-style reproduction, and finally, 3) assessing the existing and potential contribution of dinosaur research to this area of study.

AVIAN REPRODUCTION

"I think, that, if required on pain of death, to name instantly the most perfect thing in the universe, I would risk my fate on a bird's egg." T. W. Higgins (1863)

Numerous features distinguish the reproductive biology of living birds from those of other extant vertebrates (Table 1). Although the features listed here are common to extant species, they are not universal and do not necessarily represent avian synapomorphies. Many (e.g. parental care, eggshell microstructure) have ambiguous phylogenetic distributions (Tullberg *et al.*, 2002; Varricchio & Jackson, 2004; Grellet-Tinner in press). Certainly, this list (Table 1) could be expanded by including other aspects associated with reproduction such as migration, sexual display, courtship, or embryonic development. However this summary represents a starting point for discussion.

Birds are exclusively oviparous and possess only one functional ovary and oviduct (Gill, 1990). A single egg occupies the reproductive tract at a time and this may facilitate the development of the asymmetric shape that typifies avian eggs (Smart, 1987). Egg components (albumen, membrane, shell) form sequentially in specialized regions of the oviduct. Closely spaced organic centers on the upper surface of a two-layered proteinaceous membrane give rise to a structurally layered calcite eggshell, typically with straight narrow pores (Gill, 1990). In some species, a proteinaceous cuticle covers the exterior of the egg and contains cryptic coloration (Board & Sparks, 1987). Because birds lack egg retention, each egg is laid immediately after formation, at a maximum rate of one per day (Gill, 1990). Eggs are relatively large and energetically expensive to produce (Blueweiss *et al.*, 1978).

Except in rare cases, e.g. megapodes, Egyptian Plover (Seymour & Ackerman, 1980), eggs remain unburied in open nests where adults incubate by direct body contact (Gill, 1990). Consequently, egg turning appears significant for the proper development of most avian embryos (Deeming, 2002). Several egg features are associated with open nests: relatively low porosity that prevents desiccation; variable eggshell color for camouflage; and chalazae, proteinaceous chords within the albumen, that maintain proper embryo orientation during egg turning (Rahn, 1987).

During development, an air cell forms within the blunt end of the egg; this air pocket allows late-stage chicks to inflate their lungs prior to hatching (Rahn *et al.*, 1979). Although eggs may be laid days apart, delayed incubation by adults commonly results in synchronous hatching of the young. Chicks range from altricial to precocial depending on the species but universally show rapid growth (Vleck & Hoyt, 1987).

EGG PRODUCTION

- Exclusively oviparous
- Single functional ovary and oviduct
- “Assembly-line” oviduct
- Egg Production at 1/day maximum
- Female sperm storage
- No egg retention

EGGS

- Large eggs
- Asymmetric egg shape typical
- Eggshell microstructure
 - multi-layered calcitic shell
 - narrow shell units
 - closely spaced organic centers
 - possible cuticle layer
 - two layered membrane
 - low porosity
 - straight, narrow pores typical
- Air cell present within egg
- Chalazae
- Variable egg color

NESTING

- Eggs exposed, uncovered by sediment or vegetation
- Incubation by brooding
- Delayed incubation
- Egg rotation

YOUNG

- Synchronous or asynchronous hatching
- Precocial to altricial
- Rapid growth, adult size in less than 1 year

PARENTAL CARE

- Predominantly bi-parental
- Includes
 - care of eggs
 - care of young

Table 1.— Features that typify avian reproduction. Note that these are not necessarily universal or unique to Aves. See text for references.

Most birds achieve full size within a year.

Birds exhibit extensive parental care. With the exception of brood parasites and some megapodes, one or both sexes of all bird species care for eggs and young (Ligon, 1999). Although biparental care occurs in over 90% of all living bird species (Wesołowski, 1994), it is the prevalence of male care either in biparental or strictly paternal care systems which is most unusual (Ligon, 1999).

ORIGINS OF AVIAN REPRODUCTION

"From our perspective as mammals, both empirical facts and theory make the evolution of maternal care easy to appreciate. The development of sole paternal care in birds is less intuitively obvious." J. D. Ligon (1999)

Multiple hypotheses outline the origin of modern avian reproduction. Approaches range from phylogenetic to largely theoretical, with that of Elzanowski (1985) representing the only model based primarily on fossil evidence. Although differing in style, these hypotheses represent three broad categories that emphasize biparental, maternal, or paternal care as the primitive or ancestral condition in birds. A brief review of a sample of these models from Kavanau (1987), Wesołowski (1994), Burley and Johnson (2002), and Tullberg *et al.* (2002), provides a context for discussing dinosaur reproduction.

Biparental Care

Tullberg *et al.* (2002) phylogenetically analyzed the parental care systems of extant amniotes. Using a phylogeny with paleognathes as the sister group to neognathes, they found that results differed depending on the choice of character transformations. With four unordered character states of no, female, male and biparental care, the most parsimonious interpretation has maternal care ancestral to archosaurs, while the primitive condition of Aves remains ambiguous. Using ordered transformations, maternal care remains ancestral to archosaurs, but biparental care becomes the primitive condition in birds. In an earlier phylogenetic analysis, McKittrick (1992) also found biparental care as primitive for birds.

Kavanau (1987), among others (Kendeigh, 1952), proposed an extensive model for the origin of avian reproduction that incorporates biparental care nearly throughout (Table 2). Kavanau (1987) envisioned five stages moving from reptilian avian-ancestors to ancestral birds: In stage 1, an ectothermic and scaled "stem-reptilian ancestor" produced multiple eggs from both ovaries by polyautochronic ovulation. Adults buried the eggs, relying on indirect solar radiation for incubation. Although initially there was no post-ovipositional care, biparental care increased during this stage to eventually include nest guarding and young-attendance. The partially arboreal "pre-Aves" of stage 2 bore feather-like scales but remained ectothermic. These adults attended multiple

clutches, shading, exposing or burying eggs and thus incubating eggs by direct or indirect solar energy. Later in stage 3, the "primitive pro-Aves" developed a form of endothermy, feathers and some parachuting capabilities. Ovulation was polyallochronic with females "double clutching", producing two sets of eggs in rapid succession from alternate ovaries. Male and female would then brood the two clutches separately with parental care extending to the protection of young after hatching. The feathered "advanced pro-Aves" of stage 4 exhibited some flight capabilities. Females possessed two ovaries alternately producing a single egg via monoallochronic ovulation. Nest-bound (nidicolous) young may have evolved in this stage necessitating greater parental care. Finally by stage 5, the "ancestral birds", now fully endothermic and flight capable, possessed a single functional ovary and oviduct. As in most modern birds, male and female adults jointly attended a single clutch.

Stage	Description	Physiology/ Integument	Behavior	Ovulation	Nesting	Parental Care
1	stem reptile	ectothermic, scaled		polyautochronic: multiple eggs from 2 ovaries	eggs buried	no post hatching care to increased biparental care (guarding of eggs and young)
2	pre-Aves	ectothermic, feather-like scales	partially arboreal	polyautochronic: multiple eggs from 2 ovaries	eggs buried	parents attend multiple clutches; clutch manipulation
3	primitive pro-Aves	primitive endothermy, feathers	parachuting	polyallochronic: multiple egg sets from alternating ovaries	2 clutches brooded separately by male & female	protection of young
4	advanced pro-Aves	primitive endothermy, feathers	some flight capability	monoallochronic: 1 egg from alternating ovaries	possibly nest- bound young	greater parental care
5	ancestral bird	fully endothermic	flight capable	monochromic: one ovary/oviduct	1 clutch	biparental care

Table 2.— The five stages of Kavanau (1987) in the evolution of avian reproduction.

Maternal Care

Burley and Johnson (2002) propose a model independent of a specific phylogeny and with female-only care as the ancestral state of birds (Fig. 1A). Initial conditions in stage I, "basal archosaurs", consisted of a promiscuous mating system, eggs buried and incubated in a reptilian fashion, and maternal care limited to nest guarding. Later several factors increased offspring survival within "ancestral archosaurs": 1) larger eggs and /or decreased clutch size, 2) surface nesting permitting both larger eggs through sequential rather than en masse laying and endothermic brooding, and 3) an increase in mate choice by females. Associated changes included greater maternal care and a male-biased sex ratio.

An increase in consortship, the interactions between male and female during and after courtship, marked stage II in "ancestral archosaurs". This consortship increased paternity certainty and initiated male care. By stage III, 'Mesozoic birds', females actively selected for increased male care. Consequently, both males and females invested more in mate choice. As parental participation increased, it allowed for the eventual evolution of more altricial young, monogamy, and greater parental care within

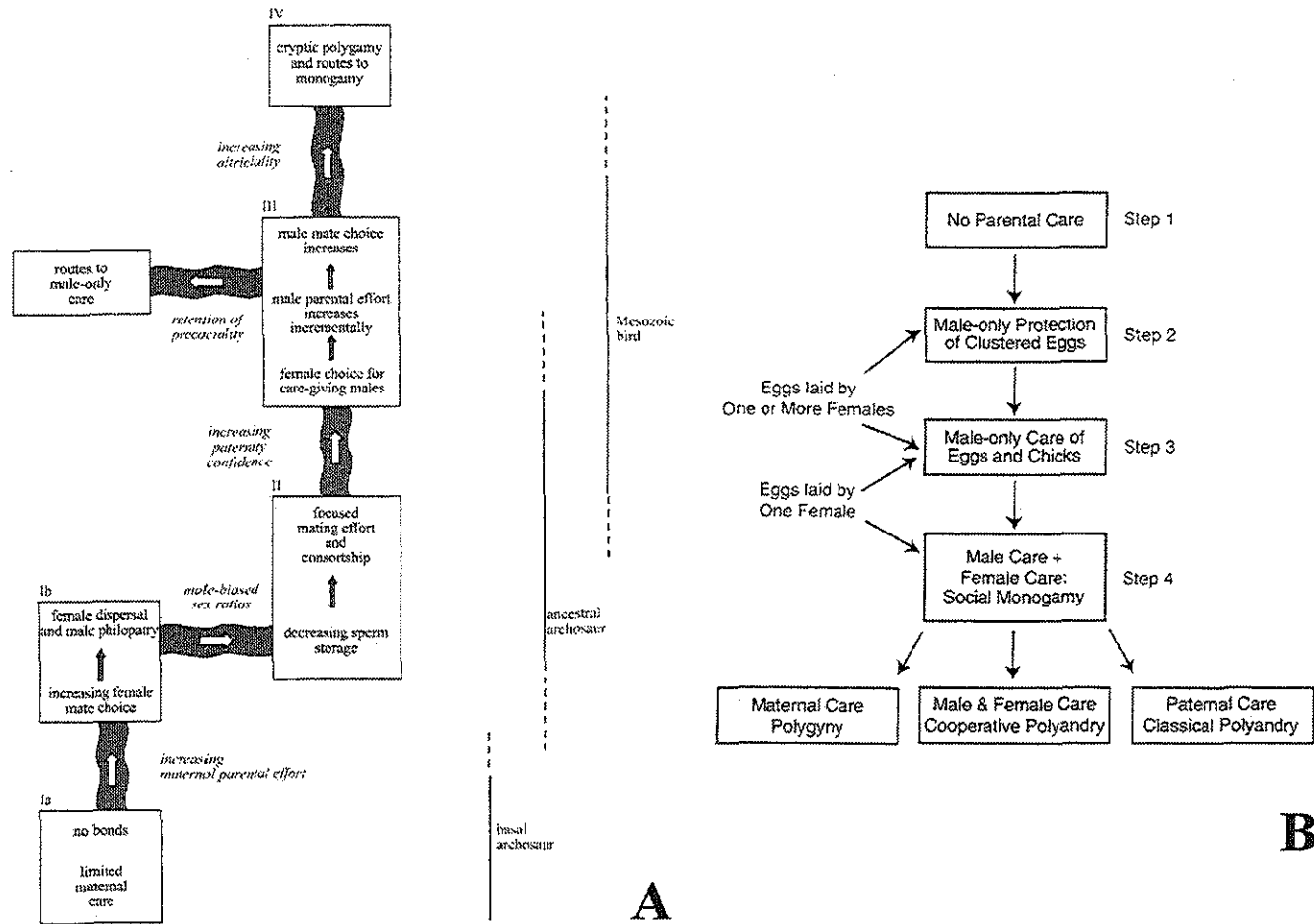


Figure 1.— Schematics for **A**, the maternal-care first model of Burley and Johnson (2002) and **B**, the paternal-care-first model of Wesołowski (1994) as presented by Ligon (1999).

stage IV. Male only care may have arisen from stage III where selection favored precocial young.

Paternal Care

Wesolowski (1994) presents one of several hypotheses (Elzanowski, 1985; Van Rhijn, 1990; Ligon, 1999) favoring paternal care as the ancestral condition in birds. Developed through a "cost-benefit economical approach of behavioral ecology" combined with a historical perspective, this model proposes a transition from an avian ancestor with no parental care to paternal, and then biparental care within birds. Associated with these changes is an initial increase then a decrease in egg size. The hypothesis proceeds through four steps (Fig. 1B) with Steps 1 and 2 occurring as or after flight evolved (Wesolowski, 1994; Ligon, 1999). Step 1 begins in bird ancestors with no parental care. Selection initially favored larger eggs perhaps to accommodate large, superprecocial chicks capable of flight. The high-energy demands of producing large eggs in turn necessitated sequential ovulation in females as well as the male-only care of Step 2. Males, without the energy demands of egg protection were free to maintain territories and care for clustered eggs. These clutches may have been produced by multiple females as in some modern ratites (Handford & Mares, 1985).

The next significant innovation consisted of incubation by brooding. This accelerated embryonic development and coadapted parent with eggs. As the male became an efficient incubator, eggs and embryos became more dependent on parental care. With brooding established, a further shift to paternal care of eggs and young, Step 3, required only a minimal change in behavior and energy expenditure. Selection switched once care of young became entrenched: Females could now produce smaller eggs with altricial young provided they chose a good male caregiver. This eventually favored social monogamy and biparental care of Step 4.

DINOSAURS AND THEIR IMPLICATIONS FOR AVIAN REPRODUCTION

"It is time to abandon debate in theropod origin of birds, and to proceed to investigate all aspects of the biology of birds in light of their own theropod origin." R. O. Prum (2002)

Can dinosaur research truly have an impact on investigations into the origins of avian reproduction? Examination of various reproductive hypotheses shows that they largely focus on behavior; parental care of eggs and young, mate choice, mating strategies, and consortship are traits unlikely to preserve unambiguously in the fossil record. Nevertheless, these same hypotheses either directly or indirectly incorporate features that are potentially preservable or inferable for dinosaur taxa. For example, attributes like integument (scales vs. feathers), skeletal adaptations for flight, egg and clutch size, nest form, and hatching developmental stage, all play a role in various

reproductive hypotheses and are known for at least some dinosaurs. Other inferable features include the number and function of oviducts and the methods of egg incubation. Consequently, the fossil record of dinosaurs provides a mechanism to test these various hypotheses on the origins of avian reproduction. We briefly review these various features as currently understood for dinosaurs before using them in evaluating several of these reproductive hypotheses.

Integument

A number of recently described specimens, primarily from the Lower Cretaceous of Liaoning Province, China, demonstrate that a variety of theropods possessed more elaborate integument than previously envisioned. Representatives of Compsognathidae (Chen *et al.*, 1998; Currie & Chen, 2001), Ornithomimosauria (Perez-Moreno *et al.*, 1994), Therizinosauroida (Xu *et al.*, 1999a), oviraptorosaurs (Ji *et al.*, 1998) and Dromaeosauridae (Xu *et al.*, 1999b, 2003) display a range of simple filaments, feather-like structures, and true symmetric and asymmetric feathers. The wide taxonomic distribution indicates that feather-like structures were primitive to Coelurosauria and possibly an even more inclusive theropod clade. Functions of these integuments may have included insulation, display and parachuting flight (Ji *et al.*, 1998; Currie & Chen, 2001; Xu *et al.*, 2003).

Flight Adaptations

Most phylogenetic analyses now place the Deinonychosauria (dromaeosaurids and troodontids) as the sister group to birds with a divergence in the Late Jurassic (Norell *et al.*, 1999; Sereno, 1999; Holtz, 2000). The phylogenies indicate the presence of several flight adaptations in the common ancestors of these groups: furcula, semi-lunate carpal, pneumatic bone, shortened trunk, vaned feathers, and a sternum with ossified ventral ribs (Norell & Makovicky, 1997; Sereno, 1999; Xu *et al.*, 2003).

Egg Size

For most body sizes birds produce significantly larger eggs than reptiles (Blueweiss *et al.*, 1978). Because only a few dinosaur eggs possess embryonic material necessary for taxonomic identification, data on relative egg size remains somewhat sparse. Large eggs minimally occur in lambeosaurines (Horner, 1999) and the maniraptorans *Oviraptor* (Dong & Currie, 1996), *Citipati* (Clark *et al.*, 1999), and *Troodon* (Varricchio *et al.*, 1997). These eggs are smaller than those predicted for similarly sized birds, but exceed by several times those expected for a reptile (Blueweiss *et al.*, 1978). Thus, two independent trends of enlargement may exist within Hadrosauridae and Maniraptora.

Clutch Size

In contrast to egg size, overall clutch weight tends to be larger in reptiles than birds for adult body sizes greater than 9 kg (Blueweiss *et al.*, 1978). The sparse available data for dinosaurs includes clutches of smaller than average (*Maiasaura*,

titanosaurid), average (lambeosaurine), and larger than average weight (*Lourinhanosaurus*, *Troodon*, *Oviraptor*) (Table 4). The demands of embryonic gas exchange in the closed environments of underground or vegetation-mound nests may have prohibited large clutches in some dinosaurs (Seymour, 1979; Seymour & Ackerman, 1980) like *Maiasaura* and titanosaurs. In contrast, the three theropods possess clutches from 1.6 to over 4 times heavier than predicted values for both reptiles and birds. These large clutches could reflect some sort of communal or multi-female nest as observed in modern ratites (Handford & Mares, 1985).

Nest Structures

Despite the preservation of large numbers of fossil clutches, dinosaur nests remain relatively uncommon (Carpenter, 1999). This may reflect an inherent depositional bias against the preservation of nest structures (Chiappe *et al.*, 2004). For example, nests excavated in mud and filled by muddy flood plain deposits leave no discernable nesting trace. In addition, where dinosaurs buried eggs underground or in mounds (Mikhailov *et al.*, 1994), subsequent pedogenic processes may have destroyed any identifying sedimentary features. Nesting traces (Plate 1) or nests inferred from close spatial relationships between adult and eggs, include those of the hadrosaur *Maiasaura peeblesorum* (Horner & Makela, 1979), a titanosaurid from Argentina (Chiappe *et al.*, 2004), *Troodon formosus* (Varricchio *et al.*, 1999), and the oviraptorids, *Citipati* (Clark *et al.*, 1999) and *Oviraptor* (Dong & Currie, 1997). Nests of *Maiasaura* are represented by green mudstone infilling bowl-like depressions within brown mudstone (Horner & Makela, 1979). Titanosaurids deposited clutches (Plate 1B) within open excavations and did not bury eggs in sediment (Chiappe *et al.*, 2004). Eggs of both oviraptorids and *Troodon* appear to have been laid partially exposed in sediments, the latter within a shallow bowl with a raised rim (Plate 1A) (Clark *et al.*, 1999; Varricchio *et al.*, 1999). These nests remain somewhat controversial. Deeming (2002) interprets *Oviraptor* nests as fully buried and therefore not subject to adult incubation. Varricchio *et al.* (1999) viewed *Troodon* nests as likely indicative of brooding, whereas Carpenter (1999) proposed the structures represented either vegetation mounds or nest-guarding by adults.

Hatchlings

The developmental state of hatchling dinosaurs has been assessed through both gross visual inspection and histologic work. The ornithomimid, *Orodromeus*, and the theropods *Troodon* and *Citipati* appear to have been precocial (Geist & Jones, 1996; Horner *et al.*, 2001). Geist and Jones (1996) suggested a precocial hatchling stage for hadrosaurs like *Maiasaura* based on gross inspection. However, histologic features indicate a more "semi-altricial" condition (Horner *et al.*, 2001). This interpretation has led to the inference of parental care of nest-bound young (Horner & Weishampel, 1988; Horner *et al.*, 2001).

Elzanowski (1981) observed that embryos of the enantiornithine bird, *Gobipteryx minuta*, possessed well-ossified forelimbs and pectoral girdles relative to their hind limbs and proposed that chicks hatched in a superprecocial state capable of flight. From this, Elzanowski (1985) developed a paternal-care first model for the origin of avian

reproduction, later expanded by Wesofowski (1994).

Oviducts

Several commonly preservable features may reflect the number and function of ovaries and oviducts: the arrangement of eggs within clutches, and egg size, shape and microstructure. Most dinosaur clutches consist of a random arrangement of eggs and provide no definitive information on the number of reproductive tracts. In contrast, clutches of the theropods, *Oviraptor*, *Citipati*, and *Troodon* exhibit a paired-egg pattern (Dong & Currie, 1996; Varricchio *et al.*, 1997; Clark *et al.*, 1999). Similar egg arrangements occur in other clutches with unidentified theropod affinities (Sabbath, 1991; Carpenter, 1999). Interpretations generally consider these patterns indicative of the primitive retention of two functional ovaries and oviducts (Sabbath, 1991; Mikhailov *et al.*, 1994; Varricchio *et al.*, 1997; Larson, 2000). Although disputed (Clark *et al.*, 1999; Larson, 2000), Varricchio *et al.* (1997) further argue that egg pairing in *Troodon* together with the large and asymmetric shape of the eggs, indicate sequential ovulation comparable to modern birds. The presence of a pair of eggs in the abdomen of *Sinosauropteryx* supports this interpretation (Chen *et al.*, 1998). The occurrence of multilayered pathologic eggshell in both modern reptiles and dinosaurs has been used as an argument for the presence of a "reptilian-like" reproductive tract in dinosaurs (Hirsch, 1994). Recent documentation of similar pathologies in birds now falsifies this hypothesis (Jackson & Varricchio, 2003).

Among the variety of eggshell morphologies exhibited by dinosaurs, several have been recognized as "ornithoid" or "avian-like" (Hirsch & Quinn, 1990; Mikhailov, 1992). Until recently, the erroneous assignment of these eggs to ornithischians obscured their true phylogenetic affinities to theropods like oviraptorids and *Troodon* (Norell *et al.*, 1994; Varricchio *et al.*, 2002). Recent work highlights several egg features common to birds and non-avian theropods (Zelenitsky *et al.*, 2002; Varricchio & Jackson, 2004). Shared features include straight, narrow pores; closely spaced prismatic shell units; two or more structural layers; and squamatic structure (Hirsch & Quinn, 1990; Mikhailov, 1997; Zelenitsky *et al.*, 2002; Varricchio & Jackson, 2004). Cladistic analysis of eggshell structures indicates that no single structural feature can differentiate avian from non-avian theropod eggshell, and argues for a similarity in oviduct function (Varricchio & Jackson, 2004).

Incubation

The lack of nesting structures associated with most dinosaur clutches contributes to the difficulty in assessing whether dinosaurs laid their eggs in vegetation mounds, buried them in sediments, or left them exposed for brooding (Carpenter, 1999). The best potential examples of the latter are the associated eggs and adults of *Citipati* and *Oviraptor*. Despite the exceptional preservation their interpretation remains debatable. Dong and Currie (1996) favor an adult incubating and protecting its eggs whereas others (Norell *et al.*, 1995; Clark *et al.*, 1999) propose that oviraptorids may not have applied heat to the clutch despite the brooding-like posture. Instead, this posture may have served as protection by shading the eggs from direct sun. Deeming (2002) interprets the oviraptorid clutches as fully buried, and both Deeming (2002) and Carpenter (1999)

argue that the insufficient contact between adult and eggs prohibited brooding. By comparison, the more compact *Troodon* clutches expose the upper portions of eggs and may have been better suited for brooding (Plate 1A) (Varricchio *et al.*, 1999). Regardless of the exact interpretation of the adult oviraptorids, their postures over the clutches imply some form of parental care of eggs (Norell *et al.*, 1995; Dong & Currie, 1996; Clark *et al.*, 1999; Deeming, 2002).

In modern taxa, eggshell structure reflects the incubation environment (Deeming, 2002). Unfortunately many dinosaur eggshell varieties (e.g. Dendroolithidae, Megaloolithidae) lack modern structural analogs. Physiologically important eggshell soft tissues like membranes and pore plugs (Board, 1982; Kern & Ferguson, 1997) rarely preserve, further complicating functional interpretations. Water vapor conductance values of many dinosaur eggs exceed those of modern birds, indicating a buried mode of incubation (Seymour, 1979; Seymour & Ackerman, 1980; Sabath, 1991; Mikhailov *et al.*, 1994; Deeming, 2002). Nevertheless, some eggs have values approaching those of birds (Deeming, 2002). Furthermore, the conductance values for eggs of *Citipati*, *Oviraptor* and *Troodon*, where clutches may have been partially exposed, have not been investigated.

Hypothesis evaluation

Having reviewed both the models on the origins of avian reproduction and the relevant information on dinosaurs, the hypotheses can now be evaluated (Table 3). For Tullberg *et al.* (2002), the existence of oviraptorid adults guarding or incubating eggs provides definitive evidence of parental care within dinosaurs. Unfortunately, this analysis requires information on the sex of these care-giving individuals, information currently unavailable. Nevertheless, determining the distribution of parental care among dinosaurs would be important for potentially resolving whether the parental care present in modern crocodylians and birds is homologous or convergent.

	Tullberg <i>et al.</i> 2002	Kavanau 1987	Burley and Johnson 2002	Wesolowski 1994
Integument		+		
Flight apparatus		+		--
Egg size			+	+
Clutch size			--	+
Nest structure		+	+	?
Hatching state		--		?
Oviduct function		?		+
Incubation	?	?	?	+

Table 3.— Comparison of the fossil evidence for non-avian dinosaurs and several hypotheses on the origin of avian reproduction. Symbols are "+", correspondence between fossil evidence and hypothesis; "--", disagreement; and "?", ambiguous relationship.

Some aspects of dinosaur evolution match well with Kavanau's (1987) model. Corresponding with predicted morphological changes, various theropod groups develop more elaborate integumentary structures eventually leading to true feathers. This leads

to gliding or some flight capabilities in animals like *Microaptor* (Xu *et al.*, 2003). Further, theropods like oviraptorids and *Troodon* conform closely to Stage 2 and 3, "pre-Aves" and "primitive pro-Aves". These theropods probably possessed some feather to feather-like coat, partially exposed clutches, and brooding or brooding-transitional behavior (Clark *et al.*, 1999, Varricchio *et al.*, 1999). In contrast, nests and nest structures of earlier theropods, ones possibly corresponding to Stage 1 or 2 animals, remain unknown except for the massed-egg clutch of *Lourinhanosaurus* (Mateus *et al.*, 1997).

Oviduct function in this model appears contradictory to the dinosaur data. The model proposes a shift in ovary function from the production of multiple eggs from both ovaries (polyautochronic ovulation), to alternating ovaries (polyallochronic), to alternating single eggs (monoallochronic), to finally a single egg from one ovary (monochronic) (Kavanau, 1987).

Although massed eggs for sauropods and the allosaurid theropod, *Lourinhanosaurus*, may represent plesiomorphic retention of polyautochronic ovulation, egg pairs in coelurosaurians like *Sinosauropteryx* (Chen *et al.*, 1998) and *Troodon* (Varricchio *et al.*, 1997) may indicate a shift to the monoautochronic condition (one egg simultaneously from each ovary) prior to the monochronic ovulation in modern birds. But this progression is built largely upon the interpretation of egg-pairs and remains controversial (Clark *et al.*, 1999; Larson, 2000). Currently, no evidence exists to clarify the number and function of reproductive tracts in basal birds.

The apparent absence of nidicolous, altricial young in non-avian theropods and basal birds clearly contradicts with Kavanau's model. Where known, these groups produced precocial to superprecocial young (Elzanowski, 1981; Geist and Jones, 1996; Horner *et al.*, 2001).

Theropods correspond in part to the "ancestral archosaurs" of Stage I and II in the Burley and Johnson (2002) model. They exhibit an increase in egg size and an overall trend towards surface nesting with the possibility of both sequential ovulation and brooding. However, increased rather than decreased clutch sizes in these theropods differ from the model (Table 4). Some other dinosaur clades (e.g. sauropods, hadrosaurines) may exhibit decreasing clutch sizes, but these groups are phylogenetically distant from birds. Overall, much of the Burley and Johnson (2002) model presents no features with significant preservation potential, thus limiting the assessment value of the fossil data.

In Wesolowski's (1994) four step model, the evolution of flight plays a potential role within Step 1. If one considers flight as evolving in a later step, then there is good correspondence between trends in non-avian theropods and model Steps 1 and 2. Theropods show a trend towards both increasing egg and clutch size, and hatchlings appear precocial and nest fleeing. Clutches are significantly larger than predicted values (Table 4) and may imply communal, multi-female nests. Additional correspondence occurs if egg pairs within partially buried clutches indicate sequential ovulation and if brooding evolved within theropods like oviraptorids and *Troodon*.

Pivotal in the interpretation of this model are the Enantiornithines. They play a primary role if flight evolves within Step 1, for most of the evolution of avian

reproduction would then, according to this model, occur within basal birds. If Enantiornithines represent a divergent offshoot, perhaps reflected in their unusual growth and histology (Elzanowski, 1981; Chinsamy & Elzanowski, 2001; Padian *et al.*, 2001), then much of the origin of avian reproduction could lie primarily within non-avian theropods. If the latter interpretation proves correct, then this model might predict that those theropod adults closely associated with egg clutches would be male.

Taxon	Adult Wt.	Egg Wt.	# Eggs in Clutch	Clutch Wt.	C _r	C _b
<i>Matiasaura</i>	4000 kg	0.98 kg	20-25	20-25 kg	230 kg	100 kg
Lambeosaurine	4000 kg	4.60 kg	22	100 kg	230 kg	100 kg
Titanosaurid	7000 kg	0.87 kg	15-34	12-30 kg	370 kg	144 kg
<i>Lourinhanosaurus</i>	176 kg	0.65 kg	34	22 kg	14 kg	9 kg
<i>Oviraptor</i>	40 kg	0.42 kg	22-30	9-13 kg	4 kg	3 kg
<i>Troodon</i>	50 kg	0.48 kg	22-24	11-12 kg	5 kg	4 kg

Table 4.— Egg and clutch weights for those dinosaurs with identifiable eggs and embryos. Cr and Cb are the predicted clutch weights for respectively an adult reptile and bird of equivalent body size. Equations are derived from modern reptilian and avian data (Blueweiss *et al.*, 1978). Dinosaur data from Horner (1984, 1999), Anderson *et al.* (1985), Durham *et al.* (1989), Dong and Currie (1996), Peczki (1995), Mateus *et al.* (1997), Varricchio *et al.* (1997), Antunes *et al.* (1998), and Chiappe *et al.* (1998).

CONCLUSIONS

"The egg is a key feature of avian reproductive biology and is the raison d'etre for the bird-nest incubation unit." D.C. Deeming (2002)

The application of dinosaur reproductive information to models on the origin of avian reproductive biology not only allows assessment of the hypotheses but also highlights those areas of dinosaur reproduction that warrant further research. Among the models, Kavanau (1987) developed a close link between the progressive development of morphologic characters (e.g., integument and flight adaptations) and reproductive features. However, the absence of altricial young among non-avian theropods and basal birds represents the most significant contradiction with the fossil record. Some aspects of the Burley and Johnson (2002) model corresponded well with the theropod evidence and may reflect a conscious effort to incorporate it. Theropods show an increase in egg size associated with possibly sequential ovulation and brooding. Because much of this model is constructed on behavioral aspects, it largely remains untestable with fossil information. Among the models, that of Wesolowski (1994) perhaps shows the best

conformation with the fossil record of theropods, provided flight evolves relatively late compared to the relevant reproductive features. The morphologic changes of Kavanau (1987) combined with the reproductive transitions in Wesolowski (1994) would fairly accurately represent the fossil record of theropods and birds. However, the most parsimonious phylogenies (McKittrick, 1992; Tullberg *et al.*, 2002) favor biparental care or a maternal-care model as in Burley and Johnson (2002).

To better address the debate over the origins of avian reproduction, significant areas of dinosaur reproduction require further investigation. These include:

- > Determining the level of parental care among various dinosaur groups. This may represent a difficult task given the nature of interpreting behavior from the fossil record.

- > Discerning the sex of adult individuals associated with eggs or hatchlings.

- > Discovering and documenting nesting structures and clutch geometry. These have the potential to provide necessary information on incubation mode and may also reflect oviduct function.

- > Determining the distribution and significance of egg pairing and whether it is indicative of sequential ovulation.

- > Estimating the water conductance values for critically important eggs like those associated with adults or potentially exposed clutches. Egg porosity remains an under-utilized tool in understanding incubation.

- > Documentation of embryos with sufficient details to allow taxonomic assignment of eggs and eggshell. If eggs can be assigned to a taxon it provides important information on relative egg and clutch size and provides a phylogenetic context for study of the specimens.

It is hoped that this discourse can lead both to the refining and revising of hypotheses on the origin of avian reproductive biology as well as stimulate further work on dinosaur research.

If doubts remain about the significance of dinosaur studies for understanding avian reproduction, we suggest that one examine a theropod egg like those of *Troodon*. Current information shows these eggs to conform closely to those of birds in shape, size and microstructure (Varricchio *et al.*, 1997, 2002; Zelenitsky *et al.*, 2002; Varricchio & Jackson, 2004). Consequently, if the egg is "the *raison d'être* for the bird-nest incubation unit" (Deeming, 2002), then the origins of avian reproduction likely lie among non-avian theropods.

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PLATE 1

Nesting traces with egg clutches.

A, Nest within a hard muddy calcrete for the theropod *Troodon formosus* from the Late Cretaceous of Montana. The plaster jacket at the center of the nest covers the upper portions of a clutch of 24 eggs. Originally, a soft mudstone blanketed both the nest structure and the upper portions of the eggs. The lower portions of the elongate eggs lie within the calcrete. Length of tape measure is 1 m.

B, Sauropod nest from Auca Maheuvo, Argentina excavated into a fine to medium grained, horizontally bedded sandstone and containing 18 hatched or eroded eggs. A massive sandstone rim nearly surrounds the perimeter of the egg-containing depression while mudstone fills the depression. Paintbrush in foreground measures 15 cm. For additional details see Chiappe *et al.* (2004).

