Review

Roots of avian evolution: clues from relict reproductive behaviors

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Remarkable, previously little known, relict reproductive behaviors of small parrots are detailed here. Because of the highly conservative nature of brain evolution, neural circuitry for many such primitive behaviors is preserved in functional condition. These behaviors can be elicited by exposing birds to appropriate conditions during breeding cycles. Founded largely on clues from these elicited responses, six main-line avian evolutionary stages are postulated, being described primarily in terms of lifestyles and reproductive practices at each stage. The progression began with small, ectothermic, shallow-nesting theropodan ancestors of birds. In warm, equable Mesozoic climates, the eggs were shallowly covered by dry vegetative debris and incubated solely by climatic heat. The following ectothermic surface-nesting ancestors of Stage 2 maintained sustainedly higher incubative temperatures by appropriately exposing and/or covering eggs with dry or moist vegetative debris, and alternately midday shading them from direct insolation with the parental bodies. Rapid double-clutching became adaptive in Stage 3, with the achievement of primitive endothermy. Higher core and incubative temperatures of Stage 4 and continued rapid double-clutching permitted more annual breeding episodes. In more seasonable early Cretaceous climates, sequential single-clutching again became adaptive in stage 5. Modern birds comprise Stage 6. Mates in Stages 1 and 2 maintained close nest vigilance from nearby, overhead resting sites in vegetation, jumping or parachuting to protect nests from small egg-predators. Pervasive selection for these practices led to skeletal adaptations for arboreality and integumentary adaptations for thermal insulation and increased drag. These practices and their selective effects are the proposed roots of avian evolution. Feathers and flight evolved with continued selection along these lines, with gliding achieved in Stage 3 and sustained wing-flapping flight in stage 4.

Key words: Origin of feathers and flight, nesting practices, egg and chick care.

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INTRODUCTION

The origin of birds is "one of the oldest and most vexing problems of evolutionary history;" some "biologists.....argue.....that the roots of avian evolution remain shrouded in mystery" (Dingus and Rowe, 1998), with the origin of feathers and flight "even more imponderable" (Padian and Chiappe, 1998a). Much progress has been made since these words were written. Interest has been heightened, particularly, in recent years by discoveries of

spectacular late Jurassic-early Cretaceous fossils of small-bodied, feathered, higher coelurosaurian theropods in 1996-1997 (Ji and Ji, 1996; Ji et al., 1998), followed by that of 'four-winged' forms, some with asymmetrically-vaned feathers (Xu et al., 2003; Zhang and Zhou, 2004) in western Liaoning Province, China, and elucidation of the avian nature of the brain and inner ear of *Archaeopteryx* (Dominguez Alonzo et al., 2004).

Another contributing finding was new osteological evidence of the theropod ancestry of *Archaeopteryx* from a "Thermopolis" specimen with excellent bone preservation, and confirmation of its possession of a hyperextenddable second toe. This blurred the distinction between archaeopterygids and basal deinonychosaurs (troodontids and dromaeosaurs), even questioning the monophyly of Aves, as currently recognized. Thus, reanalysis of data showed *Archaeopteryx* and *Rahonavis* to be outside a clade that included *Confuciusornis* and Deinonychosauria (Mayr et al, 2005).

The origin of feathers remains contentious. Some workers regard the paired, elongate, integumentary appendages of the tiny, late Triassic (220 Myr ago) archosaur, *Longisquama insignis*, to be homologous with avian feathers (Jones et al., 2000). Most workers regard them as an adaptation primarily for gliding, and merely convergent with feathers (see Paul, 2002; Witmer, 2002), showing that there was extensive experimentation in feather-like scales before the advent of feathers (Feduccia, 1996).

The oldest evidence of feathered dinosaurs derives from early Jurassic filamentous impressions associated with theropod tracks in western Massachusetts (see Kundrat, 2004). Impressions of feathers are preserved with traces of sitting that bear integumentary structures along the outlines of the pre-pubic and ischiadic impressions. Useful comparative models for these filamentous integumental structures are extant palaeognathous down feathers and similar structures of the feathered theropods from the Liaoning deposits. Their morphologies are congruent with Prum's Stage II (Prum, 1999), and support the thesis that plumulaceous morphologies evolved before the origin of the rachis and the planar vane (Kundrat, 2004).

The Lacustrine sediments bearing the Liaoning theropodan fossils date to the late Jurassic-early Cretaceous period, 124-128 Myr ago (Ji and Ji, 1996; Ji et al., 1998; Zhou et al., 2003). Their filamentous integumentary structures, including 'pinnate feathers' clearly possessing a rachis and barbs (Norell et al., 2001; Xu et al., 2001), appear homologous, if not structurally identical, to avian feathers.

Most discoverers of these fossils regard them to be flightless or gliding dinosaurs. Their feathers were considered to be of non-avian origin, characteristic of the entire clade of (non-gigantic) coelurosauria, a group of theropodan dinosaurs that includes Aves and several other groups. However, the discovery of an exquisitely preserved Late Jurassic, Solnhofen, higher coelurosaurian theropod, *Juravenator starki* (Campsognathidae), paradoxically lacking feathers, but with scaled skin around the tail and hind limbs (Göhlich and Chiappe, 2006), raises some doubts about the thesis of non-avian feather origin. Other workers, of whom Paul (2002) is the leading advocate, regard feathered (excluding such occurrences as filamentous protofeathers) 'nonavian' theropods as secondarily flightless birds. This is essentially the position held here, except allowing for possible secondarily glideless and even secondarily parachuteless occurrences. Still other workers deny any bird-dinosaur relationship, attributing the striking similarities to convergent evolution (refs. in Paul, 2002:216).

Various schemes for reproductive aspects of early avian evolution from reptilian forerunners have been formulated on the basis of current behavior and theoretical constructs (Clutton-Brock, 1991; Ligon, 1999). In the following treatment, highest priority, as regards significance for early avian evolution, is given to the previously unknown (except Kavanau, 1987, 1988) relict normal and experimentally elicited care of eggs and chicks by captive birds in spacious, partially transparent nest boxes. This applies particularly to components of behavior that occur early in breeding cycles and appear to retrace primitive ancestral practices.

Three species of small parrots were studied: Cockatiels (*Nymphicus hollandicus*), Peach-faced Lovebirds (*Agapornis roseicollis*), and Budgerigars (*Melopsittacus undulatus*) (Kavanau, 1987, 1988). Their care of eggs and chicks under currently unnatural surface-nesting conditions appears to illuminate ancestral practices at times when surface-nesting was the natural condition. It was not known previously that these ancestral practices, which were presumed to be inaccessible, could be revealed simply by exposing some birds to appropriate conditions at appropriate times.

Provine (1984) suggested that animals with fairly recent major structural and behavioral evolutionary changes would be the most promising subjects to begin "excavation for the artifacts of our behavioral past." But the detected relict psittacine behaviors suggest that one may aspire to recover much more ancient behaviors, even those of birds' early theropodan ancestors.

Inferences from relict behaviors usually favor one of the conflicting positions taken by current workers of different 'schools' of avian flight, feather, and parental-care evolution, but they raise different questions. Instead of directing attention to whether flight evolved 'trees down' or 'ground up,' they focus on why locating nests at shallow depths would have brought into play selective pressures for the 'trees-down scenario.

It is reasonable to assume that vegetative heights were the only safe, generally available locations for small the-

ropodan ancestors of birds to maintain close nighttime watch over ground nests in mild, equable, late Triassic-early Jurassic climates. In this view, the 'roots of avian evolution' owe to two principal, pervasive selective pressures. One of these pressures continuously 'funneled' these small forerunners into resting sites at low vegetative heights, to maintain close watch over nest sites {with accompanying selection for small size, long arms, increased respiratory efficiency, long distal toe bones, large first toe, etc., to facilitate climbing; see Paul, (2002)}. The other favored the offspring of close-guarding parents that gained quickest access to nests threatened by small egg-predators by jumping to the ground. An inability of climbing dinosaurs to descend quickly and easily with fingers and toes (see Paul, 2002) would have selected for an initial jumping descent.

Instead of deciding how, or which, selective pressures for aerodynamic versus insulative functions of integumentary specializations could have led to feather evolution, the focus is on why selection for both functions would have originated together upon the initiation of either shallow- or surface-nesting. Thus, selections for both aerodynamic and insulative specializations are proposed to derive from daytime foraging and nighttime presence in, and leaping from, cool heights in vegetation. Selection for neither function, alone, is thought to have given rise to fully-developed feathers. If there were only insulative selection, for example, one would expect fur or down (see, also, Feduccia, 1999).

In the past, decisions concerning whether male-only, female-only or biparental care was primitive were based on phylogenic analyses. Within the present paradigm, attention is focused on why selection would have favored, if not mandated, biparental care by shallow- and surface-nesting theropodan ancestors evolving from deep-nesters (that had provided no care).

Independent origins of favorable integumentary modifications for feather-like structures, parachuting, steering, gliding, possibly even flight, assume greater likelihood when one directs attention to the probable existence of these pervasive selective pressures, Previously unthinkable to many, this scenario also has gained plausibility following the discovery of homoplasy in the mammalian middle ear, specifically that ear bones (and derived molar features) appear to have evolved independently at least three times (Rich et al., 2005).

The view of most workers is that feathers and flight evolved in a small, highly predaceous, gracile, bipedal theropodan lineage. Morphological differences between enantiornithid and ornithurine birds indicate that there were at least two independent avian radiations during the Mesozoic, with separate pathways to flight system modifications (Rayner, 2001). From the point of view adopted here, a further major radiation of birds and near-birds in the mid-to-late Mesozoic was back to earth -- becoming secondarily flightless.

The recent discovery of endosteally-derived bone tissues in *Tyrannosaurus rex* hindlimb elements (Schweitzer et al., 2006) is consistent with the theropod-bird evolutionary relationship adopted here, as well as proposed avian and theropodan reproductive strategies. The endosteally-derived tissues are thought to be homologous to avian "medullary bone," unique to female birds, particularly ratites (Schweitzer et al., 2006). They provide an ephemeral, easily mobilized, buffering source of calcium, needed for the production of calcareous eggshells (Sturkie and Mueller, 1976). Should this objective means of fossil gender discrimination prove to be widely applicable, it may have far-reaching significance in future studies.

BACKGROUND

In the first six following sections I consider phenomena that have made the present synthesis possible, beginning with general considerations of normal and relict reproductive behaviors. There follows a section on results of conventional phylogenetic approaches, as compared to some of those based on the study of relict behaviors. After that, I consider the heretofore little exploited neural substrates for the preservation of these relics. Following that, I treat the specific relict reproductive behaviors contributing to this synthesis. Next I consider the inhibitory controls for the expression of relict behaviors. But the behavioral relics are accompanied by and partly based on, and synchronized with, the also heretofore little exploited hierarchical development of ovarian follicles, which are treated next. The following six sections, beginning with the discoveries and significance of 'non-avian' feathered theropods, return to paleontological considerations and other pertinent matters. Lastly, are treated the postulated six stages of main-line avian evolution, with emphasis on the factors influencing the evolutionary transitions between them.

NORMALLY EXPRESSED AND EXPERIMENTALLY ELICITED RELICT REPRODUCTIVE BEHAVIORS

As suggested above, fossils are not the only 'hands on' objects for studying avian evolution. Aside from obvious avian embryonic 'recapitulations,' and normal and adventitious structural atavisms, clues also derive from relict reproductive behaviors and their partially underlying cycles of ovarian follicular development and atresia (Kavanau, 1987, 1988, 1990). Relevant experimental and 'normal' situations encountered by small, captive breeding parrots in spacious, partially transparent nest boxes usually lead to clear-cut 'adaptive' responses, either for present conditions or for past presumptive primitively encountered conditions (see below).

Although some workers lament that "behavior doesn't fossilize," in reality, it appears to have fossilized abundantly -- in the neural circuitry of vertebrate brains. Unlike structural atavisms, most 'fossilized' behaviors are inconspicuous. Some occur 'normally' at certain times under certain conditions. But without close surveillance these are unlikely to be noticed. Others have only been elicited experimentally. Many seemingly provide windows into the practices of birds' remote theropodan ancestors. Retention of these rich suites of relict behaviors may be attributed largely to;

(a) An intrinsically highly conservative evolution of vertebrate brains.
(b) Resulting conservative, discrete stages in ovarian follicular maturation and atresia (involved in the regulation of ovarian hormonal secretions).
(c) The indirect encoding and polygenic basis of behaviors; and
(d) An immunity of unexpressed behaviors from adverse selection.

A contributing factor may be the insulation of small parrots' main-line ancestors from many selective pressures, by an apparently long-standing practice of nesting in naturally-occurring, highly-protective, vegetative hollows.

The rarity of previous observations of avian relict behaviors hinges on the crucial need for virtually continuous, unobtrusive surveillance of the behavior of members of families and colonies, both in and out of partially transparent nests, before, during, and after breeding. To elicit the behaviors, eggs, chicks, nest sites, and ambient conditions must be manipulated to approximate circumstances earliest ground-nesting ancestors might have encountered, both routinely and exceptionally.

PHYLOGENETIC ANALYSES AND THE PRESENT APPROACHES

Although inferences drawn from fossils of nests, eggs, embryos, juveniles, and 'adult' dinosaurs give hints of advanced reproductive behaviors, other information is virtually impossible to elucidate from the fossil record (Horner, 2000). Heretofore, the other principal approach for drawing conclusions about ancient practices has been the comparative phylogenetic method. For roughly the past 25 years this has been broadly applied to a key consideration -- the evolution of parental care.

Concerning the earliest form of such care in birds or their ancestors, various analytic methods have been brought to bear, such as cost/benefit analyses, male, female, and life-history strategies, molecular phylogenies, statistical reconstructions of behavioral characteristics, field studies of parental behavior, etc.,

together with logical deductions therefrom. But no broadly accepted conclusion has been drawn from these studies.

Investigators fall into two camps. Those favoring male-only care as being primitive are Van Rhijn (1984), Elzanowski (1985), Handford and Mares (1985), Wesolowski (1994, 2004); Ligon (1999), and Vehrencamp (2000). Those favoring biparental or female-only care are Kavanau (1987), McKitrick (1992), Székely and Reynolds (1995) (shorebirds), Varricchio et al. (1999), Burley and Johnson (2002), Prum (2002), Reynolds et al. (2002), and Tullberg et al. (2002).

In her phylogenetic approach, McKitrick (1992) arrived at the same conclusion as mine (Kavanau, 1987), that biparental incubation is primitive and that it arose from an ancestral condition in which neither parent incubated. My treatment, however, was within a paradigm that included the relict reproductive behaviors described below.

In this regard, and concerning some other aspects of avian evolution, the relict reproductive responses bring to bear completely independent lines of evidence. The first to occur, and apparently the oldest such response detected in my parrots, namely, "leaving eggs at lights-off, with immediate return at lights-on" is a strong, though indirect, indication of primitive biparental care. Thus, while it is observed characteristically in the female -- the nighttime incubator -- male Cockatiels also have been observed to engage in this relic. Taken together with other considerations, it is highly indicative of both ectothermy and biparental care in earliest shallow-nesting theropodan ancestors (see below).

While these relict avian reproductive responses have been detected only in three species of small parrots, they have thus far also been sought only in these species. Their presumed general applicability to avian evolution, awaits a similar paradigm of testing with other avian species, particularly with those in which both parents incubate. Some of these relict behaviors provide ideal dependent variables for experimental studies. But no less significant for the primitive and later ancestral modes of parental care postulated here were the accompanying permissive or constraining Mesozoic environmental (meteorological and ecological) conditions.

Another pertinent example of the phylogenetic approach is that of Garner et al. (1999). They proposed a "pouncing proavis" model to ambush prey, including increasingly improved, drag-inducing distal control surfaces, as an alternative to the 'trees-down' and 'ground-up' scenarios. In my corresponding model (Kavanau, 1987), I postulated that the crucial, initial selective pressure for jumping from vegetation was not for hunting, but for nest protection -- quick, energy-efficient, access to the ground and nearby nest -- a component of the proposed 'roots of avian evolution.' Occurring initially from relatively low heights, nest-access jumps would not then have required control of descent pathways. A third pertinent phylogenetic analysis is that of

Brightsmith (2005), suggesting that tree-cavity nesting is the ancestral state among parrots.

In the present treatment of early avian evolution, I use a data set of known avian and reptilian behaviors, but supplement it with the previously unknown relict reproductive behaviors described immediately below, and numerous recent, pertinent paleo-discoveries. I postulate a main-line evolutionary pathway traversing six principal stages, possibly beginning as early as late Triassic, with small-bodied, bipedal, ectothermic theropods, with nests buried at shallow depths.

THE NEURAL SUBSTRATE FOR CONSERVATIVE BEHAVIORAL EVOLUTION

Relationships most pertinent to conservative behavioral evolution are subsumed in Stebbins' (1969) principle of conservation of organization: Whenever a complex, organized structure has become an essential adaptive unit of a successful group of organisms, the essential features of this unit are conserved in all the evolutionary descendants. Applying this principle specifically to nervous systems, it follows that many neural input-output behavioral relationships are tightly coupled. Once established they typically persist in homologous circuits of descendant species (Jerison, 1973, 1976).

Similarity of behavior, in fact, may well be decisive when other evidence is equivocal or conflicting (Simpson, 1958). Below the level of orders, taxonomists increasingly give greater weight to behavioral evidence. Traditional systematic groupings have been altered on the basis of behavioral criteria in numerous instances. Although this dependence on behavioral evidence was questioned early by some workers, there has since been a quantum leap in the abilities of ethologists to document and analyze behavioral units in detail. Thus, it appears that behavioral data can be treated in a manner necessary for a rigorous phylogenetic analysis (McLennan et al., 1988). Motor components tend to be more conservative than perceptual ones and releasers (Mayr, 1958, 1980). Because muscles employed in the relict responses of small parrots are used in many adaptive movements, they retain the potential for full expression.

Moreover, habits and behavior generally are deeply rooted, usually products of very ancient evolution. Species-specific behavioral patterns are extraordinarily stable, genetically, and likely to be far removed from direct gene action. Thus, links between genotype and phenotype in behavioral ontogeny (and underlying neural circuitry), are complex and more indirect than in the establishment of any other biological process. Stability of behavioral patterns also is a consequence of enormously varied patterns of causal sequence by which gene mutations usually effect changes of behavior (Provine, 1984; Dumont and Robertson, 1986). Time and again phylogenies reconstructed using behavioral traits have mirrored those based entirely on morphological characters (McLennan et al., 1988).

Various properties of the vertebrate brain -- the most complex and probably least variable tissue -- show that its evolution is highly conservative, and relatively infrequently subject to hereditary abnormalities. Many, if not most, neural pathways are phylogenetically very stable (Jerison, 1973; Levi-Montalcini, 1987). These pathways guide both the reproductive behaviors treated here and their underlying physiology. At one level, this evolutionary inertia has been viewed as an extreme manifestation of a like property of all organ systems. The earlier an embryological event occurs, the greater the number of subsequent embryological processes dependant upon it and the greater the likelihood of its being conserved.

At another level, evolutionary inertia is largely attributed to the difficulty of altering central neural patterns. In a sense, these become 'insulated' from selection, which can act only indirectly on higher level integrative mechanisms involving complex, widespread neural circuits (Sperry, 1958; Dumont and Robertson, 1986). Intrinsically conservative bases for neural function also can be specified at the level of networks and neurons (Marder et al., 1987; Getting, 1988; Harris-Warrick, 1988).

A key consequence of these network properties for evolution, most pertinent here, is that natural selection cannot physically eliminate most pathways for obsolete functions. Positive selection continues to act on them because, as noted above, their neurons also are components of pathways for adaptive functions. Accordingly, selection for loss of neural functions operates largely through highly specific inhibitory mechanisms (Hamburger, 1971; Freeman and Vince, 1974; Gottlieb, 1988 and below). Because part or all of neural circuitry for simpler or similar behaviors typically becomes incorporated into circuitry for new responses, much central neural circuitry for ancient behaviors still may be present in descendants. In consequence, as also illustrated by the present studies, many behaviors of the past may be 'revived' by appropriate stimuli and/or disinhibition, provided that effector systems remain fully functional.

RELICT REPRODUCTIVE BEHAVIORS OF SMALL PARROTS

The following findings derive from seven years of intensive experimental and observational studies of Cockatiels, Peach-faced Lovebirds, and Budgerigars. They occurred at both domestic facilities and at UCLA, mostly described in detail elsewhere (Kavanau, 1987). They consisted of very close observations of minimally disturbed, confined (and sometimes 'unconfined') birds, after long accommodation to my almost continuous presence.

Leaving eggs at lights-off, with immediate return at lights-on

Introducing this relic, upon transition to night in the wild, the parent bird is in a snug, continuously dark nest-cavity, where it stays for the night. Upon this transition occurring in the experimental circumstances, however, the parent is in a spacious, flat, nesting area, exposed to light, as it was during the entire day. Such circumstances occurred only in the remote evolutionary past when avian ancestors were nesting on the ground but left the nest at night. Upon these circumstances being encountered today, they trigger in the modern bird the same responses that they elicited in the remote past, namely, the bird leaves the spacious, flat nest and seeks safe shelter for the night at an outside elevated perch.

The striking, consistent, very likely oldest (and first appearing) relict reproductive response described below presumably dates to the ectothermic, pre-incubative stages of theropodan ancestors of birds. It was noted in hens of all three species, most impressively in Cockatiels, both in nest boxes with transparent sidepanes and in open floor-nests. Early in the breeding cycle, before initiating nighttime incubation, hens (sole incubator among Budgerigars and Lovebirds), typically left the eggs for the night within minutes of the lights being extinguished. But they immediately returned if the lights were restored.

They engaged in such departures and returns repeatedly if lights were turned off and on in succession, usually as 'nighttime' was approaching but sometimes also in the early morning after having returned to the nest in the light. Returns typically were essentially immediate, sometimes amounting to simply turning around and returning if still in the act of leaving. The nest and eggs were regained within an average of only ~10 s in one test of four cycles with a Cockatiel hen (the lights were turned off four times for several minutes and then turned back on again). Her times before departures at lights-off averaged ~86 s

I interpret this strikingly consistent, previously unknown, behavior to be a recapitulation of that of the birds' ectothermic ancestors. Thus, at dusk the ancestors presumably discontinued foraging in the nest vicinity and sought safe, nearby nocturnal quarters for rest and nest-surveillance, with return therefrom during dawn the following morning. In general, the only safe nocturnal resting quarters that also would have allowed nest surveillance and ready nest re-access, would have been at moderate heights in nearby vegetation. Accordingly, such heights are believed to have been their nocturnal destination. This relatively clear-cut relict behavior was the main clue to the proposed 'roots of avian evolution, and the finding that led to numerous additional experimental tests.

The departing ancestral parents must have been ectothermic, since it would have been maladaptive for endotherms to leave eggs unincubated for the night, They

might have been leaving foraging sites in the vicinity of their shallowly-buried nests in Stage 1 ('shallow-nesting ancestral theropods') or leaving such sites in the vicinity of surface nests in Stage 2 ('surface-nesting nonavian theropods'), with the nests already having been concealed, and the eggs kept warm for the night, with decomposing vegetative debris.

From their resting and surveillance quarters in overhead vegetation, the parents could have expeditiously jumped or parachuted to the ground to protect nests from small egg-predators. The shallowly-buried eggs in Stage 1 are postulated to have been incubated solely by climatic heat, while the eggs in surface nests of Stage 2 are postulated to have been kept warmer continuously through parental care -- including burial in decomposing vegetation at night, and appropriate other covering with dry vegetative debris or shielding alternately with the parental bodies during the day.

It would have been adaptive for Stage 1 ancestors to return to nests or their vicinity without delay in the morning to ensure egg concealment and safety. This could account for the immediate return to the nest and eggs during lights-on tests. Contrariwise, time elapsing before leaving the nest vicinity at dusk (at 'lights-off' during tests) would not have been critical.

The large, and otherwise inexplicable, disparity in the two response times greatly strengthens the interpretation of their significance, particularly for the alternative of concealing eggs at night by burial in decomposing vegetative debris (as opposed to their being shallowly buried continuously). It also testifies to the apparent lengthy persistence, even of quantitative aspects, of relict responses.

The 86 s average delay before leaving the nest box at lights-off probably is the consequence of a lack of urgency. The immediate response at lights-on suggests that the present abrupt presentation of light triggers a return that would have taken place at some ancestral threshold light level during dawn, probably sunrise. The existence of this essentially immediate-response-relic provides a rich substrate for further experimentation, including confirmation, with other species and conditions. This test also was performed with male Cockatiels. Since the female is the nighttime incubator, as in most avian species, one might not expect males to retain this relict response. Since they do exhibit it, and the response must trace to an ectothermic ancestor, it is one of several indications that biparental care was primitive in birds' theropodan ancestors (see, also, the treatment of Stage 1).

Strong disinclination to expose eggs in light

This relict behavior has been seen only in birds that engage in the above relic, most strikingly by female Cockatiels. They will not leave eggs exposed in light in 'transparent' nest boxes (as opposed to conventionally

opaque, dark nest boxes) in the identical circumstances in which they leave them in darkness. Rather, they tenaciously shield the eggs from light exposure by standing or crouching above them. This behavior is believed to trace back to the 'surface nesting nonavian theropods' of Stage 2. I suggest in the following that this act, by ancestral parents:

(a) Shielded eggs in open nests from midday insolation and overhead view.

(b) Exposed eggs only to early morning and late afternoon low-angle insolation.

It is noteworthy that male Lovebirds, though they no longer otherwise participate in egg care, retain this relic. On those infrequent occasions when the sitting hen left the partially transparent nest box briefly during the day, her mate replaced her by standing over eggs that would otherwise have been exposed to light and view (Kavanau, 1987).

Repelling incoming mates

A sitting Cockatiel's repelling of a mate attempting to relieve it in incubating eggs and/or brooding chicks in spacious laboratory nest boxes, reveals an unusually high degree of possessiveness that would not be revealed in exchanges at the snug nest holes utilized in the wild. The sitting mate sometimes merely adopts a threat posture, sometimes hisses or pecks but, occasionally vigorously repels the returning mate, hen or cock, from the nest box.

A returned bird sometimes engages in incessant, superfluous grooming of its sitting mate, seemingly seeking to dislodge it through unending irritation. Despite a sitting bird's aggressive acts, incoming mates persist tenaciously in efforts to reacquire the clutch, returning repeatedly and remaining lengthily at the mate's side. These acts become more vigorous as hatching approaches. Similar great possessiveness and reluctance to yield eggs, previously unknown in Cockatiels, is known in other species, mostly large sea birds with open nests (Armstrong, 1947).

Double-clutching

On some occasions, after lengthy competition, Cockatiel mates split the clutch and incubated the eggs individually, often lengthily (Kavanau, 1987). This behavior and the repelling of incoming mates strongly suggest an ancestral practice of rapid double-clutching. It is postulated that it occurred during both stages of 'pro-aves' (Stages 3 and 4). Combined with the acquisition of endothermy and continuing favorable climates, it is the chief basis for attributing double-clutching to these two stages. Competition for the eggs must be regarded as a relic; because it could play no role today. Highly-valued, dark, 'cozy' nests in tree-hollows are employed and for-

aging pressures leave little time to compete for eggs.

Appropriating eggs

This action aims at direct egg takeover, and could be more primitive than the methods described above. Only Cockatiels (in which both parents incubate) have been observed to appropriate eggs from under sitting mates. At no time do mates compete for the same egg. Each simply watches as the other carefully 'extracts' an egg from beneath it, usually equally carefully recovering it shortly thereafter, also without opposition. This manifestation of egg possessiveness and careful egg handling also is a likely relic of times when mates incubated separate clutches. Another tactic is to nudge the mate off the eggs, but this is not unique to Cockatiels (Heinroth and Heinroth, 1959; Welty, 1982; Ball and Silver, 1983).

Routine searches

When incubating, or merely shielding a clutch, Cockatiels and Peach-faced Lovebirds routinely search for and recover errant or buried eggs. This occurs by gently probing or 'plowing' with the bill in the substrate of wood shavings. Significantly, searches are confined to the incubative area and portions of its periphery reachable therefrom with the bill. This behavior also appears to be a relic, harking back to ancestral times of nesting on yielding substrates. Thus, eggs in nests in tree-holes used by Cockatiels and Budgerigars could not become concealed under conditions existing today (see below). But these searches would have been highly adaptive in primitive nesting conditions, when eggs in ground nests were concealed by cover during absences.

These behaviors could be holdovers from times before or during incubative care. Eggs at Stage 2 likely were covered with decomposing vegetative debris at night, to protect, conceal, and keep them warm. In those ancient times, such debris was not yet 'loaded' with arthropod repellants, is known to have been more abundant and of different composition, and would have generated more heat than occurs today (Smart and Hughes, 1973).

Directed searches —- 'appeased' by a single egg or chick

These searches are highly adaptive for nesting on yielding substrates. On returning to the nest, and finding all eggs 'missing,' hens (and male Cockatiels) of all three species appeared to become 'agitated.' They proceeded to search the incubative area and its close environs. Although this behavior has not yet been reported for any other bird, its existence in small parrots suggests that it is widespread in other birds in similar circumstances. Searches consisted both of visual 'ground' scanning, and

probing or plowing the shavings with the bill. It does not occur, however, in the presence of just a single egg or chick (likewise, in clutch splitting by Cockatiels, the birds are 'appeased' by a single egg or chick).

A tested male Cockatiel was 'appeased' by caring for a fostered chick in a nest pan, 'ignoring' a chick, apparently but not certainly recognizable as its own (that is, feathered with eyes open), just outside the nest pan. The latter chick, however, was cared for promptly when relocated to just inside. On three occasions a female Cockatiel appropriated an egg from her clutch, placed at a former nest site (where she would not incubate it), rolled it to the new oviposition site, and incubated it there. On no occasion did she seek to reacquire a second egg (Kavanau, 1987).

Since these birds are hole-nesters, and Cockatiels and Budgerigars today oviposit on hard surfaces, with little or no bedding, searches for buried eggs must be relics from times of nesting on yielding ground. Moreover, the searches were highly stereotyped. No probing occurred beyond the bill's reach from the incubative area (but when a chick was present, eggs might be displaced further, and also were searched for at more distant locations).

Distant visual searches

The following remarkable search behaviors are known only for Cockatiels in spacious nest boxes and open floor nests. When a returning Cockatiel found all eggs 'missing,' it first searched beneath the incubative area. If even a single egg was uncovered, 'normal' care of that egg was resumed. If not, an incoming bird in a nest box raised its head and peered intently at the upper level of the nest box walls. This behavior is highly suggestive of engagement in a stereotyped behavior for searching at a distance from a ground nest.

If unsuccessful in finding an egg, when nesting on the cage floor, the bird sometimes climbed to a vantage point and peered intently at the far ground surrounding the incubative area, as well as outside the enclosure in all directions. Afterward, it also sometimes searched the floor 'on foot.' These quite remarkable distant visual searches of Cockatiels appear to be relics of ancestral egg care, when nesting occurred in shallow scrapes on flat substrates sufficiently compact for eggs to roll or be blown away, or be displaced accidentally. They probably date to after the earliest stage of nesting on yielding substrates (see below). 'Distant visual searches' also occur when all young are 'missing'.

Bursts of scratching on smooth surfaces

This action by Cockatiels and Lovebirds (not tested with Budgerigars) occurred when nest bottoms were smooth and hard. When wood shavings became displaced, eggs could roll about freely. Incubating birds attempting to 'cover' them, unleashed a quick burst of foot scratching movements. These actions clearly were intended to excavate a shallow depression in a surface upon which eggs otherwise could roll freely.

In connection with this behavior, it is postulated below that surface nests in Stage 2 were the evolutionary end-products of excavating increasingly shallow burial sites for fewer eggs, in areas of decreasing extent. Accordingly, the clutches would, at first, have been buried in earth, humus, or other readily excavated substrates, particularly as eggs in Stage 1 are thought to have been located in the vicinity of shading vegetation. Since eggs would not have rolled freely on readily yielding substrates, it is unlikely that this relic dates to earliest surface nesting. Accordingly, the response probably dates to times after surface nesting was established, when nests were being built directly as scrapes on fairly compact ground.

Defective eggs rolled away or hidden

Once surface nesting had begun, it would have been adaptive to remove overtly defective eggs to a distance and/or conceal them. This behavior, observed here in Cockatiels, is known in many ground-nesting birds (Welty, 1982). Since wild Cockatiels nest in tree hollows, it also appears to be a relict adaptation for ground nesting.

The finding that the non-sitting Cockatiel sometimes disposed of eggs is significant. Except in some colonial species, only the parent engaged at the nest removes eggshells (Tinbergen et al., 1962). This relic is another suggestion that primitive egg care probably was biparental.

Brood-site fidelity -- 'ignoring' displaced chicks

Cockatiels brooding eggs and chicks in open nests 'ignored' one of their chicks whose eyes had not yet opened when it was placed just outside the nest, even when it was their only chick. When, as yet unrecognizable chicks are removed to another location, parents continue to incubate remaining eggs, usually 'ignoring' the removed chicks. When replaced in the nest, the otherwise 'ignored' chicks are tended to immediately.

In essence, when eggs and chicks are in the nest together, the welfare of the chicks has highest priority. But when as yet unrecognizable chicks are placed outside the nest, the eggs are the sole focus of attention. Once feathered and old enough to be recognized (10 days of age, with eyes open), Cockatiel chicks usually have highest priority (Kavanau, 1987; but see the possible exception under "Directed searches -- 'appeased' by a single egg or chick").

This relict behavior strikingly illustrates how neural circuitry for a parental care practice that was adaptive tens of millions of years ago, may continue to determine

present-day behavior, even in experimental circumstances in which it would doom the offspring. It appears to be a relic from, and to suggest the existence of, times when ancestors of Cockatiels nested in colonies, when it would have been maladaptive to 'rescue' unrecognizable chicks outside the nest.

Such behavior also is known in certain colony-nesting albatrosses (Bartholomew and Howell, 1964) but it could not occur in tree-holes. While nothing is known of their possible colony-breeding ancestors, possession of this relic by Cockatiels, is consistent with the present theses, since the bulk of avian colony breeders belong to the more primitive orders (Collias and Collias, 1984).

The existence of relict behaviors -- the main thesis of this and my previous related works (Kavanau 1987, 1988) -- apparently has come to be recognized by Dingus and Rowe (1998). They state, though without reference, "Not all of its [the genome's] programs are used at once, and some may lie dormant for long periods….older programs can still be activated….occasionally with unfortunate consequences…..As old programs are triggered, either in nature or the lab, we sometimes get a glimpse of the past."

Oviposition-site fidelity

Experiments with hens of Cockatiels and Lovebird showed that fidelity to oviposition sites overrides that to eggs and/or former nest sites (Kavanau, 1987). Fidelity is so great that a Lovebird hen repeatedly abandoned, and subsequently reclaimed, her clutch within a 14-cm-diameter nestbowl, when the bowl was simply moved back and forth, only 14 cm from, and then back to the site of oviposition. Distance-wise, this was the equivalent of simply transferring the same eggs back and forth between two fixed, adjacent nest bowls. This relic behavior, which also would doom the offspring (it could not occur within nests of Lovebirds or Cockatiels today), also illustrates a remarkable awareness of landmarks. Such fidelity would ensure that, among ancestral colony nesters, parents only incubated their own clutches.

Displaced nestlings do not stray

When Cockatiel nestlings are displaced from nests, all their locomotion becomes rotary, in a tight circle. This occurs even a day or two after the eyelids first open (but probably before an ability to focus). This would be adaptive in nests in small, shallow scrapes on flat ground, ensuring that nestlings would not stray. Since the behavior, if it occurred, would be adaptively neutral in a tree-hole nest, it also can be regarded as a ground-nesting relic.

Lightly-buried nestlings become silent and still

Fully mobile Budgerigar nestlings usually congregate in a heap, cheeping 'agitatedly' and 'jockeying' for position within the heap. But if covered with wood shavings, they tend to cease all activity, usually with beaks extending from the heap to facilitate breathing. This also occurs in some ground-nesting birds (Maclean, 1974; Howell, 1979). Such behavior in hole-nesters would appear to be a relic of times when young in surface nests were covered during parental absences, or times of danger.

ROLES OF NEURAL INHIBITORY CONTROL MECHANISMS

Inhibitory nerves are present from earliest embryonic stages at which networks generate bursts of activity, and inhibitory mechanisms underlie the precise adjustments that result from sensory input during post-hatching behavior (Hamburger, 1971; Freeman and Vince, 1974). During ontogeny, the neural circuitry for a behavior may be present at a particular stage, but the behavior may occur only if an existing neural inhibition is removed.

These circumstances are illustrated by certain predominantly vestigial but well-manifested responses in man, such as the palmar grasp and rooting reflexes of infants. They may be elicited by appropriate stimuli in normal individuals. In some circumstances, however, they become expressible only after release of inhibitory influences, as may occur after frontal lobe lesions or spinal cord disease (Luhan, 1968; Steegmann, 1970; Matthews, 1982). Thus, the neural circuitry supporting incubation may be present in the males of all three species studied but be activated or disinhibited only in Cockatiels.

A bird's being mature does not imply that the normal processes and pathways for reproductive behaviors are ready for use. Rather, mobilization of neural and physiological pathways follows a hierarchical course, a consequences of changes in hormones and neurohumors that 'open' initial or antecedent pathways. As discussed above, this occurs, at least in part, by blocking inhibitory influences. A well known example is integration of nest-building behavioral patterns of domestic canaries into functional sequences. Performance of one specific activity (and accompanying altered hormonal states) stimulates the next (Hinde, 1970).

In nest-building movements by Great Cormorants, *Phalacrocorax carbo*, breeding behavior develops, as a rule, in ascending stages. Concluding a breeding season, the same stages are traversed in descending order -- as also was observed to some degree with the birds of this study -- only to develop again in the same sequence in subsequent seasons (see Kortland, in Fentress and McLeod, 1986).

PRESUMPTIVE HIERARCHICAL DEVELOPMENT OF OVARIAN FOLLICLES

As noted above and elaborated below, the reproductive behaviors of small parrots also develop hierarchically. But hierarchical reproductive phenomena do not apply only to behavior. These phenomena also appear to derive from, and interact with events in the reproductive organs, particularly the ovary, in which follicular development, maturation, and atresia are under complex, conservative, neuromodulatory control. The basic hormonal patterns involved in these processes seemingly were established very early in vertebrate evolution (Callard and Lance, 1977).

Female birds enter their reproductive life with a finite number of reproductive cells. Primary oocytes and follicles, each one innervated by hundreds of sympathetic and parasympathetic fibers (Burden, 1978), undergo several kinds of selection. The selections In Budgerigars appear to retrace the phylogenetic progression of sizes and numbers of ancestral ripe follicles, putatively giving valuable clues to past clutching practices. These apparent ovarian recapitulations appear to underlie the well known phenomenon of birds adhering tenaciously to ancestral incubative patterns and habits (Ball and Silver, 1983), which are surprisingly unresponsive to ecological conditions (Skutch, 1957; Drent, 1972; Smith, 1979).

In its undeveloped state the left ovary of Budgerigars consists of a mass of follicles ~1 mm in diameter. An apparent phylogenetic progression of growth and atresia of cohorts of these follicles occurs during breeding, I draw upon this progression as a guide to clutching practices in my main-line synthesis of avian evolution.

Similar ovarian morphology and development also is seen during the reproductive cycles of other birds, including those that build nests (Budgerigars do not). Nest building often is coincident with follicular growth, as exemplified in the domestic canary, *Serinus canarius* (Hutchison et al., 1968) and the Barbary or Ring Dove, *Streptopelia risoria* (Cheng, 1974; Hutchison, 1977). In Budgerigars, however, ovarian follicular stages have been documented in great detail. Just as with the listed behavioral relics, the generality of findings for successive cohorts of ovarian follicles for other avian species remains to be assessed.

In the quiescent state the avian ovary is a small, flat, yellow organ with numerous small (< 1 mm) follicles. In the active state it is a large organ composed of 5 to 6 large follicles, graded in size, and filled with yellow yolk, and a larger number of smaller follicles filled with white yolk (Tienhoven, 1961). Some stages of growth and ovulation of these follicles are stimulated or regulated by gonadotrophin. Some exterior growth and maturational effects are mediated by various steroid hormones synthesized by the growing follicles (Guraya, 1978).

The ultimate source of ovarian control presumably resides in the brain. As noted, hundreds of neural fibers directly innervate primary oocytes and follicles (Burden, 1978). From the numerous follicles present at the beginning of a breeding cycle, ancient neural mechanisms of the conservatively evolving brain seemingly induce similarly conservative development of a certain small number of follicles and suppress the development and growth of others, which become atretic.

Because those selected grow yolky eggs, fewer still are selected to continue growth and maturation. Eventually a hierarchy of follicular sizes is formed, with its peak being large, preovulatory, yolky follicles whose ovulation during the breeding cycle determines clutch size (Guraya, 1978). In Budgerigars, a graded follicular series forms 3 - 4 days after the hen enters the nest box, which is approximately 6 days before the first egg is laid. The onset of nesting behavior depends on the secretion of ovarian hormones (low levels of ovarian estrogens).

Regarding the maturation of female reproductive cells in Budgerigars, from a phylogenetic point of view, I propose that:

(a) The upper range of the condition of 10 -20 synchronously developing largest follicles (1.0 - 1.5 mm in diameter) corresponds to the pre-ovulatory condition in each ovary of deep-nesting basal ectothermic theropodan ancestors, with up to 40 eggs laid *en masse*.

(b) The lower range of this condition corresponds to the 'shallow-nesting ancestral theropods' of Stage 1 (ectothermic), with, say, 10 eggs from each ovary (20 eggs per clutch), perhaps laid in two episodes several days apart.

(c) The condition of 2 to 5 synchronously developing largest follicles (2.0 - 2.5 mm) corresponds to the 'surface-nesting nonavian theropods' of Stage 2 (ectothermic), with up to 10 eggs per clutch, also laid in more than one episode;

(d) The condition of one largest follicle and 5 to 8 (but as many as 8 to 10) smaller ones forming a graded series (4 - 12 mm), marks the onset of primitive endothermy, with one egg from each ovary laid every day or second day (monoautochronic ovulation, as follicles in the graded series ripen), and corresponds to rapid double-clutching (two broods per ovarian cycle is common in birds) by ancestors in surface-nesting Stages 3 and 4, with fewer than 10 eggs per clutch; and

(e) The graded series also applies to sequential single-clutching in Stages 5 and 6, with only the left ovary functional in most species. Same-size cohorts of maturing and atretic follicles in reptiles (Byskov, 1978; Saidapur, 1978) probably also recapitulate past ovipositional practices.

There is no more convincing illustration of the potential for conserved breeding practices, and avian relict reproductive behaviors to provide clues to avian evolution, than the primitive nesting and egg care of birds' closest living relatives, crocodilians, as compared to those of

turtles. Although their probable common ancestor dates back 280 Myr, aspects of ancient practices of both groups have been conserved to a striking degree. Females of both of these anatomically greatly divergent forms use the hind feet, blindly and meticulously, to dig the nest and check the fall of eggs into it (Neill, 1971). Dinosaur nest excavation also is suspected to have been a hind limb activity (Coombs, 1989).

DISCOVERIES AND SIGNIFICANCE OF 'NONAVIAN' FEATHERED THEROPODS

One of the recently discovered Liaoning feathered theropods was a chicken-sized basal compsognathid coelurosaur, *Sinosauropteryx prima,* with a filamentous fringe of densely-packed, probably tubular, integumentary structures. These seem to resemble most closely the plumules of modern birds, having relatively short quills and long filamentous barbs (Chen et al., 1998). Some workers consider them to be first-stage precursors of true feathers (Padian et al., 2001; Prum and Brush, 2002). Chattergee (1997) and Chen et al. (1998) suggested an insulative origin.

Also discovered were fossils of feathered, turkey-sized, basal caudipterygians, *Caudipteryx zoui*. They had relatively short forelimbs and modern-looking, more or less symmetrical, clearly avian contour-feather fans on advanced bird-like hands and a shortened tail. Some of their remarkably avian features are not seen even in *Archaeopteryx* (Witmer, 2002). An original insulative function also was proposed for them (Ji and Ji, 1996; Ji et al., 1998).

Workers who do not support a theropodan origin, question *Caudipteryx* being a flightless dinosaur, considering it, rather, to be a secondarily flightless bird of other derivation (refs. in Paul, 2002:216), Subscribers to the theropodan secondary flightless origin, view *Caudipteryx* and other bird-like dinosaurs, as dating from the Cretaceous, because they were flightless descendants of middle Jurassic birds. Only when they lost flight, and were selected for increased size, did they more often become part of the Cretaceous record (Paul, 2002, and below) and contribute to the impression of a stratigraphic disjunction. Other workers regard them as "feathered nonavian dinosaurs" (Zhou and Hou, 2002) that have compellingly shown that feathers had their origin within theropod dinosaurs (Chiappe and Dyke, 2002; see, also, Padian and Chiappe, 1998b; Prum, 2002; Dyke and Norell, 2005), or as stages in avian evolution from dinosaurs (Ji et al., 1998).

In this connection, Padian et al. (2001) comment, "If the neatly parallel barbs of the feathers of *Caudipteryx* and *Protarchaeopteryx* reflect the presence of barbules, then clearly barbules evolved before flight did, but why?" To this discordance, we can add the stout-, even grotesque-forelimbed *Mononykus olecranus,* "perhaps the most startling recent finding" (Chiappe, 1995) and

Alvarezsaurus, whose potentially secondary flightless characters are exceptionally well developed. Of them, Chiappe remarks, "placement of these bizarre creatures within Aves [which he nonetheless finds fully justified] has created a great deal of controversy." Dingus and Rowe (1998) ask, "If *Mononykus* is not a bird, then where does it fit? Why does it have a keeled sternum like other ornithurines….fused wrist bones, a bony sternum, a pelvis with a back-turned pubis, like other maniraptors….a shortened tooth row, a stiff tail, and a tall ascending process in the ankle, like other tetanurines. Why is its skeleton hollow and its foot equipped with a first toe set far below the ankle joint, like other theropods?" Also, the orbit is connected to the infratemporal fenestra, among archosaurs a condition known exclusively in birds (Chiappe, 1995).

The secondarily flightless scenario (see, also, below) parsimoniously accounts for these seemingly paradoxical findings. Although Padian et al. (2001) do not adopt it they regard it as the simplest explanation. They do, however, conclude that, "either feathers evolved independently in several coelurosaurian lineages, or our understanding of coelurosaurian phylogeny needs revision." In addition to possessing a number of other avian features, the presence of a mass of gizzard stones, together with tooth loss, in *Caudipteryx*, indicate an advanced state of herbivory (Feduccia, 1999; Martin and Czerkas, 2000), not inconsistent with its being secondarily flightless.

One scarcely can overemphasize that a presence of feathers and widespread secondary flightlessness in the fossil record, likely has been greatly obscured by the improbability of feather preservation at sites other than inland water habitats (with fine-grained sediments) and closely neighboring terrestrial environments (Davis and Briggs, 1995). Thus, no unequivocal fossil feather is known prior to those of *Archaeopteryx* in the late Jurassic (Paul, 2002; Witmer, 2002), and, indeed, sediments from which all the Mesozoic feathered fossils from China were recovered are lacustrine.

Though the impression given above is that considerable disagreement still exists concerning the ancestral affiliations of birds, most cladistic approaches lead to the conclusion that birds descended from predatory dinosaurs, closely affiliated with sickle-clawed dromaeosaurs (closest relatives of *Archaeopteryx*). This view was greatly reinforced by the discovery of the astonishingly *Archaeopteryx*-like, sickle-clawed *Sinornithosaurus* (Xu et al., 1999). This relatively long-limbed theropod was one of the best adapted for life in the trees, and offers the best fossil evidence to date for both the "trees-down" and secondarily flightless hypotheses (Paul, 2002).

EARLY SELECTIVE PRESSURES FOR THE ORIGIN OF FEATHERS

Selection for the slightest fringe of drag-increasing, scale-

like feather equivalents in terrestrial-arboreal theropods would have offered an immediate advantage in making jumping and 'free-fall' descent easier and safer, evolutionarily en route to flat, stiffened integumentary structures and parachuting and steering. Some workers believe this selection, alone, could have led to the evolution of a tubular follicle, presumably the initial event in feather evolution (Savile, 1962; Bock, 1986; U. Norberg, 1990; Prum, 1999). The high adaptedness of jumping, parachuting, steering, and gliding is evident from their independent, widespread evolution among vertebrate classes (Norberg, 1990; Paul, 2002).

As gliding evolved from strict parachuting, such skin extensions would have had to form airfoils for lift (Balda et al., 1985), but not for steering and slowing descent. Many workers assert that flapping flight is far more likely to have evolved from arboreal gliders than from gliding or running cursors (Norberg, 1985; Peters and Gutmann, 1985; Rayner, 1985; Tarsitano, 1985). Norberg's models show that evolutionary transitions from gliding to active flight are mechanically and aerodynamically feasible, with presumptive adaptive advantages for every step along the hypothetical route. Padian et al., 2001; see, also, Hopp and Orsen 1998), suggested the view, partially subscribed to here, that feather-like structures may have been at least partly selected for, at some stage, for parental thermoregulation of eggs in nests.

Specifically, I suggest two principal early selective pressures for the origin of feathers, both of which, acting together, probably were essential to achieve fully-developed flight (see, also, Dawson and Hudson, 1970). One was for drag-increasing adaptations to facilitate jumping from heights. Any fringing integumentary extensions also would disrupt the body outline, which might aid in concealment. The other was insulative:
(a) Against loss of heat during presence at heights in vegetation at night, and in greater exposure to breezes while foraging in trees and shrubs by day.
(b) To shield parents from intense, midday insolation, as they bodily shaded eggs in surface nests in Stage 2, a common avian practice in arid lands (Campbell and Lack, 1985).

The germ of this latter selection, broadly speaking, was suggested by Regal and others (see Regal, 1975). Both the overnight safety of arboreal sites and selective pressures in their cooler microclimates also have been suggested by Bock (1986; see, also, refs. in Feduccian, 1996).

As noted, I propose that a selective pressure for quick access to the ground and nest from overhead vegetative sites -- a component of the proposed 'roots of avian evolution' -- was the crucial one that directed some dinosaurs along the path toward increased arboreality and flight. Body size probably was differentiative, either facilitating or precluding arboreal agility. I write above, "path toward increased arboreality and flight," because

some of the theropods that took that path might have abandoned it before achieving flight, not progressing beyond parachuting and steering (Stage 2) or gliding (Stage 3). Rather than subsequently following the coelurosaurian phylogenetic tendency toward miniaturization, they might have followed the tyrannosaurid trend toward progresssively larger size.

This could account, for example, for the recent finding of filamentous branched 'protofeathers' in the earliest known tyrannosauroid, the small, gracile, Liaoning *Dilong paradoxus* (Xu et al., 2004). To the discoverers, the branched filaments indicated that this "important modification" occurred early in coelurosaurian evolution. But a secondarily glideless or parachuteless interpretation was not considered. Such an interpretation could no less account for 'feathers' in other Liaoning theropods lacking various signs of ancestral adaptations for flight.

The smallest 'nonavian' basal dromaeosaur, *Microraptor zhaoianus,* occurred in the same Liaoning deposits (Xu et al., 2000). Its integument consisted of the 'typical filamentous coat,' suggesting that feathers or their degenerate remnants were present among dromaeosaurids. Their feet were well adapted for upward climbing, comparable to those of arboreal birds.

Although most small predatory dinosaurs show such adaptations, those of *Microraptor* were suited for upward climbing to a greater degree (Paul, 2002). They also possessed a highly mobile hand-wrist complex, and unique caudal vertebral adaptations for balance control (Ostrom, 1990). Some specimens displayed a prominent fan of feathers at the tail tip (in extant birds, providing for lift, enhanced maneuverability, and braking during landing).

Some workers concluded that these theropods were primarily cursorial ground-dwellers, not adapted for arboreality (Padian et al., 2001; Prum and Brush, 2002; Zhou et al., 2003). However, this would not rule out their having had ancestors that parachuted and braked with their symmetrically-vaned feathers (see below).

Feather-vane symmetry is significant, because vanes in many feathers of modern volant birds are asymmetrical, indicative of advanced aerodynamic functions, at the least for gliding (Feduccia and Tordoff, 1979). Asymmetry is essential for feather bending and rotating, with angles of attack automatically adjusted by appropriate pitching movements during wing beats (R. Norberg, 1985). Symmetrical feathers serve only a few simple aerodynamic functions: braking and parachuting through drag, and rudder action (Paul, 2002).

The discoverers of 6 new specimens of 4-winged dromaeosaurids (*Microraptor gui*) at the same locale in China (Xu et al., 2003), adopted somewhat altered views. Possessing symmetrically- and asymmetrically-vaned, wing-like arrays of pennaceous primary and secondary feathers on both fore and hind limbs, Xu et al (2003). proposed that these theropods were pre-adapted for

flight, probably could glide, were ill suited for a terrestrial existence, and represented an intermediate stage between flightless 'nonavian' theropods and birds. Also, that they were arboreal -- like *Archaeopteryx,* an upward trunk-climber (see Tarsitano, 1985; Yalden, 1985; Feduccia, 1993). Discovery of relatively long, distinctively curved, pennaceous feathers, mainly along the outer side of the tibiotarsus of a Liaoning enantiornithine fossil by Zhang and Zhou (2004), tends to support the views of Xu et al (2003). Here, these dromaeosaurids are considered to be aberrant offshoots from stages 4 or 5 of the main line.

It is scarcely conceivable, that feathers, with their marvelous, damage-limiting modular structure, almost airtight vanes, and ability of these vanes to reform broken barb-to-barbule linkages on preening, could have evolved independently of fine-tuning by selection for advanced aerodynamic adaptations. As has been emphasized by Feduccia (1985), "feathers are by far the most complex derivatives of the integument to be found in any vertebrates…allow a mechanical and aerodynamic refinement never achieved by other means….would represent gross 'overkill' for insulatory structures….provide the most convincing argument against feathers having evolved initially in the context of thermoregulation."

Early avian ancestors ground nested, just as did their theropodan forerunners (Clark et al., 1999), and as also do their palaeognathous large, ground-bird descendants today, retaining or replicating ancestral reproductive practices (Paul, 1994). But they increasingly invaded arboreal, and eventually aerial, habitats. [use of "arboreal" in the following, in relation to Mesozoic avian practices, connotes abilities to ascend, forage, rest, and travel on and among trunks, branches, and fronds, but not implying early nesting in trees (Feduccia, 1999).].

My Stage 4, 'Advanced pro-aves' (including *Archaeopteryx*), lacking a fully reversed first toe (merely spread medially), apparently were only facultative perchers (Mayr et al., 2005). There can be little doubt, however, that primitive birds (my 'Ancestral birds' of Stage 5) were accomplished perchers. This is attested by their enlarged, more curved, foot claws, and longer, more distally placed, and strongly reversed hallux (Padian and Chiappe, 1998b). Early ancestors, as also many contemporary birds, were more or less 'at home' in both habitats. Though small-bodied ancestors of birds were becoming increasingly well adapted for arboreality, coexisting terrestrial adaptations long remained crucial.

THE SECONDARILY FLIGHTLESS SCENARIO

There is highly suggestive evidence, marshalled incisively by Paul (2002), that the coelurosaurian theropods -- *Protarchaeopteryx*, dromaeosaurs, troodonts, caudipte-

rygians, oviraptosaurs, and therizinosaurs -- have descended from small, more advanced fliers than *Archaeopteryx*. This category also most probably includes avimimids, and potentially includes alvarezsaurs, believed to have been close to, if not within, Aves.

Paul (2002) points out, for example, that the large-brained troodonts and velociraptors share so many bone designs with living birds that the conclusion that they are secondarily flightless offshoots of ancient birds is almost inescapable. He outlines in considerable detail how their bird-like bodies probably originally developed as adaptations for climbing, perching, gliding, and ultimately flight.

The evidence suggests that there were multiple losses of flight occurring at various stages of avian evolution, including its very beginning, even under harsh, dangerous circumstances that would seem to have favored strong flight performance (Paul, 2002). In this scenario, parsimony and logic favor flight as the causal agent of bird-like pectoral girdles, arms, and tails of these bird-breasted dinosaurs.

"Secondary flightlessness even explains why all avepectoran [bird-shouldered] dinosaurs diverged from classical theropods in terms of brain development, poor sense of smell, and feeding habits: that is, because their ancestors were small, smart fliers that lived in a 3-dimensional world and did not hunt big game" (Paul, 2002).

"….flight was lost fairly often among sophisticated flying birds in the Mesozoic and Cenozoic." It was especially likely to have been lost by basal flyers, and lost more than once (Paul, 2002). In being lost, paedomorphosis (retention of infantile characters) has been a major component. But there also is a trend to peramorphosis, where the skull, trunk and legs become proportionately overdeveloped, as in the ratite-like features in some Cretaceous dinosaurs. "It is ironic that flight….the prime stimulus for the origination of the avian clade, has been discarded in favor of flightlessness time and again in both aquatic and terrestrial groups exploiting new adaptive niches" (Chattergee, 1997).

"Once flight is abandoned….the selective pressures to reduce and eliminate the costs of growing and maintaining the flight apparatus are very strong….complete alteration to ground-bound forms that differ significantly from the flying ancestors may require only a million years or less….some island birds seem to have lost flight and dramatically reduced their flight apparatus in just generations…." (Paul, 2002). Among the first features to regress are the expensive flight muscles, particularly the pectoralis major and supracoracoideus, and the furcula normally degenerates into two clavicular splints.

In one view, loss of flight occurred at least as early as foot-propelled early Cretaceous divers, not too far removed from *Archaeopteryx* (Feduccia, 1999). Moreover, secondarily flightless birds may have retained flight-related adaptations (improved neural, muscular, and

skeletal systems) that gave them a competitive edge over non-fliers whose ancestors had never flown (Paul, 2002). Though Paul has been the chief proponent of the secondarily flightless dino-bird scenario, the possibility has not been overlooked by others (refs. in Paul, 2002:224).

In the other view, favored here, some of the secondarily flightless dino-birds referred to above may have begun to appear in small numbers as early as the middle Jurassic. Avian flight probably was being lost (and feathers regressing) at every major stage of its development. "….the most birdlike dinosaurs date from the Cretaceous because they were offshoots, rather than predecessors, of the early fliers in the Jurassic" (Paul, 2002).

In the following, as mentioned above, many of the recently discovered nonavian, flightless, feathered theropods are regarded as secondarily flightless birds. For them, at least, the designation, "nonavian," is misleading. Those feathered theropods not so derived are regarded as secondarily glideless or even parachuteless. In Witmer's (2002) assessment of secondarily flightless proposals, "….present some problems for testing by phylogenetic analysis….merit the scrutiny that they have never adequately received….have the distinct advantage that all supposed time discordances basically disappear…. the evolution of birds and theropods is hopelessly intertwined….are decidedly untidy, yet they still should receive serious consideration, and this will happen only when they are framed in explicit phylogenetic terms." But there are many impediments to such framing.

Of course, evolution toward flight could as well have been reversed at any intermediate condition, say gliding or parachuting, producing secondary glideless or parachuteless theropodan descendents of members of my postulated Stage 2 or 3. Such phenomena might have led to various grades and suites of adaptations for aerial niches less advanced than those achieved by active fliers (see Table 11.1 and p. 155 in Paul, 2002). These might have been identified as flightless 'non—avian' theropods but, nonetheless, might have evolved as the result of selection for aerodynamic adaptations en route to parachuting or gliding. An ex-treme example, might be *Sinosauropteryx,* with its filamentous fringe of integumentary structures resembling the plumules of modern birds (Chen et al., 1998), possibly employed in arboreal pursuits, including parachuting from vegetative heights to the nest site, yet lacking any other potentially secondarily flightless character (Paul, 2002).

And, if the proposal for the 'roots of avian evolution' is near the mark, selective pressures would ever have 'funneled' ground-nesting small theropods into heights in vegetation, with crucial needs, and selection, for rapid descent to the nest -- with heavy selection favoring the origin of aerial adaptations. Specifics and details of how adaptations for an aerial existence and flight may have come about in a "trees down" scenario have been dealt with extensively elsewhere (see Norberg, 1990; Paul, 2002, Chapter 6).

ECTOTHERMS OR ENDOTHERMS?

One of several long-standing issues among vertebrate paleontologists concerns dinosaurian thermal physiology. Although the most common early dinosaurs (prosauropods of the early Triassic; not in the avian lineage) grew at the fast rates typical of dinosaurs, these rates were affected by environmental factors, which typically is true of and suggests that they were ectotherms (Sander and Klein, 2005). Findings generally suggest that tyrannosaurids had determinate growth (Erickson et al., 2004). Other data suggest that some dinosaurs had greater growth rates than extant reptiles, growing most rapidly as juveniles; others may have grown at moderate rates observed in both reptiles and mammals, but with considerable rate variation between groups (Paul, 2002; Erickson et al., 2004). *Tyrannosaurus rex* reached effectively full size in less than 20 years, a growth rate comparable to that of the African elephant, which has a similar mass and time to achieve maturity (Horner and Padian, 2004).

For the putative endotherms of interest here, recent studies (Ricqlès et al., 2001) have made considerable progress. Studying, and drawing upon other studies (including those of Chinsamy et al., 1998), of fossil materials, within a comprehensive paradigm of bone growth and microstructure, several conclusions were drawn. These include:

(a) Theropodan hatchlings (such as *Coelophysis, Allusaurus*, and *Troodon*) in all size classes grew relatively rapidly to juveniles, implying the possession of some form of high, sustained metabolic rates;

(b) The histological features of basal bird and closely related 'nonavian' theropod bones suggest attainment of an essentially endothermic grade of thermal physiology; and

(c) All fossil taxa with hair or feathers, or similar structures, covering the body, probably possessed a generally endothermic level of physiology.

In the view held here, these conclusions receive strong support from the likelihood that many of the closely related 'nonavian' theropod bones, were those of secondarily flightless birds or secondarily glideless forms, in whom a primitive-to-advanced, though not yet tachymetabolic, grade of endothermy might be expected (see below). `But the above studies cast little light on the grades of endothermy achieved.

In this domain, some relict reproductive behaviors discussed above provide supplemental information. They strongly indicate the existence of early stages of evolution of birds in which eggs were attended by both parents, but were not incubated by body heat, implying ectothermy.

But the relict behaviors would not preclude climatically facilitated rapid growth of nestlings and juveniles.

I had already postulated a gradual acquisition of fully elevated core temperatures of endothermy by ancestors of birds (Kavanau, 1987), suggesting core temperature increases in the following sequence (some name designations updated): Stage 1. 'shallow-nesting ancestral theropods,' ectothermic; Stage 2. 'surface-nesting nonavian theropods,' ectothermic; Stage 3. 'primitive pro-aves,' endothermic (32 - 34°C; revised from 30 - 32°C); Stage 4. 'advanced pro-aves' (including *Archaeopteryx*), endothermic (~36°C); Stage 5. 'ancestral birds,' endothermic (~38°C); Stage 6. modern birds, 41 - 42°C.

In this connection, a sufficiently advanced level of homeothermy (constant core temperature and an accompanying finely-tuned chemostatic system), has great adaptive value. But the appropriate value of the core temperature is much dependent on the niche occupied. Concordant with this scenario, Paul (2002) concluded that "the debate on dinosaur energetics is no longer about whether they were tachyaerobic, but how much so, how early, and how well they thermoregulated."

In fact, the mere presence of some dinosaurs at high latitudes that are devoid of other reptiles, strongly suggests endothermic capabilities to cope with colder climates (Paul, 2002).

HIERARCHICAL DEVELOPMENT OF FEATHERS

Accompanying paleontological advances has been our understanding of feather development. Following Prum and Brush (2002), the cylindrical follicle and feather germ are general features that characterize all feathers; therefore they should be considered the defining features of feathers. Feather development proceeds hierarchically through a series of transitional stages, each marked by a developmental evolutionary novelty -- a new mechanism of growth -- in which advances at each stage provided the basis for the next evolutionary innovation.

Examples representing every stage of the Prum-Brush model are thought to exist among the diversity of extant feathers (see Prum and Brush, 2002). The structural gradation between the scutate scales on a bird's tibiotarsus and the feathers on the thigh appear to confirm the thesis that feathers can be regarded as highly modified scales (see Padian and Chiappe, 1998b). Indeed, developmental experiments can transform early avian scales into feather short buds, consistent with the broad homology thesis (Prum and Brush, 2002).

COCKATIELS ARE RELATIVELY UNSPECIALIZED

DNA hybridization and other evidence are consistent with the view that parrots are the descendants of an ancient lineage with no close living relative (Sibley and Ahlquist,

1990). Since parrots reach their greatest diversity in South America (25 genera) and Australia (26 genera), it has been suggested that their evolution took place in Gondwana (Briggs, 2003).

Of the three species studied, relict behaviors appear most prominently in Cockatiels, small members of the Cacatuidae family. Cockatiels lack elaborate courtship displays; nothing about their morphology, appearance, habits, or ecology, suggests a high degree of specialization. Importantly, both sexes are intimately associated with egg and chick care. Relict care components, both those that are spontaneous and those that have been elicited, appear to be conserved from times when eggs were laid at shallow depths or on flat ground in primitive scrapes. Nothing of the origin, evolution, or relatedness of Cockatiels belies the view that many ancestral features are retained.

The habit of nesting in tree hollows, probably the earliest mode of tree-nesting, by Cockatiels and many other Australian parrots (Brightsmith, 2005) may date to tens of millions of years ago (Thomson, 1950). The comparative safety provided by this practice, together with intrinsically conservative brain evolution, and an inability of selection to act on unexpressed behaviors, likely provided a stabilizing influence on many behaviors of tree-hole nesters, and could be partly responsible for retention of very ancient circuitry for relict behaviors in the avian lineage (Kavanau, 1987).

Cockatiels seemingly have retained primitive ground-nesting adaptations to an exceptional degree, with both sexes giving the eggs an extraordinarily high degree of attention. Accordingly, they are ideal experimental animals for attempting to reconstruct these ancient adaptations and their probable sequence of evolution. Interest in this phenomenon derives not so much in the behavioral adaptations, themselves, though some are remarkable, but in broader implications, namely, the accessibility of much ancient neural circuitry, and accompanying potentials for phylogenetic inferences.

POSTULATED STAGES IN MAIN-LINE AVIAN EVOLUTION

Overview

Stage 1. 'Shallow-nesting ancestral theropods:' ectothermic, stepwise clutch assembly, sequential single clutching, solely climatic incubation, ~ 20 eggs/clutch, biparental care, foraging in and near vegetation, access to threatened nests by jumping and parachuting from overhead resting and surveillance sites in vegetation

Stage 2. 'Surface-nesting nonavian theropods:' ectothermic, stepwise clutch assembly, sequential single clutching, sustained, enhanced climatic incubation, ~10

eggs/clutch, biparental care, advancing arboreality, access to threatened nests by jumping, parachuting, and steering from overhead resting and surveillance sites in vegetation.

Stage 3. 'Primitive pro-aves*:'* primitively endothermic (32 -34℃), stepwise clutch assembly, rapid double-clutching, parental incubation of separate clutches, < 10 eggs / clutch, biparental care, advanced arboreality, access to threatened nests by gliding

Stage 4. 'Advanced pro-aves,' (including *Archaeopteryx*); endothermic (~36℃), stepwise clutch assembly, rapid double-clutching, parental incubation of separate clutches, < 10 eggs/clutch, biparental care, advanced arboreality, sustained wing-flapping flight, some nesting in tree hollows and fronds

Stage 5. 'Ancestral birds:' endothermic (~38℃), stepwise clutch assembly by monovulation in multiple episodes, sequential single-clutching, biparental incubation and care, only left ovary in most, improved flight capabilities, tree-nesting widespread

Stage 6. Modern birds: endothermic (largely 41- 42℃), stepwise clutch assembly by monovulation in multiple episodes, largely sequential single--clutching, parental incubation, mostly biparental care, only left ovary in most, modern flight capabilities, tree-nesting and herbivory widespread

Detailed treatments

Stage 1. 'Shallow-nesting ancestral theropods'

Times and identity: Presumptively favorable times and upper weight limits can be suggested. Earliest favorable Mesozoic times for burying eggs at shallow depths would have been in the warm, equable climates of the late Triassic-early Jurassic periods (225 - 175 Myr ago). In most predatory dinosaurs of these periods, an absence of big brains, flight-modified pectoral girdles, arms, tails, and forward-facing eyes (for improved navigation in complex arboreal niches), seemingly owes to the very poor fossil record of small forms. In any event, there is no substantial evidence of avian flight earlier than the middle Jurassic, a period spanning over 17 Myr, and potentially secondarily flightless characters do not become numerous until later Jurassic times (Paul, 2002).

Most small, predatory dinosaurs had scansorial adaptations. To permit some degree of arboreal agility, upper weight-limits would have been in the range of 10 - 20 kg, roughly turkey- to-dog-sized. Size reductions would have followed, as adaptations discussed below. At the time of first achieving flight (that is, becoming sustainedly airborne), size probably was in the range of pigeons,

crows, and gray squirrels (up to 500 g) (Paul, 2002). Although the protodinosaurs from which the group evolved would have been relatively small (< 1 m long; < 1Kg), the earliest theropod of which we have appreciable knowledge is *Coelophysis bauri* of the late Triassic. Having been in the adult range of ~3½ m and up to ~35-45 kg, it far exceeds the size limit for arboreal agility. The "nearly identical" early Jurassic, *Syntarsus,* reached the lesser adult weight of 25 kg (Dodson, 1997).

Some later Mesozoic theropods (Tetanurines) with origins not far removed from *Coelophysis*, continued the "coelurosaurian" tendency toward miniaturization, with great diversification potential. It is among these, with forelimbs strikingly resembling those of birds (exapted for the flight stroke; Padian et al., 2001), that the earliest avian forerunners perhaps are to be sought. However, there is no reasonably complete skeleton of any small, predaceous dinosaur until the late Jurassic, almost 100 Myr after the form most likely originated (Dingus and Rowe, 1998). Small size, and being limited to interior habitats, greatly reduced the probability of preservation.

Equable Mesozoic climates as the key event-- eggs buried at shallow depths -- midday shade: The eggs being buried at depths by earlier theropodan ancestors very likely possessed rigid shells with large pores. For them, relatively deep burial was at, say, 20 - 30 cm; but possibly up to 60 cm (Cousin et al., 1994), with the precise depth of burial being much dependent on substrate composition.

Deep burial gave added security from predators, maintained relatively constant temperature and moisture, and accommodated many eggs (piled or multilayered). Since Mesozoic temperatures in deep nests would have been lower than at the surface, development was slower, and oxygen requirements could have been met under existing conditions of relatively slow gas exchanges.

The key facilitator of the transition from relatively deep to shallower burial (at, say, 10 - 20 cm) of eggs, and eventually to surface nesting, is postulated to have been the warm, equable, greenhouse climates of the late Triassic-early Jurassic. Among smaller reptiles burying eggs at depths, these climates would have brought into play strong selection for egg location at shallower depths and the surface, where higher temperatures would have accelerated embryonic development.

However, shallowness of depth would have been limited by the then high gas conductances of calcareous dinosaur eggshells -- 8-16 times as great as in birds (Moratalla and Powell, 1994). While these high conductances would have benefited embryonic development in deeply buried nests, at higher humidity and typically lower oxygen levels, eggs near or at the surface would have been highly vulnerable to evaporative water loss.

For these reasons, I propose that avian ancestors passed through a relatively lengthy period of shallow nesting

-- at progressively lesser depths -- as selection for lesser eggshell gas conductances occurred. Eggshells would have evolved from basic dinosaurid types, with multi-canaliculate or protocanaliculate, highly conductive pore systems, to basic ornithoid types, with the angusticanaliculate, much less conductive (ratite), pore systems of theropods and birds (Mikhailov et al, 1994).

Eggs buried at depths of ~10-20 cm would have had a key advantage of being re-accessed readily, making it possible for ancestors of stage 1, for the first time, to build-up clutches in more than one ovulatory episode. By allowing lesser egg burdens, this would have been highly adaptive for small theropods in terrestrial-arboreal habitats. After clutch completion, eggs buried in these shallow nests would have been guarded but undisturbed until near term and hatching. Only say, 1/2-sized partial clutches (smaller total size, perhaps about 20 eggs) might have been ovulated concurrently, that is, 5 eggs from each ovary, in two episodes several days apart. With shortened incubative periods, there could have been more reproductive episodes, probably even year-around breeding in some locales.

By this means -- sustained increased incubative temperatures at shallow depths, and increased survival of offspring through nest guarding and close hatching and post-hatching parental care -- a greater reproductive potential could have been achieved. This is the most likely selective pressure for such parental investment by dinosaurs (Coombs, 1989). At first, an increase in egg size, favoring greater survival of hatchlings, would have been adaptive, but selection for smaller eggs would have become pervasive with progressively increasing arboreality (see below).

A change from *en masse* oviposition to stepwise assembly of clutches would have conferred no advantage to large dinosaurs. But for small-bodied theropods, foraging in vegetation, the advantages would have been considerable. As postulated earlier, the key selective pressure differentiating some small-bodied theropodan ancestors of birds from larger dinosaurs that remained terrestrial, probably hinged on body size.

At risk of falling prey to larger dinosaurs and cynodonts, these small-bodied ancestors would have had to seek safe resting quarters during inactive periods that, nonetheless, permitted close surveillance and ready nest access. Sites in overhead vegetation probably were the only feasible option -- an aspect of the proposed 'roots of avian evolution.' A comparable common tendency exists today in ground birds, which seek to elevate themselves from the ground during inactivity to reduce predation risks (Dial, 2003).

The general occurrence of various types of sounds as clutches of shallowly-buried eggs approach term has far-reaching consequences. Without close parental surveillance of nest sites and protection of nests from small egg predators at these times, and subsequent hatching

and post-hatching care, neither shallow- nor surface-nesting would have been feasible.

These constraints also partially account for my proposal of a primitive status for biparental care. Thus, it seems highly unlikely that only one parent could have fulfilled these demanding needs. In another aspect, the needs would have been considerable, because partial clutch assembly at relatively constant temperature might have lengthened the hatching period.

In these postulated circumstances, the presence of suitable vegetation also would have been constraining. Thus, an absence of nearby, safe overhead resting sites would indirectly have limited the shallowness of depth suitable for nests. In some locations, then, shallow- and surface-nesting might have been feasible only for comparatively large reptiles, not in the avian line. In those locations relatively deep nesting would have remained the only feasible option for small reptiles, for whom neither the 'roots of avian evolution' nor eventual flight would have materialized.

Another prerequisite for egg survival at the shallow depths envisioned would have been to locate nests out of direct midday insolation, that is, in midday-shaded areas. Otherwise, overheating risks would have been too great. Looking ahead, virtually every avenue of analysis of circumstances that probably came into play in the postulated progression of main-line avian evolution leads to major roles for arboreality, heights in vegetation, and decomposing and dry vegetative debris.

Practices of female crocodilians provide illuminating, supportive present-day correlates for selective nest placement, even when relatively deep. Nests of American Alligators (*Alligator mississippiensis*) usually are shielded by dense overhead vegetation, and often are located at a tree's base; also true of Nile Crocodiles (*Crocodylus niloticus*). Female American Alligators will dig nests as far as 75 m from the shore, in order to site them in tree shade (Neill, 1971). The critical variable of daily temperature fluctuations in shaded nests of *Crocodylus johnstoni* never exceeds 2°C, compared to 6°C in unshaded nests. The fact that egg-chamber temperatures are near the eccritic value is largely a climate/environmental phenomenon, not a consequence of nest design (Coombs, 1989).

Illustrating the feasibility of favorable nest placement by avian ancestors, many birds orient nests to obtain warmth of morning sun; others situate them for midday or continuous shading; still others minimize wind impact by placement on leeward sides of vegetation or other objects, or exploit cooling winds. Some birds even seasonally reorient nest entrances (Bartholomew et al., 1976).

Nest surveillance and guarding; influences of insectivory: For reasons stated above, powerful selection would have favored descendants of theropods burying

eggs at shallow depths in midday shade. However, no gain would have been achieved by accelerating development and shortening vulnerable periods, if accompanying risks occasioned by shallow burial were increased excessively. So, theropods benefiting most from such practices would have been those that reduced risks through virtually continuous, close, nest-site surveillance.

Only small-bodied, ancestral theropodan pairs that foraged 'near' their shallowly-buried nests could have maintained close surveillance, protected the nest, and insured integrity of its overlying protective cover. Close surveillance would have been crucial for shallow nests, with sometimes noisy occupants, located predictably near vegetation in midday shade.

Nest-guarding by female crocodilians also is of interest in these regards: the nests, themselves, and their near vicinity, are the foci of female defense behavior; attacks commonly are discontinued once the female reaches the nest (Coombs, 1989).

Having chosen a shallow site, built up, and buried the clutch, females would have been first, within a given reproductive episode, to maintain surveillance and care of the nest. But selection would have favored the offspring of pairs in which the males joined earliest in these activities. This is another of the bases for proposing monogamy and biparental care at this earliest departure of theropodan ancestors from deep nesting. Indeed, monogamy and biparental care occur in over 90% of living birds. This, alone, raises the likelihood that these traits are plesiomorphic, that is, that they are primitive to the theropodan ancestors of birds.

However, even if male care of shallowly-buried nests could somehow have been dispensed with, male assistance in hatching (even of superprecocials) and both hatching and post-hatching (of precocials) probably would have been needed (see above and below). In any event, male participation in both nest and chick care would have been obligatory with the use of surface nests. But at a non-excessive energetic cost, the practices discussed above would have been feasible only for theropods for whom adequate prey existed in the nest vicinity, near enough to allow the needed close nest surveillance. Smallest theropods would have been favored, since they could have subsisted in the smallest foraging regions.

The onset of warm, equable climates also would have provided highly favorable environments for large insects, which existed in great abundance through much of the pertinent times. This is an important consideration because, in all likelihood, these small theropods were largely insectivorous.

Inasmuch as free claws of early birds' hands suggest bush-, shrub-, or tree-climbing, it is probable that their near ancestors were scansorial as well (Norberg, 1990; Zhou and Farlow, 2001). Theropods were well equipped for snaring insect prey with sideways-flexing wrist joints,

making possible sudden rotating and whipping forward of the hand (Padian and Chiappe, 1998a, b), part of a predatory stroke from which the flight stroke may have evolved (Padian, 2001).

Multiple quick body movements, including springing, to capture small prey, particularly from tree trunks and branches, often would have been followed by descent trajectories from increasing heights. This would have increased selection for drag-increasing integumentary modifications that lessened the likelihood of injury. With the gradual perfection of such foraging capabilities, this selection would have become increasingly significant.

Shallow burial -- terrestrial-arboreality -- territoriality: Considering small-bodied theropods that buried eggs at shallow depths in midday shade, not only would access to vegetative heights have provided safe, near vantage points for nest surveillance and ready nest approach, terrestrial-arboreality would have made the resource region more defensible, both by expanding it vertically into vegetation, and contracting it horizontally.

Rapid direct descents from vegetation that strongly selected for increased integumentary drag also would have favored increased insulative modifications, leading to the comparatively rapid beginnings of evolution of feather-like structures. Insulative selection would have increased because windiness usually increases at greater heights by day and, most particularly, because presence at heights at night would have entailed exposure to cooler air.

Foliage has far more hiding places and food for insects, large and small, than bare ground (Viohl, 1985), making it a little tapped resource for sharp-sighted vertebrate insectivores. Small insects and habitat complexity favored small, quick and agile theropods, capable of moving among small limbs, where they could flush insects from hiding.

Acute vision also appears to have been possessed by small theropods, judging, for example, from *Coelophysis* skulls. Large orbits, surrounded by sclerotic ossicles (also seen in *Archaeopteryx*), suggest large eyes, accommodation, and resistance to deformation, conferring very acute vision and perception (Colbert, 1995; Paul, 2002; Dominguez Alonzo et al., 2004).

Arboreal habits, in and of themselves, result in strong selection for reduced body size, and clutches of smaller and/or fewer eggs. Smaller eggs and clutches also would have facilitated maintenance of needed surface uniformity above shallowly-buried eggs. Small body size allows support by smaller branches, reduces terminal speed of free fall with limbs spread, etc. (see Kavanau, 1987:590-593).

Together with selection for agility and lesser weight in arboreal habitats, by virtue of lesser clutch burdens, selection for smaller eggs also would tend to lead to adult size reduction. Increased oxygen demands, occasioned

by climbing in vegetation, may account for part of the putative increased respiratory efficiency of bird-like theropods (Paul, 2002).

Selection for ancestral theropods that home based hunting in the vicinity of shallow nests and vegetation, and repelled potential small egg-predators therefrom, would provide a basis for the origin of territoriality, also exhibited by male crocodilians during the mating season (Coombs, 1989; Magnusson and Lima, 1991).

But a male's remaining in the vicinity of the nest presupposes monogamy and some degree of post-ovipositional mate consortship. Terrestrial-arboreality, coupled with male territoriality, provides a likely means of achieving this. It would have been accomplished by females depositing eggs in their mates' relatively closely circumscribed territories, and remaining there, participating in nest guarding and hatchling care (amounting to territoriality of females, as well). In a comparable example, the male Dwarf Caiman, *Paleosuchus trigonatus*, is strongly territorial, with the smaller female's home range contained within his (Magnusson and Lima, 1991).

Implications of nest-site surveillance for care of young: Achievement of the above-described stage also has implications for the evolution of offspring care. Unlike circumstances for many reptiles that bury eggs at depths, and take no part in hatchling care, it would have been adaptive for parents maintaining close surveillance of shallowly-buried nests, also to tend to basic needs of hatchlings.

At first, this would have included digging out buried, hatching eggs, assisting in hatching and, probably, hatchling grooming, most of which even crocodilians accomplish today. As noted earlier, such actions would have been crucial because of the sounds emitted by young at, or nearing, full-term. Moreover, full-term young likely employed hatching calls, which apparently have remained a universal feature among crocodilians. They are the necessary and sufficient releaser of the nest-opening response by the male or female parent, though usually the latter.

By synchronizing hatching, such vocalizations promote hatchling survival. Crocodilian vocalizations, which can occur many hours before hatching, increase in frequency, intensity, and complexity as hatching approaches (Ewert, 1979; Coombs, 1989). Many incubating avian parents are highly responsive to such pre-hatching vocalizations (Drent, 1975; Kavanau, 1987).

Post-hatching care might well have lasted several days, and constituted a pre-adaptation for closer parental care of the eggs and nests in the following postulated surface nesting of Stage 2. Post-hatching care of young likely consisted of protecting and, probably, escorting in crèches (juvenile crocodilians are spontaneously gregarious; Coombs, 1989) to facilitate food acquisition.

The best evidence for such ancestral parental care comes from much later Cretaceous times, in a dinosaur not in the avian lineage (see Meng et al., 2004, and below).

To this juncture, except for the relic, "leaving eggs at lights-off, with immediate return at lights-on," my proposals for early avian evolution have been based mostly on known behavior and physiology of reptiles and birds, on their implications for clutches buried at shallow depths, and on paleo-findings. For the succeeding postulated evolutionary stages, however, I rely extensively on relict breeding behaviors, paleoclimatology, and paleoecology.

Stage 2: 'Surface-nesting nonavian theropods'

Fossil record and general considerations: Dinosaurian fossil records are notoriously incomplete (Horner et al., 1992). Most familiar fauna were inhabitants of warm, lowland areas with lush vegetation and numerous streams, swamps, and lagoons. Most of the fossil findings that might be pertinent to breeding practices of the 'surface-nesting nonavian theropods' of this stage are for dinosaurs that are not in the avian lineage, or date to much later times than the late Triassic, including fossils considered here to be those of secondarily flightless birds. In view of the relative paucity of information, all breeding practices judged to be pertinent are taken note of, beginning with dinosaurs not in the avian lineage.

Late Triassic remains of nests and eggs that might give clues to breeding practices of the postulated Stage 2 'surface-nesting nonavian theropods' are fragmentary. In the oldest dinosaur nest from those times, eggshell fragments and hatchling skeletons of prosauropods, *Mussaurus*, were found, without evident nest type or egg arrangement (see Moratalla and Powell, 1994). This finding suggests that nest building and, possibly, parental care were already developed. Other pre-Cretaceous prosauro-pod findings included an early Jurassic clutch of 6 partial eggs and associated juvenile bones (Moratalla and Powell, 1994).

Most convincing evidence of post-hatching dinosaurid parental care comes from recent discoveries in Liaoning sediments (Meng et al., 2004). A single adult ornithischian dinosaur, *Psittacosaurus sp.* (also not in the avian line) was found clustered with 34 remarkably complete and undisturbed juveniles, all of the same size and same body attitude. All retained articulated, 3-dimensional form in upright, lifelike postures.

Occurring predominantly in late Cretaceous strata were nests and eggs of oviraptorids, considered here to be secondarily flightless. These were in fairly good condition, but only few species were represented (Carpenter and Alf, 1994; Moratalla and Powell, 1994). On some occasions, such as might have materialized in quickly developing sandstorms, rapidly buried, articulated adult

specimens were preserved with nests and eggs. Four out of 17 of these specimens were in positions indicative, at the least, of protecting the partially-buried eggs (e.g., sitting atop a clutch with their axial skeletons lodged in the space in the clutch center, devoid of eggs). This occurred with eggs and adults of toothless maniraptorans, including *Oviraptor philoceratops* and *Citipati osmolskae,* in Gobi redbeds. These tended to be much larger than those of the postulated much earlier Stage 2 ancestors (Norell et al., 1994, 1995; Dong and Currie, 1998; Clark et al., 1999; Grellet-Tinner et al., 2006).

From 22 to 30 elongate, angusticanaliculate, ornithoid-ratite type, slightly-tapered eggs usually were laid in pairs. These lay horizontally or subhorizontally, with the slightly more tapered pole slightly tilted toward the nest center -- devoid of eggs -- in up to three superimposed layers. This distribution suggests production and laying of single egg pairs (Norell et al., 1995; Dong and Currie, 1998; Clark et al., 1999; Grellet-Tinner et al., 2006). Except that only one egg typically is laid now, this accords with a secondary flightless origin of oviraptorids, probable offshoots of Stage 4 or 5.

Eggs lay in tightening circles from bottom to top, so that covered nests would have formed mounds, suggesting parental manipulation (Dong and Currie, 1998). The existence of these multilayered egg clutches, putatively forming mounds, suggests that some seasonal late Cretaceous climates and nest locations were favorable for embryonic development without parental incubation. Also, that beyond guarding (say, sitting atop), the nest-mound received minimal pre-hatching attention. An embryo in an egg in one such nest had its head tucked near the knees, with bones nearly fully ossified, indicating precociality (Norell et al., 1994, and below).

The above conclusions concerning egg-laying practices are supported by the finding of a pair of shelled eggs within the oviducts of an oviraptorosaurian specimen from late Cretaceous deposits in Jiangxi Province, China (Sato et al., 2005). It is unlikely that more than one pair of shelled eggs at a time could have been held within the specimen's body. Accordingly, it was concluded that each of the paired oviducts simultaneously produced a single egg (monoautochronic ovulation), with multiple laying needed to complete a clutch. Similar conclusions were reached by Chen et al. (1998) concerning a pair of eggs within the body cavity of their exceptionally well preserved specimen of *Sinosauropteryx prima*.

A question of great interest pertains to egg aerial exposure, as altered by cover. In the case of an oviraptorid parent and nest, Dong and Currie (1998) suggest that the center of the nest had been filled with sand (presumably to take the weight of the protectively-brooding, parent), and that the eggs were probably not buried when sat upon. Coombs (1989) asserts that decomposing vegetation probably covered all dinosaurid eggs, and that the common presence of un-

stratified fill suggests that most, if not all, Mesozoic dinosaurs partially or completely buried eggs at one time or another during development.

Partial burial in soil assured that the eggs would not be moved, and could receive direct parental contact, probably being incubated by a combination of both (Horner, 2000). Although Varricchio et al., 1999) know of no evidence for vegetative cover of *Troodon* eggs, such cover cannot be ruled out (Carpenter, 1999).

Troodon formosus, a medium-sized (40-50 kg) coelurosaur was discovered in association with eggs, eggshell fragments and nests in late Cretaceous strata of North America (Varricchio et al., 1997, 1999). The largest clutch, within a rimmed bowl-shaped depression (1 x 1 m), contained up to 24 eggs. These were paired (best seen in bottom views, because of close-packing at the top) and standing vertically at a slight angle with their blunt (air-cell) end uppermost, and inclined toward the clutch center. In one nest, an adult lay in contact with at least 10 unhatched eggs. These eggs likely were incubated using both contact with soil and body heat (both parents may have brooded). But even when nest covering was employed in Stage 2, it is not proposed that cover was present at all times.

Troodon young apparently were precocial (established from embryonic bone; Ricqlés, 2001) like those of oviraptorids, receiving no post-hatching nest care. Varricchio (1997) noted that several features of troodontids showed close relationships with birds, but he did not entertain the possibility of troodontids being secondarily flightless.

Troodon is thought to have nested in dry upland habitats that probably experienced wide daily temperature fluctuations. Their nests were spaced at distances suggesting colonial nesting and careful tending of eggs (Horner and Gorman, 1988). The similarity of the paleoenvironments of *T. formosus* with those of pluvianids (including Egyptian Plovers; Howell, 1979) today, coupled with nest structures and clutch arrangements that resemble each other, suggest that *T. formosus* could have engaged in nesting and incubative behaviors similar to those of pluvianids (Grellet-Tinner et al., 2006). *T. formosus* young (originally misidentified as *Orodromeus* (see Varricchio et al., 1997), though precocial, apparently grew to ~1/2 adult size before leaving the nest vicinity (Horner, 1994), though they left the nest, itself, soon after hatching (Varricchio et al., 1997).

A well preserved nest of about 12 therizinosauroid eggs (~ 70 x 90 mm) was found in sediments from the earliest of the late Cretaceous (75 Myr ago) of the Nanchao formation in the Henan Province, China. Some of the eggs contained embryos at least 67% developed. These had well-to-exquisitely preserved bones and teeth and remnants of what seem to be soft tissues, such as cartilage, muscle, and possibly skin. The hatchlings doubtless were superprecocial and able to chase down prey and consume suitable plants (see Pannisi, 2004).

Teeth of the youngest embryos resembled those of other theropods, while those of the oldest had achieved greater similarity to those of herbivores.

The early Cretaceous therizinosaur, *Beipiaosaurus inexpectus*, is known to have had integumentary feather-like structures similar to those of *Sinosauropteryx* (Xu et al., 1999). Though their implications for late Triassic-early Jurassic Stage 2 avian ancestors may be limited, these findings also are consistent with therizinosaurs being secondarily flightless.

Troodontids are perhaps the most convincing example of Cretaceous secondary flightlessness; accordingly, it is appropriate to elaborate further on their properties that are indicative of, if not actually confirming, their descent from flying ancestors. Conventionally, these are regarded as pre-adaptations for flight that originated among theropods (see Grellet-Tinner et al., 2006). Thus, Troodontids had the largest relative brain sizes (encephalization quotient of 5.8) of dinosaurs, in the range of living birds (Barsbold, 1997). In view of the highly conservative nature of vertebrate brain evolution, already noted, many would regard this finding, alone, to be persuasive evidence of troodontid secondary flightlessness.

Buttressing this conclusion, troodontids also possessed very thin-walled, fragile bones, forwardly-directed, exceptionally large eyes (Fiorillo, 2004), laterally-placed optic lobes, and many sharply pointed, cusped teeth, suggesting the partial retention of insectivory (Varricchio, 1997). In still a further indication of secondary flightlessness, *Mei long*, a 53-cm-long subadult troodontid, presumably buried while sleeping or resting, was in a 'life posture' identical to the stereotypical 'tuck-in' sleeping and resting posture of many birds (Xu and Norell, 2004).

Moreover, significant differences in polar size and shape of eggs of *T. formosus* (creating a marked polar asymmetry, as opposed to being merely tapered) indicate the presence of a fully developed air cell like those of modern birds. Additionally, in contrast to other known theropods but similar to modern birds, troodontid eggshells lack surficial ornamentation (Grellet-Tinner et al., 2006).

Mesozoic fossil avian eggs and embryos: Until recently, Mesozoic fossil avian eggs were extremely rare. Two kinds associated with embryos were known only from late Cretaceous Gobi sites (Mikhailov, 1992). An ovoid type belonged to the neornithine, *Gobipipus*. The other, symmetrically ellipsoidal, is attributed to an enantiornithine, *Gobipteryx* (Chattergoo, 1997).

The following Phu Phok fossil eggs are included here because they match the egg size of small extant passerines and display avian characters in their oval shape and eggshell microstructure. Recently, Buffetaut et al. (2005) found four very small, goldfinch-egg-size (1.15 cm^3), fossil eggs in an early Cretaceous outcrop of red rocks in Phu Phok, northeastern Thailand, While the eggs' surficial ornamentation is typical of 'non-avian' saurichian dinosaurs, the 3-layered prismatic structure of its eggshell is known only in extant and fossil eggs of birds. The authors suggest that the eggs derive from a very small, feathered maniraptoran similar to the theropods from the western Liaoning Province of China, considered here to have been secondarily flightless birds.

One of the Phu Phok eggs contained a theropod embryo encased in calcite. No theropod egg clearly associated with skeletal material displaying such a minute size had previously been discovered. In other such known fossil associations the eggs do not possess the typical avian oval shape caused by a fully developed air cell at the large end, or the 3-layered shell typical of Mesozoic and modern birds (Buffetaut et al., 2005).

Dozens of well-preserved, small (lesser volume than *Gallus gallus* eggs) asymmetrical avian eggs were found in late Cretaceous, non-marine sandstone units in Neuquén, City, Patagonia, Argentina (Schweitzer et al., 2002). A described egg contained partially articulated or minimally displaced embryonic bones, allowing the first unequivocal assignment of prismatic trilaminate eggshell structure found in extant neognathes to a basal avian lineage.

The remains are phylogenetically bracketed between the two avian nodes Ornithothoraces and Ornithuramorpha, for the first time allowing the association between the morphology of avian Mesozoic eggs and a particular clade of basal birds. All indications are that the extinct bird that laid these eggs had similar nesting practices to extant birds and a modern avian reproductive system.

The oldest, best preserved avian embryo is a feathered precocial, enantiornithine-like fossil in its final developmental stage, in early Cretaceous Liaoning shale (Zhou and Zhang, 2004).

Ancestral pre-incubative practices and Cockatielian behavior: The transition to Stage 2, probably dates to the late Triassic-early Jurassic in times of limited seasonality, universally warmer than today. In this enduring favorable climate, it would have been adaptive to achieve 'open' surface-nesting, as soon as eggshell gas conductances precluded excessive water loss (basic ornithoid types). As an extreme example of 'open' nests, those of ratites are simple ground depressions, or a patch of flattened vegetation (Coombs, 1989).

In those climates, more rapid embryonic development would have been achieved by maintaining the temperature of the eggs in the eccritic range throughout the day and night, using protective and warming cover as needed. Cover at different times would have consisted of either dry or decomposing vegetative debris, or the shading or shielding parental bodies, as described below. These various covers commonly are used today.

At this surface-nesting stage, one expects sequential laying of multiple clutches per season, probably year around (crocodilians also may lay clutches sequentially; Ferguson, 1985). This practice would have taken full advantage of the prevailing climates, and more rapid embryonic development, facilitated by the close, 24 h, parental egg care. Egg laying every 2 or 3 days, would have built up clutches of about 10 eggs. Relative to Stage 1, there would have been advances in hatchling and nestling care, in arboreality, in insectivory, and in accessing threatened nests by jumping, parachuting, and steering from nearby overhead resting sites in vegetation.

The most revealing, and probably the most ancient, of the relict egg-care responses is, "leaving eggs at lights-off, with immediate return at lights-on." This, and the relic discussed below, occurred most consistently among hens of Cockatiels in pre-incubative and early post-incubative breeding. The behavior is identified with ectothermic stages, when the eggs putatively were either shallowly-buried without nighttime care, or kept warm at night by a layer of decomposing vegetation. Sometimes Cockatiel hens only perched inside the nest box, or nearby, outside, in the male's company. The latter behavior is consistent with the proposal that during inactivity in Stages 1 and 2, both parents maintained nest surveillance from safe, nearby overhead sites.

Another relict behavior, probably dating to Stage 2 (observed both in open nests and nest boxes with transparent side panes), was the strong disinclination of attending birds to leave eggs exposed in 'daylight,' in circumstances in which they left them readily in darkness. They tenaciously stood or crouched over them. As discussed below, this behavior probably served to shield eggs from direct midday insolation and view, still the habit of many birds in hot environments (Welty, 1982; Kavanau, 1987, under "egg care"). It also would have allowed exposure only to low-angle, early morning and late afternoon insolation.

Only after laying the third or fourth egg, do small parrots begin to incubate at night. Peach-faced Lovebird and Budgerigar hens, when not yet incubating, also sit only loosely on exposed eggs in open nests or "transparent" nest boxes, through much or all of daytime periods. This begins at "lights-on" and ends at "lights-off." Many other species also begin incubating with the third or penultimate egg and show comparable pre-incubative behaviors (Eisner, 1961; Mead and Morton, 1985).

Before Cockatiels came into breeding, a supplied egg usually evoked great interest. It might have been touched and moved about, tucked under the breast momentarily and even competed for, but usually was not relocated to a former incubative area, shielded, or guarded. Apparently physiological conditions had not yet attained a lowered threshold for activation, or disinhibition, of neural circuitry for the latter responses. But once Cockatiels had begun to court and mate, neural circuitry and ovarian secretions

for the next stage of egg care had begun to be mobilized. Then, fostered eggs exposed to light were shielded and guarded by day, but abandoned at night.

Reconstructing egg care: The transition from shallowly-buried to 'surface' nests is thought to have increased reproductive potential, driven mainly by selection for shorter periods of embryonic development, brought about in clutches of fewer eggs kept at higher average temperatures 'around the clock.' With embryonic periods more closely circumscribed, egg vulnerability would have been less, and parents also would have had greater control over egg exposure. The behaviors associated with the transition to surface nesting probably can be reconstructed from current practices and the reviewed relict behaviors (Kavanau, 1987, and above).

Consider, first, the most likely route for nighttime egg care using surface nests. Relict behavior of the three species studied implies nighttime departure from the vicinity of buried or surface nests ("leaving eggs at lights-off, with immediate return at lights-on"). During nightly absences from surface nests, it would have been adaptive to cover eggs with a shallow layer of decomposing vegetative debris, say about an hour before sunset. Such cover would have concealed eggs, provided a source of heat, retained heat already absorbed and produced metabolically, and insulated eggs from cooler ambient air. This postulated practice assumes that eggs at this stage were of a basic ornithoid type, with low gas conductive pore systems; otherwise the gaseous environment of decomposing vegetation or microbial respiration would have been unfavorable for developing eggs exposed to it for the night.

In the morning, eggs would have been uncovered about an hour after sunrise. A camouflaged parent would have begun to shield them from overhead view, allowing only low-angle insolation (recall the relic, "strong disinclination to expose eggs in light"). Both parents could have foraged during the hour before sunset, and dusk (after eggs were buried), and during dawn and the hour after sunrise (before they were uncovered). These are favorable foraging times, with flying insects out in great abundance (Pough, 1973).

Covering and uncovering eggs in surface nests with sand, soil, down, or plant matter at certain times of 24 h cycles, are common practices (Maclean, 1974, 1976; Skutch, 1976; Howell, 1979). Although crocodiles are not surface nesters in the sense considered here, since they do not cover and uncover their eggs daily, their ecology and reproductive habits provide the best comparable egg-care examples. In today's less favorable circumstances for vegetative decomposition than in past times (Smart and Hughes, 1973), these processes raise the temperature 1 - 5°C, compared to the mean in ambient air (Ferguson, 1985).

Parental daytime care: Eggs could not simply have been left covered with decomposing debris during the day, as they would have overheated. At some time in the early morning, as ambient air temperature rose, effects of the combined heat would have exceeded eccritic values. If the decomposing debris were removed early in the morning, and replaced by dry debris, ambient heat could not have kept the eggs sufficiently warm. At this time, exposure to relatively low-angle (15 - 30°) insolation, as adjusted by parental shielding, could have provided a heat buffer, supplementing the gradually increasing ambient heat, to maintain the eccritic temperature. Precisely this need for the warmth of the morning and evening sun has long been suggested as one reason for the open nests of small birds in cool and temperate climates (Collias and Collias, 1984).

The same events, in reverse order, could have occurred in late afternoon, before covering eggs for the night. Of course, to receive relatively low-angle insolation in early morning and evening, nests would have had to have line-of-sight exposure then, with low-lying peripheral surface vegetation giving partial cover to an attending, camouflaged parent.

Parental alternation in midday foraging and shading: As noted above, for surface-nesting ancestors to benefit fully from favorable climatic conditions, and higher average incubative temperatures -- mindful of contemporary widespread practices (Drent, 1975; Kendeigh et al., 1977; Howell, 1979) -- it is suggested that nests were not located in cooler shaded areas during midday hours. But to prevent overheating at these sites, body shading of the eggs would have required the alternate participation of both parents, another basis for proposing primitive biparental care.

Just as today, prolonged direct exposure on clear days at low and medial latitudes would have been intolerable for a single parent, even if initially possessing primitive integumentary insulation. Even for nest-guarding crocodilians, with their great heat capacity, nearby shade is thought to be important for thermoregulation (Coombs, 1989). The cost of such close egg attention as midday body shading probably would have been more than offset by the benefits of shortened reproductive periods, greater flexibility of care, and protection from egg predators.

Close alternate attention to eggs during hot midday hours is the strategy employed today by some open-nesting birds, such as Dusky Flycatchers, *Muscicapa adusta* (Morton and Pereyra, 1985), and Gray Gulls, *Larus modestus* (Collias and Collias, 1984). Such close attention to eggs in surface nests by Stage 2 ancestors would have had antecedents in the guarding and periodic checking of shallowly-buried nest sites in Stage 1, essential for the survival of term and near-term young. In certain intervals between midday heat, and mid-morning and mid-afternoon periods of lesser warmth, air temperatures would have been at or near eccritic values.

During nest absences at these times, eggs could have been concealed with dry debris or soil and uncovered on return, the practice of many ground-nesters today (Maclean, 1974; Skutch, 1976). A relict behavior of a Lovebird hybrid also strongly suggests that covering eggs with debris during absences was a component of egg care by Lovebird ancestors. On four occasions when a single egg was laid, a hybrid hen merely covered it with nesting material, without incubating it (Buckley, 1969). This was never observed in my pure-bred birds. It appears to be a relic of earlier protective egg care of surface-nesting ancestors (some relics are expressed most readily in hybrids; Buckley, 1982).

Early ancestral surface nesters carefully attending eggs probably would have assisted hatching, followed by protection, grooming, confinement of unescorted young to the nest site, and some few days of provision of food or escorting to feeding sites. These proposed methods of ancestral parental care are moderate measured against comparable, demanding parental practices of many birds in harsh climates (Drent, 1972; Freeman and Vince, 1974; Maclean, 1976; Zerba and Morton, 1983).

The earliest evidence of lengthy parental care of dinosaur hatchlings comes from the body proportions and poorly developed dentition of articulated embryos of the early Jurassic herbivorous prosauropod, *Massospondylus carinatus* (Reisz et al., 2005), again not in the avian line.

Selection for feather-like integumentary structures and feathers: With achievement of Stage 2, the most powerful selection for integumentary adaptations would have come into play. These were the continuing ones for greater drag and heat retention of Stage 1, but they also would have included the crucial selection for midday heat-shielding from insolation. Taken together, I suggest that these selections accelerated the evolution of integumentary adaptations that led to feathers, and facilitated endothermy and flight.

Such selective pressures have been discussed and debated in great detail elsewhere (see Chapters in Hecht et al., 1985; Paul, 2002; and papers cited earlier in "Ectotherms or endotherms?"), and need no further elaboration. This also holds for comprehensive treatments of flight origin, and pros and cons of cursorial and arboreal theories (e.g. Chattergee, 1997).

Stage 3: 'Primitive pro-aves'

Marked changes in transition to 'primitive pro-aves': These changes consisted of:

(a) Achievement of primitive endothermy;
(b) Increased arboreality and arboreal agility;
(c) Improved aerodynamic and insulative properties of feathers; and progression to gliding;

(d) Transition to rapid double-clutching, including incubation by body heat, with one clutch cared for by each parent, and with close egg contact throughout the night and much of the day; and

(e) Return to nesting in midday shade.

Acquisition of primitive endothermy also implies increased nutritional needs and foraging specializations, enlarged memory capacity, advanced information processing, and independent regulation of brain temperature (for detailed treatments, see Kavanau, 1987:554).

More extensive arboreality, with gliding, would have been accompanied by further integumentary specializations – already modified for heat shielding and retention, and greater drag -- for improved aerodynamic properties, and still further retention of body heat, facilitating the higher metabolic level of primitive endothermy. Increased arboreal agility would have been associated with lesser egg burdens -- probably only two ripening eggs every other day. Although probably of some use in taking terrestrial prey, gliding, with its limited maneuverability, probably was used primarily for transportation, conferring flexibility in selecting landing sites (Moody, 1962).

Hatchlings putatively had down and a greater, though still relatively low, rate of growth -- presumed ancestral conditions for modern birds (Starck, 1993). Such hatchlings usually require a parental heat source at night, during inclement weather, and from which to venture for exercise and foraging on readily procured food. They also require brooding until full thermoregulatory abilities are established, and usually do not fly until almost full grown (Skutch, 1976; Welty, 1982).

Endothermy, incubation, and rapid double-clutching: As noted above, the extreme reluctance of incubating Cockatiel mates to surrender eggs to one another, the equally great tenacity of the incoming bird to acquire them, and the easing of this conflict by lengthily splitting the clutch, strongly suggest the occurrence of times when each parent incubated a separate clutch; otherwise the observed extreme tenacity would have been decidedly counterproductive. In the continuing favorable climates, rapid double-clutching probably began directly upon acquisition of primitive endothermy and was facilitated by the great adaptability of ovarian function.

In a presumptive relic of this stage in another species, both Egyptian Plover mates prepare nest scrapes, but only one is adopted (Howell, 1979). The scant early avian paleontological evidence that bears most closely on this matter is indirect and weak. Thus, the even sex distribution of *Confuciusornis* fossils (see Paul, 2002) suggests that both parents attended nests. Also, many avian mates split fledgling broods, reducing chances of entire broods being lost through predation (Skutch, 1976). Pervasive selection along any channel that favors increased avian reproductive output is well known (Emlen

and Oring, 1977; Clutton-Brock, 1991; Ligon, 1999; Deeming, 2002), and is one of the bases for the postulated adoption of rapid double-clutching in the earliest circumstances that were permissive.

One can assume that care of incomplete clutches, and subsequent incubation in Stages 3 and 4 of 'pro-aves' bore many similarities to extant rapid double-clutching practices, with incomplete clutches being shallowly covered with debris and protected. An increase in reproductive potential would have accompanied the considerably greater rate of egg production at the sustained higher core temperatures (32 - 34°C), with the likelihood of accommodating more reproductive episodes per season. Rapid double-clutching assumes very productive habitats, with abundant food supplies (Coombs, 1989), in this instance including large flying insects, such as prevailed through much of the Mesozoic.

More eggs accommodated: With parental incubation:

(a) Eggs needed to be readily accessible and required greater protection; and

(b) Numbers of eggs cared for by a parent -- determined by physical constraints of body size and need for readily concealable nests -- would have been lesser. But with two separate clutches, more total eggs could have been accommodated.

Guided by putative phylogenetic stages in the growth, ripening and atresia of follicles of Budgerigars, a progression of from up to 10 eggs, in Stage 2 nests, to 6 - 9 eggs in each of two clutches in Stage 3, is suggested (Kavanau, 1987, and above). With each parent caring for half the eggs: (a) incubative efficiency would have been high (fewer eggs generally require shorter incubative periods) (Skutch, 1957; Welty, 1982); (b) each nest's eggs would have been safer from predators than if all eggs were together, since they would have occupied less space and been more readily concealed. Nest care by only one adult also tends to render nests less conspicuous (Skutch, 1976).

The male would have taken over sole care of the first clutch, while the female went on to lay and attend to the second. It would have been adaptive for mates to nest within mutual sight, and to tend to depart in alternation, with the remaining parent watching over both nests. Yellow-wattled Lapwings, *Vanellus malabaricus,* for example, maintain lengthy vigilance over unattended nests after sunrise (Drent, 1972), while males of many species guard nests from inconspicuous nearby perches (Freeman and Vince, 1974; Welty, 1982). Shared vigilance also may be a basis for colonial nesting in hole-nesting crocodilians (Coombs, 1989).

Shifting nest sites to shaded locations: With achievement of a primitive grade of endothermy, and greater independence from climatic heat, it would have become adaptive to locate nests in locations where midday body-shading was unnecessary. Eggs would have been incu-

bated during midday periods only when ambient temperatures were below the eccritic range. Within the range, they would have been concealed while parents foraged.

With core and incubative temperatures at the primitive endothermic level, relatively long nest absences would have been tolerated. However, more parental attention would come to be needed in the 'advanced pro-aves' of Stage 4, with their higher core and incubative temperatures (~36°C).

Many birds forage during periods of sufficient warmth, such as Great Tits, *Parus major,* and Field Sparrows, *Spizella pusilla* (O'Connor, 1984). The Australian Dotterel, *Peltohyas australis*, conceals eggs for long warm periods, but incubates them in cool weather (Maclean, 1968). Egyptian plovers warm the eggs at night but cool them by day with water carried in their plumage (Howell, 1979).

To survive in the Mesozoic milieu, clutch concealment would have been essential during absences, even with mates keeping watch nearby. This would have been facilitated by very simple, unstructured scrapes or hollowed-out nesting sites that would have been inconspicuous after egg concealment with light cover. For example, Egyptian Plovers level their shallow scrapes with sand (Howell, 1979).

Stage 4: 'Advanced pro-aves' (including *Archaeopteryx*)

The transition from 'primitive pro-aves' to 'advanced pro-aves' would have involved further advances in endothermy, insulative and aerodynamic feathers, size reduction, and further invasion of aerial niches. Activity therein would have included gliding and sustained, low-amplitude, wing-flapping flight of limited range. Nesting in tree-hollows and among fronds probably began in some lines.

Accompanying these changes, one anticipates an increase in relative brain size, with enlarged visual centers and coordinated changes in other brain regions associated with movements, together with expanded auditory and spatial sensory perception in the inner ear canals and other structures that coordinate head and eye movements. For *Archaeopteryx*, relative to maniraptorans (the latter also showing a trend toward brain enlargement and laterally separated optic lobes), one finds a stage further towards the modern bird pattern necessary for flight (Dominguez Alonso et al., 2004).

Another significant matter for 'advanced pro-aves' relates to habitat resources, namely the greatly abundant, rich, little tapped, source of animal proteins, the large flying insects. Of these, members of the Coleoptera, Diptera, Hemidiptera, and Tricoptera, at least, were present during the middle Mesozoic (Smart and Hughes, 1973). It is almost certain that *Archaeopteryx* was insectivorous, based on possession of moderately-to-very-sharp, stout, peg-like, conical teeth, adapted for piercing and crushing prey swallowed whole. An increasing reliance on insect prey is consistent with progressive size reduction in early avian evolution, as prey and predator size among vertebrate carnivores correlate positively (Gittleman, 1985).

More rapid egg production: Concerning the rate of egg production, ovarian function displays tremendous adaptability and potential for alterations in virtually all quantitative aspects (even influenced by diet, alone), largely independently of genetic control. Ovarian function is highly responsive to both external and internal environmental influences, as mediated by endocrine and neural control (Breitenbach et al., 1963; Gilbert and Wood-Gush, 1971; Ricklefs, 1974; Vitt and Price, 1982). Any simple, adaptive alteration in ovarian function that exists today, probably also was accessible to these avian ancestors.

Increased core temperature and metabolic rate would have supported more rapid egg production, making clutch assembly possible by laying of single eggs daily from alternate ovaries. Thereby, the maximum encumbrance of gravid 'advanced pro-aves' would have been only one ripening egg. This capability would have been selected for to achieve lowest feasible wing load-ing. The energetically highly demanding shell-deposition, a period ill-suited for other activities, would have peaked during nightly rest, with laying in the early morning -- now the common practice (Gadgil and Bossert, 1970; Ricklefs, 1974; Feare et al., 1982).

The evolutionary transition to 'advanced pro-aves' would have followed in the same adaptive trajectories that led to 'primitive pro-aves.' Partial clutches would have been given essentially the same degree of pre-incubative care in Stage 4 as in Stage 3, beginning at the time of laying. Today, one or both parents care for partial clutches to varying degrees (Maclean, 1968; Hildén, 1975; Bergstrom, 1985). The male's paternal 'urges' would have waxed following the laying of each egg of the first-clutch, until the completed clutch would have received the full pre-incubative Stage 3 care.

After the male's egg-care behavior and possessiveness had peaked, the female need merely have continued to oviposit nearby (within sight). Before incubation, eggs would have been concealed with dry debris at temperatures characteristic of non-incubative care. Incubation in both Stages 3 and 4 probably did not begin until after completion of the second clutch.

It would have been adaptive for pairs to synchronize their incubation, through lengthening of the male's non-incubative phase. Polygynous male galliforms and shorebirds may delay incubation for 6-12 days, while courting females and fertilizing a second clutch, thereby often synchronizing hatching (Mertens, 1960; Hildén,

1975; Skutch, 1976; Ridley, 1978). With an advancing grade of endothermy, and increasing core and eccritic temperatures, longer parental egg attendance would have been required. Intensiveness and efficiency of foraging also would have had to increase, with more insect prey needed per unit of time.

Selection for helpless hatchlings: Hatchlings in Stages 1 and 2 would have been precocial by virtue of their proximate reptilian ancestry. But as arboreality and endothermy advanced in main-line descendants, increasingly strong selection for smaller eggs and clutches would have favored the evolution of altricial (helpless) hatchlings (but many 'offshoots' from Stage 4 have remained precocial). Their eggs could have been smaller, by virtue of parental feeding reducing needs to store nutrients. Helpless hatchlings (in 80% or more of species today) would have contributed to selection for quicker development of young. An altricial chick is described as "….a veritable growth machine, permitting prodigious metabolism of efficiency not found elsewhere among the higher vertebrates" (Portmann, 1950).

However, discontinuous bone growth of enantiornithines, and slowly deposited, virtually unvascularized, bone tissue, suggest slower growth rates than in modern relatives (Chiappe, 1995). Quicker development shortens and completely circumscribes periods of egg and young vulnerability, and parental risks. Such shorter periods probably were crucial, because the most powerful influences selecting for brevity of incubation and quick fledging, even today, are exposure hazards, particularly predation (Cody, 1971).

Stage 5: 'Ancestral birds'

Advancing endothermy to Stage 5 was accompanied by higher core and incubative temperatures and quicker development. With longer foraging absences, occasioned by increased nutritional needs, decreasing abundance of large flying insects, and the transition of many species to herbivory, egg chilling would have become an important factor. As cooler, more seasonal Cretaceous climates began to prevail in these circumstances; selection would have favored a return to biparental incubation of single clutches. Populations colonizing more temperate regions would have pioneered this transition.

A reduced annual reproductive potential occasioned by return to biparental care of single clutches could have been offset by competitive advantages that increased lifetime reproductive success. In many lines, these advantages, and attainment of full altriciality, could have accrued from colonization of more favorable habitats and/or adoption of more secure and/or better insulated nests, favoring locations in trees.

Increased core temperatures (estimated at ~38°C), probably in the range of primitive living birds, were accompanied by evolution of vigorous, sustained, large-amplitude, wing-flapping flight. Additional selective forces leading to 'ancestral birds' would have been for those 'advanced pro-aves' with increased wing-aspect ratios, more efficient wing profiles, greatest coordination, wing flexion on the upstroke, and superior wing-feather attachments. These advances would have led to powerful flight capabilities, along with size reduction (U. Norberg, 1985; Zhou and Hou, 2002).

Tail reduction to a pygostyle (and increased pubic retroversion) marked a relatively rapid evolutionary shift from stable but less maneuverable flight, associated with long bony tails, to more dynamic, unstable flight, marked by greater maneuverability and bipedal touchdowns (Paul, 2002). Greater selection along these lines probably followed from the air/wood arboreal habitats. These would have selected for high maneuverability over stability, to follow interrupted flight trajectories caused by frequent unclear flight paths (Dr. Donald Perry; personal communication).

Increased metabolic rates would have supported more rapid production of single eggs, making one ovary and oviduct, and alternate ovarian function, superfluous. Continued selection for reduced weight probably accounts for the right ovary and oviduct having become vestigial in most birds (Romanoff and Romanoff, 1949). Genetically, this is relatively readily accomplished, and might have occurred over a comparatively brief period, evolutionarily speaking (Cody, 1966; Jones, 1978).

At any rate selection, again, but influenced by different forces, would have favored biparental care of single clutches, with one parent usually in attendance. Development of altriciality also would have favored biparental care since, within limits; such care can achieve more rapid development of young. This stage would have dated to long before development of the adaptive specializations that, today, permit lengthy chilling of eggs of some species. Two consequences of the need for sustained higher incubative temperatures were selection for more protective, insulated nests and for feeding of the incubating parent by its mate. But improved nesting conditions eventually emancipated many species from essentially continuous egg contact, and/or obligatory egg care by both parents.

Stage 6: Modern birds

Evolution of modern birds entailed a further increase in core temperatures (to ~ 41- 42°C), continuation of nesting in trees and tree-hollows in altricial lines, and almost completely helpless hatchlings. Selection increasingly favored developing embryos with greater tolerance to chilling. With the attainment of true flight, access was gained to enormously expanded ranges of habitats, leading to extensive radiations and diversity.

The combination of multifaceted interactions between

widely foraging species (acting as seed dispersing vectors), primitive angiosperms, and insect pollination, led to dominance of an angiospermous flora and development of widespread and intensive herbivory.

SUMMARY

Based on contemporary avian and reptilian practices, paleontology, paleoclimatology, and relict reproductive behaviors in three species of small parrots, six stages -— cross-sections of a continuous process -- have been postulated in main-line avian evolution from late Triassic-early Jurassic theropodan forerunners of birds to modern birds.

Stage 1 'Shallow-nesting ancestral theropods'

These ancestors were small, terrestrial-arboreal, bipedal, and gracile. They preyed on other small animals, including insects during foraging near bases of, and at low heights in vegetation, remained in the vicinity of their nest site during periods of breeding. Parents spent the night in the safety of these low heights, watching over their nest site, and jumping or parachuting to the ground to protect it from small egg-predators, absolutely crucial at times when sounds were emitted by near-term embryos and hatching.

These latter practices, the proposed 'roots of avian evolution,' selected skeletal adaptations for arboreality and integumentary adaptations for thermal insulation and increased drag. Clutches of up to 20 eggs were built up in more than one laying episode and buried at shallow depths in midday-shaded areas. They were incubated by climatic heat in warm, equable climates in more than one annual reproductive episode. Parents aided hatching, and young were groomed, protected, and probably escorted to feeding sites.

Stage 2. 'Surface-nesting, nonavian theropods'

These ancestors laid clutches of up to 10 eggs in shallow scrapes in areas exposed to midday insolation, and maintained them continuously at elevated temperatures by close parental attention. The resulting shortened periods of embryonic development allowed more annual reproductive episodes. Parents alternately shaded the eggs during midday insolation, leading to selection for heat-shielding integumentary adaptations. Eggs were kept warm at night by a cover of decomposing vegetative debris. During cooler early morning and late afternoon periods parents shielded eggs from overhead view but allowed warming by low angle insolation;

In the favorable (close to eccritic) ambient temperatures of mid morning and mid afternoon, foraging parents merely concealed eggs with dry vegetative debris.

Increased daytime foraging in trees and nighttime presence therein, maintained selection on integumentary structures for heat retention and drag. When supplemented by selection for midday heat shielding, the evolution of featherlike integumentary cover was accelerated, supporting parachuting and steering, conveying greater flexibility in the protection of the more vulnerable surface nests.

Stage 3: 'Primitive pro-aves'

These ancestors possessed primitive feathers with improved aerodynamic and insulative properties supporting primitive endothermy (32 - 34°C core temperature). In continuing favorable climates, rapid double-clutching became adaptive, with clutches of less than 10 eggs built up by laying every 2 or 3 days. Parents incubated separate clutches throughout the night and much of the day in surface nests within mutual sight. Foraging in trees included jumping after relatively abundant large nearby flying, fleeing, or stationary insects, often followed by gliding in steered descent. Hatchlings were precocial in the avian sense.

Stage 4. 'Advanced pro-aves' (including *Archaeopteryx*)

These ancestors achieved sustained wing-flapping flight and modern feathers, and foraged intensively in vegetation. Wing flapping occurred at relatively low speeds and amplitudes, with moderate lift capability. Selection to minimize wing-loading through reduced relative weight of eggs was accompanied by developing altriciality, probably correlated with beginnings of nesting in tree-hollows and among fronds. More advanced endothermy with increased core temperature (36ºC), together with alternating ovulation, led to clutch assembly (less than 10 eggs) by laying one egg every day. Rapid double-clutching remained adaptive.

Stage 5: 'Ancestral birds'

These ancestors evolved progressively improved wing-flapping ability and further increases in core temperature (~38°C), leading to modern flight capabilities. At an increased metabolic rate, egg production by a single ovary and oviduct approached that previously requiring alternate operation of paired organs, allowing regression of the right reproductive organs of females of most species. Developing embryos required higher incubative temperatures, and were less tolerant of chilling during parental absences, occasioned by increased nutritional needs in cooler, more seasonable Cretaceous climates. A

single clutch again needed attention and incubation by both parents, favoring more rapid development of altricial hatchlings. More and shorter reproductive episodes of single-clutching and/or greater longevity maintained the lifetime reproductive potential. Tree-nesting became widespread.

Stage 6: Modern birds

These attained increased core temperature (41 - 42°C) and perfected flight capabilities, together with gaining access to enormously expanded ranges of habitats, leading to extensive radiations and diversity. The adaptive value of continuous attendance to eggs came to reside largely in protection from predators, facilitated by widespread tree-nesting. A transition of many to herbivory was completed.

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REFERENCES

Armstrong EA (1947). Bird Display and Behaviour. Linsay Drummond, Ltd., London.

Balda RP, Caple G, Willis WR (1985). Comparison of the gliding to flapping sequence with the flapping to gliding sequence. In: Hecht MK, Ostrom JH, Viohl G, Wellnhofer P (eds). The beginnings of birds. Freunde des Jura-Museums, Eichstatt, Germany, pp. 267-277.

Ball GF, Silver R (1983). Timing of incubation bouts by Ring Doves. J. Comp. Physiol. 97: 213-225.

Barsbold R (1997). Mongolian dinosaurs. In: Currie J, Padian K (eds) Encyclopedia of Dinosaurs, Academic Press, New York, pp. 447-450.

Bartholomew GA, Howell TR (1964). Experiments with nesting behavior of Laysan and Black-footed Albatrosses. Anim. Behav. 12: 549-559.

Bartholomew GA, White FN, Howell TR (1976). The thermal significance of the nest of the Sociable Weaver Philetairus socius: summer observations. Ibis 117: 171-179.

Bergstrom PW (1985). Daylight incubation sex roles in Wilson's Plover. Condor 88: 113-115.

Bock WJ (1986). The arboreal origin of avian flight. In: Padian K (ed) The Origin of Birds and the Evolution of Flight. California Academy of Sciences, San Francisco, pp. 57-72.

Breitenbach RP, Nagra CL, Meyer RK (1963). Effects of limited food intake on cyclic annual changes in Ring-necked Pheasant hens. J. Wildl. Management 27: 24-36.

Briggs JC (2003). Fishes and birds: Gondwana life rafts reconsidered. Syst. Biol. 52: 548-553.

Brightsmith DJ (2005). Competition, predation and nest niche shifts among tropical cavity nesters: phylogeny and natural history of parrots (Psittaciformes) and trogons (Trogoniformes). J. Avian Biol. 36: 64-73.

Buckley PA (1969). Disruption of species-typical behavior patterns in F$_1$ hybrid Agapornis parents. Zeit. Tierpsychol. 26: 737-743.

Buckley PA (1982). Avian genetics. In: Petrak ML (ed) Diseases of Cage and Aviary Birds. Lea and Febiger, Philadelphia, pp. 21-110.

Buffetaut E, Grellet-Tinner G, Varavudh S, Gilles C, Halyan T (2005). Minute theropod eggs and embryo from the lower Cretaceous of Thailand and the dinosaur-bird transition. Naturwiss. 92: 477-482.

Burden HW (1978). Ovarian innervation. In: Jones RE (ed) The Vertebrate Ovary. Plenum Press, London, pp. 615-638.

Burley NT, Johnson K (2002). The evolution of avian parental care. Phil. Trans. Royal Soc. (London) B357: 241-250.

Byskov AG (1978). Follicular atresia. In: Jones RE (ed) The Vertebrate Ovary. Plenum Press, London. pp. 533-562.

Callard IP, Lance V (1977). The control of reptilian follicular cycles. In: Calaby JH, Tindale CH (eds) Reproduction and Evolution. Australian Acad. Science, Canberra, pp. 199-209.

Campbell B, Lack E (1985). A Dictionary of Birds. Buteo, Vermillion, SD.

Carpenter K (1999). Eggs, Nests, and Baby Dinosaurs. Univ. Press, Bloomington, Indiana.

Carpenter K, Alf K (1994). Global distribution of dinosaur eggs and babies. In: Carpenter K, Hirsch KF, Horner JR (eds) Dinosaur Eggs and Babies. Cambridge Univ. Press, New York, pp. 15-30.

Carpenter K, Hirsch KF, Horner JR (1994). Introduction. In: Carpenter K, Hirsch KF, Horner JR (eds) Dinosaur Eggs and Babies. Cambridge Univ. Press, New York, pp. 1-11.

Chattergee S (1997). The Rise of Birds. Johns Hopkins Univ. Press, Baltimore, Maryland.

Chen P-J, Dong Z-M, Zhen S-N (1998). An exceptionally well-preserved theropod dinosaur from the Yixian Formation of China. Nature 391: 147-152.

Cheng MF (1974). Ovarian development in the female Ring Dove in response to stimulation by intact and castrated male Ring Doves. J. Endocrin. 63: 43-53.

Chiappe LM (1995). The first 55 million years of avian evolution. Nature 378: 349-355.

Chiappe LM, Dyke GJ (2002). The Mesozoic radiation of birds. Ann. Rev. Ecol. Syst. 33: 91-124.

Chinsamy A, Martin LD, Dodson, P (1998). Bone microstructure of diving Hesperornis and the volant Ichthyornis from the Niobrara Chalk of Western Kansas. Cretaceous Res. 19: 225-235.

Clark JM, Norell M, Chiappe L (1999). An oviraptorid skeleton from the late Cretaceous of Ukhaa Tolgod, Mongolia preserved in an avian-like brooding position over an oviraptorid nest. Am. Mus. Novitates 3265: 1-36.

Clutton-Brock TH (1991). The Evolution of Parental Care. Princeton Univ. Press,. Princeton, New Jersey.

Cody ML (1966). A general theory of clutch size. Evol. 20: 174-184.

Cody ML (1971). Ecological aspects of reproduction. In: Farner DS, King JR (eds) Avian Biology, Vol. 1. Academic Press, New York, pp. 462-512.

Colbert EH (1995). The Little Dinosaur of Ghost Ranch. Columbia Univ. Press, New York.

Collias NE, Collias E (1984). Nest Building and Bird Behavior. Princeton Univ. Press, Princeton, New Jersey.

Coombs WP (1989). Modern analogs for dinosaur nesting and parental behavior. Geol. Soc. Am., Special Paper 238: 21-53.

Cousin R, Breton G, Fournier R, Watté J.-P (1994). Dinosaur egg laying and nesting in France. In: Carpenter K, Hirsch KF, Horner JR (eds) Dinosaur Eggs and Babies. Cambridge Univ. Press, New York, pp. 56-74.

Davis PG, Briggs DEG (1995). Fossilization of feathers. Geol. 23: 783-786.

Dawson WR, Hudson JW (1970). Birds. In: Wittow GC (ed) Comparative Physiology of Thermoregulation. Academic Press, New York, pp. 223-310.

Deeming DC (2002). Behavior patterns during incubation. In: Deeming DC (ed) Avian Incubation, Behaviour, Environment, Evolution. Oxford Univ. Press, New York, pp. 63-87.

Dial KP (2003). Evolution of avian locomotion: correlates of flight style, locomotion modules, nesting biology, body size, development, and the origin of flapping flight. The Auk 120: 941-952.

Dingus L, Rowe T (1998). The Mistaken Extinction, Dinosaur Evolution and the Origin of Birds. Freeman & Co., New York.

Dodson P (1997). Paleoclimatology. In: Currie J, Padian K (eds) Encyclopedia of Dinosaurs, Academic Press, New York, pp. 515-519.

Dominguez Alonzo P, Milner AC, Ketcham RA, Cookson MJ, Rowe TB (2004). The avian nature of the brain and inner ear of *Archaeopteryx.* Nature 430: 666-669.

Dong Z-M, Currie PJ (1996). On the discovery of an oviraptid skeleton on a nest of eggs at Bayan Mandamu, Inner Mongolia, Peoples Republic of China. Canadian J. Earth Sci. 33: 631-636.

Drent RH (1972). Adaptive aspects of the physiology of incubation. Proc. Internl. Ornithol. Congr. XV: 255-280.

Drent RH (1975). Incubation. In: Farner DS, King JR (eds) Avian Biology, Vol. 1. Academic Press, New York, pp. 333-429.

Dumont JPC, Robertson RM (1986). Neuronal circuits: an evolutionary perspective. Science 233: 849-853.

Dyke GJ, Norell MA (2005). Caudipteryx as a non-avialan theropod rather than a flightless bird. Acta Palaeontologica Polonica 50: 101-116.

Eisner E (1961). The behavior of the Bengalese Finch in the nest. Ardea 49: 51-69.

Elzanowski A (1985). The evolution of parental care in birds with reference to fossil embryos. In: Ilyichev VD, Gavrilov VM (eds) Acta XVIII Congr. Internl. Ornithol., Vol. 1. Nauka, Moscow, pp. 178-183.

Emlen ST, Oring LW (1977). Ecology, sexual selection, and the evolution of mating systems. Science 197: 215-223.

Erickson GM, Makovicky PJ, Currie PJ, Norell MA, Yerby SA, Brochu CA (2004). Gigantism and comparative life-history parameters of tyrannosaurid dinosaurs. Nature 430: 772-775.

Ewert MA (1979). The embryo and its egg: development and natural history. In: Harless M, Morlock H (eds) Turtles--Perspectives and Research. John Wiley & Sons, New York, pp. 333-413.

Feare CJ, Spencer PL, Constantine DAT (1982). Time of egg laying of Starlings *Sturnus vulgaris.* Ibis 124: 174-178.

Feduccia A (1985). On why the dinosaurs lacked feathers. In: Hecht MK, Ostrom JH, Viohl G, Wellnhofer P (eds). The beginnings of birds. Freunde des Jura-Museums, Eichstatt, Germany, pp. 75-79.

Feduccia A (1993). Evidence from claw geometry indicating arboreal habits of *Archaeopteryx.* Science 299: 790-793.

Feduccia A (1996). The Origin and Evolution of Birds. Yale Univ. Press, New Haven.

Feduccia A (1999). The Origin and Evolution of Birds, 2nd ed. Yale Univ. Press, New Haven.

Feduccia A, Tordoff HB (1979). Feathers of *Archaeopteryx:* asymmetric veins indicate aerodynamic function. Science 203: 1021-1022.

Fentress JC, McLeod PJ (1986). Motor patterns in development. Handb. Behav. Neurobiol. 8: 35-97.

Ferguson MWJ (1985). Reproductive biology and embryology of the crocodilians. In: Gans C, Billet F, Maderson PFA (eds) Biology of the Reptiles*,* Vol. 14. John Wiley, New York, pp. 329-491.

Fiorillo AR (2004). The dinosaurs of Arctic Alaska. Sci. Am. 291(6): 84-91.

Freeman BM, Vince MA (1974). Development of the Avian Embryo. Chapman & Hall, London.

Garner JP, Taylor GK, Thomas ALR (1999). On the origins of birds: the sequence of character acquisition in the evolution of avian flight. Proc. Royal Soc. London, B266: 1259-1266.

Gadgil M, Bossert WH (1970). Life historical consequences of natural selection. Am. Scientist 104: 1-24.

Getting PA (1988). Comparative analyses of invertebrate central pattern generators. In: Cohen AH, Rossignol S, Grillner S (eds) Neural Control of Rhythmic Movements in Vertebrates. John Wiley, New York, pp. 101-127.

Gilbert AB, Wood-Gush DGM (1971). Ovulatory and ovipository cycles. In: Bell DJ, Freeman DM (eds) Physiology and Biochemistry and the Domestic Fowl. Academic Press, New York, pp. 1353-1378.

Gittleman JL (1985). Carnivore body size: Ecological and taxonomic correlation. Oecologia 67: 540–554.

Göhlich UB, Chiappe LM (2006). A new carnivorous dinosaur from the Late Jurassic Solnhofen Archipelago. Nature 440: 329-332.

Gottlieb DI (1988). GABAergic neurons. Sci. Am. 258: 82-89.

Hamburger V (1971). Development of embryonic motility. In: Tobach E, Aronson LR, Shaw E (eds) The Biopsychology of Development. Academic Press, New York, pp. 27-44.

Hanford B, Mares MA (1985). The mating systems of ratites and tinamous: an evolutionary perspective. Biol. J. Linnean Soc. 225: 77-104.

Harris-Warrick RM (1988). Chemical modulation of central pattern generators. In: Cohen AH, Rossignol S, Grillner S (eds) Neural Control of Rhythmic Movements in Vertebrates. John Wiley, New York, pp: 285-331.

Hecht MK, Ostrom JH, Viohl G, Wellenhofer P (eds) (1985). The Beginnings of Birds: Proc. Internl. Archaeopteryx Conf., Eichstatt, 1984. Eichstatt: Freunde des Jura-Museums, Eichstatt, Germany.

Heinroth O, Heinroth K (1959). The Birds. Faber & Faber, London.

Hildén O (1975). Breeding system of Temminck's Stint *Calidris temminckii.* Ornis Fennica 52: 117-144.

Hinde RA (1970). Animal Behaviour. McGraw-Hill, New York.

Hopp T, Orsen M (1998). Dinosaur brooding behavior and the origin of flight feathers. In: Wolberg DL, Stump LE, Rosenberg GD (eds) The Dinofest Symposium. Philadelphia Acad. Natural Sciences, Philadelphia, p. 27.

Horner JR (1994). Comparative taphonomy of some dinosaur and extant bird colonial nesting grounds. In: Carpenter K, Hirsch KF, Horner JR (eds) Dinosaur Eggs and Babies. Cambridge Univ. Press, New York, pp. 116-123.

Horner JR (2000). Dinosaur reproduction and parenting. Ann. Rev. Earth Planetary Sci. 28:19-45.

Horner JR, Gorman J (1988). Digging Dinosaurs. Workman Publishing, New York:.

Horner JR, Padian K (2004). Age and growth dynamics of *Tyrannosaurus rex.* Proc. Royal Soc. London, B271: 1875-1880.

Horner JR, Varricchio DJ, Goodwin MB (1992). Marine transgressions and the evolution of Cretaceous dinosaurs. Nature 258: 59-61.

Howell TR (1979). Brooding biology of the Egyptian Plover, *Pluvianus aegyptius.* Univ. Calif. Publ. Zool. 113, 93 pp.

Hutchison RE (1977). Temporal relationships between nesting behaviour, ovary and oviduct development during the reproductive cycle of female budgerigars. Behav. 60: 278-303.

Hutchison RE, Hinde RA, Bendon B (1968). Oviduct development and its relation to other aspects of reproduction in domesticated canaries. J. Zool. (London) 155: 87-102.

Jerison HJ (1973). Evolution of the Brain and Intelligence. Academic Press, New York.

Jerison HJ (1976). Principles of evolution of the brain and behavior. In: Masterton RB, Hodos WD, Jerison HJ (eds) Evolution, Brain and Behavior: Persistent Problems. John Wiley, New York, pp. 23-45.

Ji Q, Ji S-A (1996). On the discovery of the earliest bird fossils in China and the origin of birds. Chinese Geol. 233: 30-33 (in Chinese).

Ji Q, Currie PJ, Norell MA, Ji S-A (1998). Two feathered dinosaurs from Northeastern China. Nature 393: 753-761.

Jones RE (1978). Evolution of the vertebrate ovary, an overview. In: Jones RE (ed) The Vertebrate Ovary. Plenum Press, London, pp. 827-840.

Jones TD, Ruben JA, Martin LD, Kurochkin EN, Feduccia A et al. (2000). Nonavian feathers in a late Triassic archosaur. Science 288: 2202-2205.

Kavanau JL (1987). Lovebirds, Cockatiels, Budgerigars, Behavior and Evolution. Science Software Systems, Los Angeles.

Kavanau JL (1988). Presumptive relict reproductive behavior in small parrots. Brain, Behav. Evol. 32: 340-352.

Kavanau JL (1990). Conservative behavioral evolution, the neural substrate. Anim. Behav. 39:758-767.

Kendeigh SC, Dol'nik VR, Gavrilov VM (1977). Avian energetics. In: Pinowski J, Kendeigh SC (eds) Granivorous Birds in Ecosystems. Cambridge Univ. Press, Cambridge, pp. 127-204.

Kundrát M. (2004). When did theropods become feathered?--evidence for pre-*Archaeopteryx* feathery appendages. J. Exp. Zool. 302B: 355-364.

Levy-Montalcini R (1987). The nerve growth factor 25 years later.

Science 237: 1134-1162.

Ligon JD (1999). The Evolution of Avian Breeding Systems. Oxford Univ. Press, New York.

Luhan JA (1968). Neurology. Williams & Wilkins, Baltimore, Maryland.

Maclean GL (1968). Field studies of the sand grouse of the Kalahari Desert. Living Bird 1968: 209-235.

Maclean GL (1974). Egg-covering in the Charadrii. Ostrich 45: 167-174.

Maclean GL (1976). Arid zone ornithology in Africa and South America. Proc. Internl. Ornithol. Congr. XVI: 468-480.

Magnusson WE, Lima AP (1991). The ecology of a cryptic predator, *Paleosuchus trigonatus*, in a tropical rainforest. J. Herpetol. 25: 41-48.

Marder E, Hooper SL, Eisen JS (1987). Multiple neurotransmitters provide a mechanism for the production of multiple outputs from a single neuronal circuit. In: Edelman GM, Gall WE, Cowan MW (eds) Synaptic Function. John Wiley, New York, pp. 305-327.

Martin LD, Czerkas SA (2000). The fossil record of feather evolution in the Mesozoic. Am. Zool. 40: 687-694.

Matthews WB (1982). Diseases of the Nervous System. Blackwell, Boston.

Mayr E (1958). Behavior and systematics. In: Roe A, Simpson GG (eds) Behavior and Evolution. Yale Univ. Press, New Haven, pp. 341-362.

Mayr E (1980). Problems of classification of birds. Proc. Int. Ornithol. Congr. XVII: 95-112.

Mayr G, Pohl B, Peters DS (2005). A well-preserved *Archaeopteryx* specimen with theropod features. Science 310: 1483-1486.

McKitrick MC (1992). Phylogenetic analysis of avian parental care. The Auk 109: 828-846.

McLennan DA, Brooks DR, McPhail JD (1988). The benefits of communication between comparative ethology and phylogenetic systematics: A case study using gasterrosteid fishes. Can. J. Zool. 66: 2177-2190.

Mead PS, Morton ML (1985). Hatching synchrony in the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*): a selected or incidental trait. The Auk 102: 781-792.

Meng M, Liu J, Varricchio DJ, Huang T, Gao C (2004). Parental care in an ornithiscian dinosaur. Nature 431: 145-146.

Mertens R (1960). The World of Amphibians and Reptiles. Harrap, London.

Mikhailov K (1992). The microstructure of avian and dinosaurian eggshell: phylogenetic implications. In: Campbell KE (ed) Papers in Avian Paleontology. Los Angeles Natural History Museum, Los Angeles County, pp. 361-374.

Mikhailov K, Sabath K, Kurzanov S (1994). Eggs and nests from the late Cretaceous of Mongolia. In: Carpenter K, Hirsch KF, Horner JR (eds) Dinosaur Eggs and Babies. Cambridge Univ. Press, New York, pp. 88-116.

Moody PA (1962). Introduction to Evolution, 2nd Ed. Harper, New York.

Moratalla JJ, Powell JE (1994). Dinosaur nesting patterns. In: Carpenter K, Hirsch KF, Horner JR (eds) Dinosaur Eggs and Babies. Cambridge Univ. Press, New York, pp. 37-46.

Morton ML, Pereyra ME (1985). The regulation of egg temperatures and attentiveness patterns in the Dusky Flycatcher (*Empidonax oberholseri*). The Auk 102: 25-37.

Neill WT (1971). The Last of the Ruling Reptiles—Alligators, Crocodiles, and Their Kin. Columbia Univ. Press, New York.

Norberg RA (1985). Function of vane asymmetry and shaft curvature in bird flight feathers; inferences on flight ability of *Archaeopteryx*. In: Hecht MK, Ostrom JH, Viohl G, Wellnhofer P (eds). The beginnings of birds. Freunde des Jura-Museums, Eichstatt, Germany, pp. 303-316.

Norberg UM (1985). Evolution of flight in birds: aerodynamic, mechanical and ecological aspects. In: Hecht MK, Ostrom JH, Viohl G, Wellnhofer P (eds). The beginnings of birds. Freunde des Jura-Museums, Eichstatt, Germany, pp. 293-302.

Norberg UM (1990). Vertebrate Flight. Springer-Verlag, New York.

Norell MA, Clark JM, Demberelyn D, Rhincken B, Chiappe LM, Davidson AR, McKenna MC, Altangerel P, Novacek MJ (1994). A theropod dinosaur embryo and the affinities of the Flaming Cliffs dinosaur eggs. Science 266: 779-782.

Norell MA, Clark JM, Chiappe LM, Dashzeveg D (1995). A nestling dinosaur. Science 378: 774-776.

Norell MA, Ji Q, Gao K, Yuan C, Zhao Y, Wang L (2002). 'Modern' fathers on a non-avian dinosaur. Nature 416: 36-37.

O'Connor RJ (1984). The Growth and Development of Birds. John Wiley & Sons, New York.

Ostrom JH (1990). Dromaeosauridae. In: Weishampel DB, Dodson P, Osmólska H (eds) The Dinosauria. Univ. Calif. Press, Berkeley, pp. 269-279.

Padian K (2001). Stages in the origin of bird flight: behind the arboreal-cursorial dichotomy. The false issues of bird origins: an historic perspective. In: Gauthier J, Gall LF (eds) New Perspectives on the Origin and Early Evolution of Birds. Peabody Museum of Natural History, Yale Univ., New Haven, pp. 265-272, 485-489.

Padian K, Chiappe LM (1998a). The origin of birds and their flight. Sci. Am. 278(2): 38-47.

Padian K, Chiappe LM (1998b). The origin and early evolution of birds. Biol. Rev. 73: 1-42.

Padian K, Ji Q, Ji S (2001). Feathered dinosaurs and the origin of flight. In: Tanke DH, Carpenter K (eds) Mesozoic Vertebrate Life. Univ. Press, Bloomington, Indiana, pp. 117-135.

Paul GS (1994). Dinosaur reproduction in the fast lane: implications for size, success, and extinction. In: Carpenter K, Hirsch KF, Horner JR (eds) Dinosaur Eggs and Babies. Cambridge Univ. Press, New York, pp. 244-255.

Paul GS (2002). Dinosaurs of the Air, the Evolution and Loss of Flight in Dinosaurs and Birds. Johns Hopkins Univ. Press, Baltimore, Maryland.

Pennisi E (2004). Newly hatched dinosaur babies hit the ground running. Science 305: 1396.

Peters DS, Gutmann WFr (1985). Constructional and functional preconditions for the transition to powered flight in vertebrates. In: Hecht MK, Ostrom JH, Viohl G, Wellnhofer P (eds). The beginnings of birds. Freunde des Jura-Museums, Eichstatt, Germany, pp.. 233-242.

Portmann A (1950). Le developpement postembryonaire. Traité de Zoologie 15: 521-535.

Pough FH (1973). Lizard energetics and diet. Ecology 54: 837-844.

Provine RR (1984). Wing flapping during development and evolution. Am. Scientist 72: 448-455.

Prum RO (1999). Developmental and evolutionary origin of feathers. J. Exper. Zool. 285: 291-306.

Prum RO (2002). Perspectives in ornithology: why ornithologists should care about the theropod origin of birds. The Auk 119: 1-17.

Prum RO, Brush AH (2002). The evolutionary origin and diversification of feathers. Quart. Rev. Biol. 77: 261-295.

Rayner JMV (1985). Mechanical and ecological constraints on flight evolution. In: Hecht MK, Ostrom JH, Viohl G, Wellnhofer P (eds). The beginnings of birds. Freunde des Jura-Museums, Eichstatt, Germany, pp. 279-288.

Rayner JMV (2001). On the origin and evolution of flapping flight aerodynamics in birds. In: Gauthier J, Gall LF (eds) New Perspectives on the Origin and Early Evolution of Birds. Peabody Museum of Natural History, Yale Univ., New Haven, pp. 363-385.

Regal P (1975). The evolutionary origin of feathers. Quart. Rev. Biol. 50: 35-66.

Reisz RR, Scott D, Sues H-D, Evans DC, Raath MA (2005). Embryos of an early Jurassic prosauropod dinosaur and their evolutionary significance. Science 309: 761-764.

Reynolds JD, Goodwin NB, Freckleton RB (2002). Evolutionary transitions in parental care and live bearing in vertebrates. Phil. Trans. Royal Soc. London, B357: 269-281.

Ricklefs RE (1974). Energetics of reproduction in birds. In: Paynter RA, Jr (ed) Avian Energetics. Nuttall Ornithological Club, Cambridge, Massachusetts, pp. 152-297.

Ricqlés A, Padian K, Horner JR (2001). The bone histology of basal birds in phylogenetic and ontogenetic perspectives. In: Gauthier J, Gall LF (eds) New Perspectives on the Origin and Early Evolution of Birds, Peabody Museum of Natural History, Yale Univ., New Haven,

pp. 411-526.

Ridley M (1978). Paternal care. Anim. Behav. 26: 904-932.

Rich TA, Hopson JA, Musser AM, Flannery TF, Vickers-Rich P (2005). Independent origin of middle ear bones in monotremes and therians. Science 307: 910-914.

Romanoff AL, Romanoff AJ (1949). The Avian Egg. Wiley, New York.

Saidapur SK (1978). Follicular atresia in the ovaries of non-mammalian vertebrates. Internl. Rev. Cytol. 54: 225-244.

Sander PM, Klein N (2005). Developmental plasticity in the life history of a prosauropod dinosaur. Science 310: 1800-1802.

Sato T, Cheng Y-N, Wu X-C, Zelenitsky DK, Hsiau Y-F (2005). A pair of shelled eggs inside a female dinosaur. Science 308: 375.

Savile DBO (1962). Gliding flight in vertebrates. Am. Zool. 2: 161-166.

Schweitzer MH, Jackson FD, Chiappe LM, Schmott JG, Calvo JO, Schmitt JG, Calvo JO, Rubilar DE. (2002). Late Cretaceous avian eggs with embryos from Argentina. J. Vert. Paleontol. 22: 191-195.

Schweitzer MH, Wittmeyer JL, Horner JR (2006). Gender-specific reproductive tissue in ratites and *Tyrannosaurus rex*. Science 308: 1456-1459.

Sibley CE, Alquist JE (1990). Phylogeny and Classification of Birds. Yale Univ. Press, New Haven.

Simpson GG (1958). Behavior and evolution. In: Roe A, Simpson GG (eds) Behavior and Evolution. Yale Univ. Press, New Haven, pp. 507-535.

Skutch AE (1957). The incubation patterns of birds. Ibis 99: 69-93.

Skutch AE (1976). Parent Birds and Their Young. Univ. Texas Press, Austin.

Smart JD, Hughes NF (1973). The insects and the plant. In: van Emden HF (ed) Insect/Plant Relationships, Royal Entomol. Soc. London 6: 143-155.

Smith HM (1979). Handbook of Lizards. Cornell Univ. Press, Ithaca, New York.

Sperry RW (1958). Developmental basis of behavior. In: Roe A, Simpson GG (eds) Behavior and Evolution. Yale Univ. Press, New Haven, pp. 128-139.

Starck JM (1993). Evolution of avian ontogenies. In: Power DM (ed) Current Ornithology, Vol. 10. Plenum Press, New York, pp. 275-366.

Stebbins GL (1969). The Basis of Progressive Evolution. Univ. North Carolina Press, Chapel Hill, NC.

Steegmann AT (1970). Examination of the Nervous System. Year Book Medical Publishers, Inc., Chicago.

Sturkie PO, Mueller WJ (1976). Reproduction in the female and egg production. In: Sturkie PD (ed) Avian Physiology, 3rd ed. Springer-Verlag, New York, pp. 302-330.

Székely T, Reynolds JD (1995). Evolutionary transitions in parental care in shorebirds. Proc. Royal Soc. London, B262: 57-64.

Tarsitano SF (1985). The morphological and aerodynamic constraints on the origin of avian flight. In: Hecht MK, Ostrom JH, Viohl G, Wellnhofer P (eds). The beginnings of birds. Freunde des Jura-Museums, Eichstatt, Germany, pp. 319-332.

Thomson AL (1950). Breeding seasons of birds. Ibis 92: 173-184.

Tinbergen R, Broekhuysen GJ, Feekes F, Houghton JCW, Kruuk H, Szulc H (1962). Egg shell removal by the Black-headed gull *Larus ridibundus* L. a behaviour component of camouflage. Behav. 19: 74-117.

Tullberg BS, Ah-King M, Temrin H (2002). Phylogenetic reconstruction of parenntal-care systems in the ancestors of birds. Phil. Trans. Royal Soc. London, B357: 251-257.

Van Rhijn JG (1990). Unidirectionality in the phylogeny of social organization, with special reference to birds. Behav. 115: 153-173.

Varricchio DJ (1997). Troodontidae. In: Currie J, Padian K (eds) Encyclopedia of Dinosaurs, Academic Press, New York, pp. 749-754.

Varricchio DJ, Jackson F, Borkowski JJ, Horner JR (1997). Nesting and egg clutches of the dinosaur *Troodon formosus* and the evolution of reproductive traits. Nature 385: 247-250.

Varricchio DJ, Jackson F, Treuman, H (1999). A nesting trace with eggs for the Cretaceous theropod dinosaur *Troodon formosus.* J. Vert. Paleo. 19: 91-100.

Vehrencamp SL (2000). Evolutionary routes to joint-female nesting in

birds. Behav. Ecol. 11: 334-344.

Viohl G (1985). Geology of the Solnhofen lithographic limestone and the habitat of *Archaeopteryx*. In: Hecht MK, Ostrom JH, Viohl G, Wellnhofer P (eds). The beginnings of birds. Freunde des Jura-Museums, Eichstatt, Germany, pp. 31-44.

Vitt LJ, Price HJ (1982). Ecological and evolutionary determinants of relative clutch mass in lizards. Herpetol. 38: 237-255.

Welty J (1982). The Life of Birds. Saunders College Publications, New York.

Wesolowski T (1994). The origin of parental care and the early evolution of male and female parental roles in birds. Am. Nat. 143: 39-58.

Wesolowski T (2004). The origin of parental care in birds: a reassessment. Behav. Ecol. 15: 520-523.

Witmer LM (2002). The debate on avian ancestry, phylogeny, function and fossils. In: Chiappe LM, Witmer LM (eds) Mesozoic Birds, Above the Heads of Dinosaurs. Univ. Calif. Press, Berkeley, pp. 3-30.

Xu X, Norell MA (2004). A new troodontid dinosaur from China with avian-like sleeping posture. Nature 431: 838-841.

Xu X, Norell MA, Kuang X, Wang X, Zhao Q, Jia C (2004). Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids. Nature 431: 680-684.

Xu X, Tang Z-L, Wang X (1999). A therizinosauroid dinosaur with integumentary structures from China. Nature 399: 350-354.

Xu X, Wang X, Wu X (1999). A dromaeosaurid dinosaur with filamentous integument from the Yixian Formation of China. Nature 401: 262-266.

Xu X, Zhao X, Wang X (2000). The smallest known non-avian theropod dinosaur. Nature 408: 705-708.

Xu X, Zhou Z, Prum RO (2001). Branched integumental structures in *Sinornithosaurus* and the origin of feathers. Nature 410: 200-204.

Xu X, Zhou Z, Wang X, Kuang X, Zhang F, Du X (2003). Four-winged dinosaurs from China. Nature 421: 335-340.

Yalden DW (1985). Forelimb function in *Archaeopteryx*. In: Hecht MK,

Ostrom JH, Viohl G, Wellnhofer P (eds). The beginnings of birds. Freunde des Jura-Museums, Eichstatt, Germany, pp. 91-97.

Zerba E, Morton ML (1983). Dynamics of incubation in Mountain White-crowned Sparrows. Condor 85: 1-11.

Zhang F, Zhou Z (2004). Leg feathers in an early Cretaceous bird. Nature 431: 925.

Zhou Z, Barrett PM, Hilton J (2003). An exceptionally preserved lower Cretaceous ecosystem. Nature 421: 807-814.

Zhou Z, Farlow JO (2001). Flight capabilities and habits of *Confuciusornis*. In: Gauthier J, Gall LF (eds) New Perspectives on the Origin and Early Evolution of Birds. Peabody Museum of Natural History, Yale Univ., New Haven, pp. 237-254,

Zhou Z, Hou L (2002). The discovery and study of Mesozoic birds in China. In: Chiappe LM, Witmer LM (eds) Mesozoic Birds, Above the Heads of Dinosaurs. Univ. Calif. Press, Berkeley, pp. 160-183.

Zhou Z, Zhang F (2004). A precocious avian embryo from the lower Cretaceous of China. Science 306: 653.