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11. Dinosaur Brooding Behavior and the Origin of Flight Feathers

THOMAS P. HOPP AND MARK J. ORSEN

Abstract: The origin of birds from within the group of theropod dinosaurs has been controversial because it is difficult to understand how wing feathers evolved through short intermediate stages before becoming long enough to generate adequate power and lift for flight. The "ground up" concept of flight evolution among cursorial dinosaurs can be criticized because there is no apparent selective pressure to drive the forelimb feather lengthening process through its earliest stages. Feather functions such as insect-trapping, hunting, and display have been proposed, but none of these require the feather length and shape that evolved by the time *Archaeopteryx* appeared.

We propose a mechanism to account for the forelimb and tail feather lengthening process, based on a behavior that exists in living birds—namely, brooding. Interestingly, despite the many known examples of modern birds that use their wing feathers in nesting and chick-rearing, there has been no previous proposal of brooding as a selective pressure in the evolution of flight feathers. We present fossil evidence that nesting and care of hatchlings could have been responsible for the development of long feathers on the forelimbs and tails of pre-avian theropod dinosaurs. It has been noted that oviraptorids incubated their nests in a posture strikingly similar to that of many modern birds, with breast and feet in contact with the eggs. However, gaps in the animal's coverage of its eggs were sufficiently large to allow solar-heating, wind-cooling, or rain-wetting effects on the exposed eggs. Comparisons to modern birds demonstrate that these gaps could have been covered by wing and tail feathers. Thus, the evolution of long feathers on the forelimbs and tail base of theropod bird ancestors could have been driven, not by flight requirements, but by the advantage of decreased environmental stress on eggs and hatchlings. Significantly, this evolutionary process would have provided brooding advantages at every increment of feather lengthening. Even the first relatively short feathers would have offered increased protection for the young.

To assess whether brooding feathers could have originated among early non-avian dinosaurs, we undertook a comparative study of dinosaur and bird skeletal anatomy with emphasis on modern birds' nesting and brooding postures. We determined the extent to which theropod dinosaurs could adopt birdlike postures while incubating eggs and tending hatchlings, and concluded that the use of long forelimb and tail feathers for brooding could readily have existed even among early theropods. Furthermore, because the skeletons of these older theropods were conducive to brooding but not flying, forelimb and tail quill feathers may have evolved in these animals to the sizes and shapes seen in Archaeopteryx in the absence of flight, whereupon they were subsequently co-opted by Archaeopteryx or a similar creature for the additional purpose of flying.

Introduction

The theory of bird origins among the ground-dwelling, cursorial theropod dinosaurs (Ostrom 1973, 1974, 1976) has a long history of controversy. A central problem is that of providing an explanation for evolution of the form and function of flight feathers, because it has been hard to see a selective advantage in the early stages of forelimb feather development in a ground-dwelling, cursorial theropod. Since the discovery of the first *Archaeopteryx* fossil in 1865, numerous hypotheses have been advanced to explain the origin of flight feathers. A number of these hypotheses have concentrated on nonflight selective pressures as the initial driving force. For example, Mayr (1960) suggested that display and sexual selection were the driving forces behind wing and tail feather development. Regal (1975) proposed that feathers were developed primarily as heat shields, and Ostrom (1979) suggested insect trapping. Dyck (1985) pointed out that the water repellency of feathers might have been of primary importance. Thulborn and Hamley (1985) proposed shading while hunting, where the wings were spread as a canopy in the fashion practiced by some modern egrets. It is plausible that all of these disparate functionalities may have, at one point or another, played a role in feather evolution. However, these proposals still leave open the possibility that other mechanisms were involved in the evolution of bird flight (Feduccia 1994).

Heilmann (1927) and Savile (1962) proposed the distinct alternative theory that feathers developed primarily for aerodynamic uses in an arboreal, gliding animal. Feduccia (1980) and others have since elaborated and advocated this concept. Such feather features as the asymmetrical vanes have been cited to indicate that aerodynamic function was critical early in feather development (Feduccia and Tordoff 1979). The proposal that pennaceous feathers evolved before downy feathers (Parkes 1966; Feduccia 1995) has been cited as a further example of flight, rather than insulation, as the original function of feathers. These as well as other arguments have been raised as objections to the cursorial origin of flight (reviewed by Ostrom 1979, 1997). Proponents of the cursorial theory have been hard-pressed to explain the driving force behind feather lengthening that must have preceded the use of wings for flight (Feduccia 1995). Advocates of the arboreal theory point out that their concept features a single consistent selective pressure, feathers as airfoils, while the cursorial theory requires a switch from one use to another at some indeterminate point in feather evolution (for example, from sun-shielding to flying).

Remarkably, both sides in this debate have neglected one of the most important aspects of avian life—brooding. Here we address the issue of flight evolution among cursorial theropods once more, this time with emphasis on a possibly critical role played by brooding. Because modern birds still, almost universally, use their wing feathers for brooding, this is the only cursorial theory that does not require a change in selective pressure. As we see it, pressure to optimize brooding has been continuous from the ancient past until today. In what follows, fossil evidence and modern bird behavior and anatomy will be cited as guides for understanding a possible mechanism for the brooding-driven evolution of wing and tail feathers.

Brooding Postures and Feather Evolution

Brooding is a vital and widespread activity of modern birds that involves egg incubation and covering of chicks by adults to provide warmth, shielding from solar heating, shelter from rain and wind, and protection from predators (Skutch 1976). With few exceptions, brooding adults assume characteristic postures in which the feet are placed medially and the wing feathers are used to cover surrounding eggs or chicks (Wallace and Mahan 1975). These postures most often

involve extension of the wings from their normal "folded" or fully flexed posture (figs. 11.1-11.3). Furthermore, the extended wings are often "drooped" or lowered toward the ground (Howell et al. 1974; Johnsgard 1993) and sometimes drawn backward at the shoulder (figs. 11.2, 11.3). These movements provide optimal cover for the chicks, which through their size or numbers may present a considerable challenge for parents to cover (e.g., the large chicks in fig. 11.3).

The discovery and description of nesting oviraptorids implied that dinosaurs may have incubated their eggs much like modern birds (Norell et al. 1995; Dong and Currie 1996; Clark et al. 2001). Unfortunately, lack of any evidence for feathers on the oviraptorid specimens made it impossible to verify whether feathers could have played a part in such incubations. Nevertheless, consideration of the postural details of nesting oviraptorids underscores the similarity of dinosaur and avian incubation. In the most complete specimen (Norell et al. 1995) the animal lies with its breast, belly, and feet in contact with its eggs (fig. 11.4), in a posture very similar to modern birds such as the ostrich (Sauer and Sauer 1966). However, forelimbs of Citipati are not in the folded posture that many modern birds use while resting or covering a nest. Rather, they are in an extended, rearward-directed orientation. This also appears to be the orientation in a second, less complete oviraptorid specimen (Dong and Currie 1996). As mentioned above, this posture is similar to one employed by birds brooding large chicks or by birds that produce large clutches of eggs. A covering of enlarged wing feathers and tail feathers would greatly improve the ability of an oviraptorid to shield its eggs from sun, wind, and rain (figs. 11.4, 11.5). Such feathers would also provide protection for chicks after hatching.

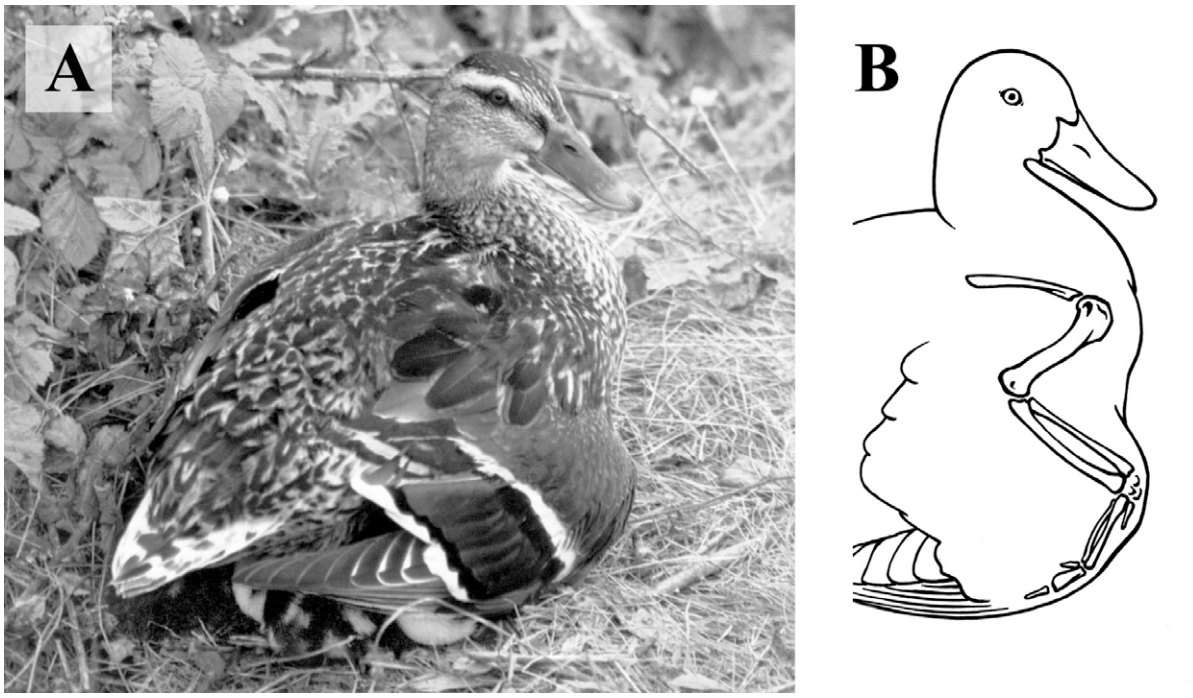

Figure 11.1. Mother duck and ducklings. A. This female mallard has lowered her wings until her wrists are near the ground, and fanned her secondary feathers to cover her brood. The light-and-dark-patterned, downy ducklings are just visible beneath the rear quarter, partially protected by the adult's backward-directed primary feathers and the tail feathers. B. Diagrammatic representation of the bone structure underlying the wing in panel A. Note the partial extension of the forelimb. (Photograph from Hosking and Kear 1985, p. 82. The original caption reads, "Mother's wings provide shelter for a brood of mallard ducklings Anas platyrhynchos." *Used with permission)*

Figure 11.2. Bonelli's Eagle shading its brood. The outstretched wing and fanned-out primary and secondary feathers are characteristic of brooding postures used by many modern birds to prevent solar overheating of eggs and chicks. (Photograph from Nicolai 1973, p. 75. The original caption reads, "Wings outstretched, an African Bonelli's eagle Hieraeetus fasciatus spilogaster *provides shade for its young." Used with permission)*

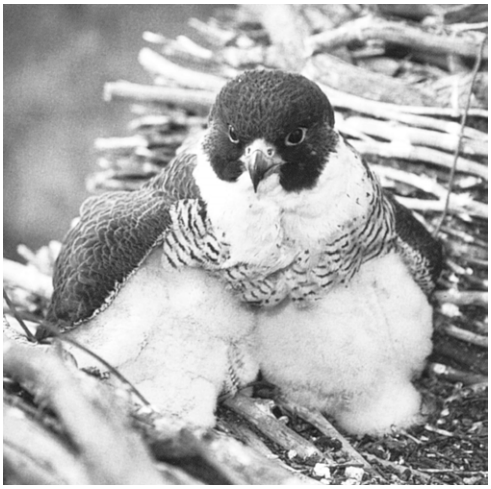

Figure 11.3. Brooding peregrine falcon Falco peregrinus *shelters her two large, downy nestlings from a rain shower. The wings are held in an extended posture similar to the forelimbs of fossil nesting oviraptorids. If deprived of parental cover, chicks often die of exposure-related hypothermia. (Photograph from Olsen 1995, p. 157. The original caption reads, in part, "Day 15: chicks no longer require constant brooding except at night and in cool weather." Used with permission)*

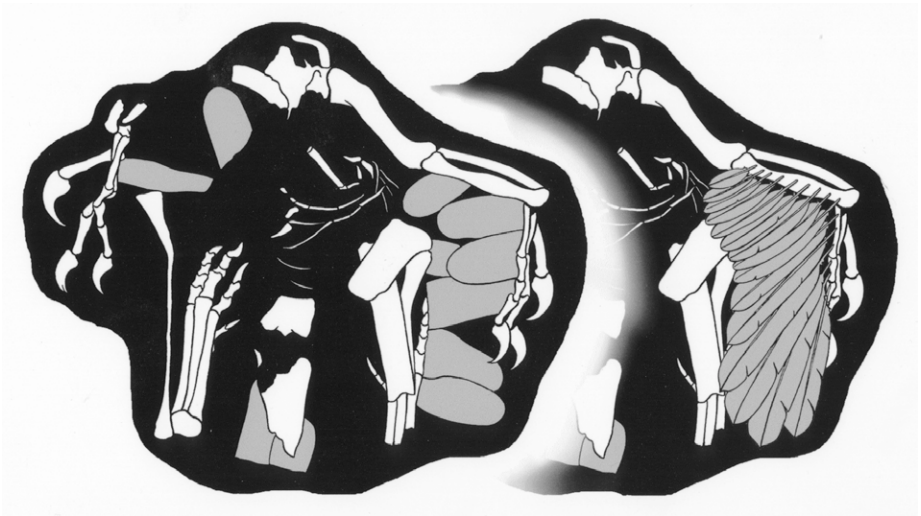

Figure 11.4. Oviraptorid nest fossil and proposed feathers. The diagram on the left represents the nesting Citipati *fossil (Norell et al. 1995; Clark et al. 2001), specimen IGM 100/979, with eggs shaded gray. The animal's breast, forelimbs, and feet were in contact with the eggs. A closely similar posture has been described for another nesting oviraptorid, IVPP V9608 (Dong and Currie 1996). Note the gap in egg coverage between the body and the forelimbs, and the supinated (thumb-outward) position of the manus. Although no traces of feathers were found in the fossil, it is noteworthy that this manus orientation would make it possible for a birdlike set of primary (originating on the manus) and secondary (originating on the forearm) feathers to cover the exposed eggs. A hypothetical set of primary and secondary feathers are illustrated on the right. Also note the* Archaeopteryx*-like juxtaposition of the metacarpals and phalanges of digits 2 and 3, suggesting that, like* Archaeopteryx, *this manus did indeed bear long feathers.*

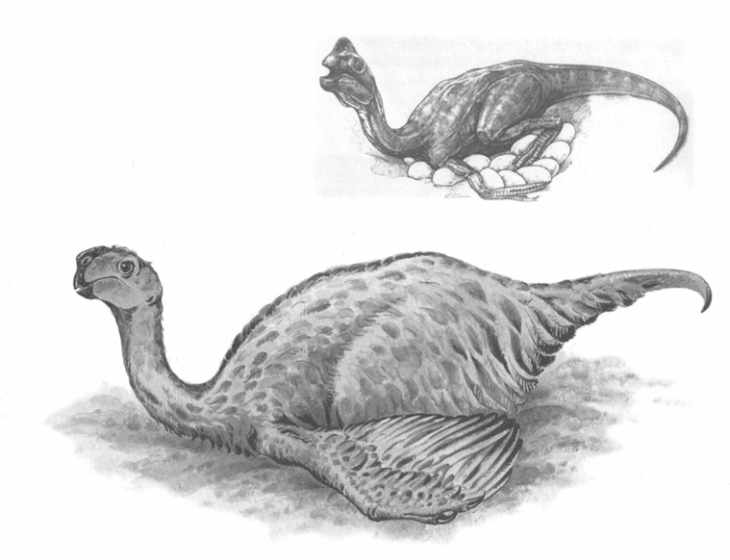

Figure 11.5. Nesting oviraptorid restored with or without feathers. A set of birdlike "wing" feathers enables this oviraptorid to cover its entire nest, with help from elongated feathers at the base of the tail and a flap of skin (propatagium) between the shoulder and wrist (painting by Mark Orsen). Inset, a featherless oviraptorid is shown in the orientation dictated by the original fossil. (M. Novacek 1996, drawing used with permission from AMNH. Notable are the areas where eggs are exposed in front of and behind the forelimb, and at the rear quarter)

A Selective Pressure for Feather Lengthening

More significantly, the forelimb position of the nesting oviraptorid fossils suggests a selective mechanism for the elongation of wing feathers. Whereas it has been hard to determine a selective pressure on a cursorial hunting animal that would drive the initial phases of evolving long forelimb feathers, there is no difficulty in seeing the selective advantage that would result from even small increases in the length of forelimb feathers on a brooding animal. Small increments of feather lengthening would have offered a cumulative selective advantage by gradually increasing the area of cover around the adult (fig. 11.6). Starting with a short-feathered oviraptorid ancestor (at left in fig. 11.6A) there would be a survival advantage in any mutation that improved the animal's coverage of larger clutches of eggs, larger broods, or both. Thus, even small increments of feather lengthening on the forelimbs would enhance breeding success.

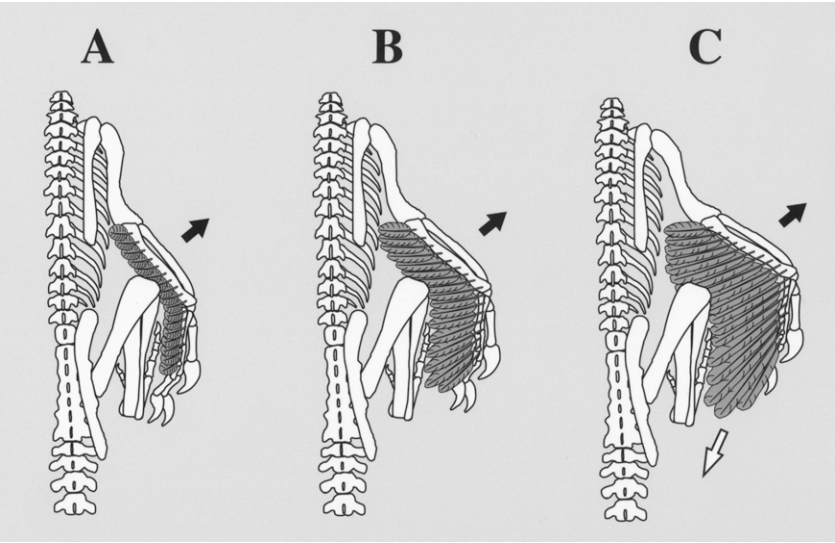

Figure 11.6. Incremental feather lengthening. Oviraptor *(C) is compared to a hypothetical short-feathered ancestor (A) and an intermediate evolutionary stage (B). As the feathers lengthen through a series of mutations, the forelimb is able to move outward (solid arrows) to accommodate larger or more numerous eggs and chicks. The open arrows indicate the area at the rear quarter where longer primary feathers, as well as tail feathers, would improve the coverage of the brood (compare to the mallard in fig. 11.1).*

Over time, a series of small elongation increments would have resulted in forelimb feathers of considerable length. We propose that these brooding feathers ultimately became long enough to be exapted for the additional use of flying, presumably in an animal smaller than *Oviraptor* (for example, *Archaeopteryx*-sized). A need to cover chicks or eggs near the rear quarter of the parent

might additionally have resulted in lengthening of the forelimbs themselves and perhaps some degree of tail feather lengthening (fig. 11.6). Both of these traits would also have helped to pre-adapt *Archaeopteryx*'s ancestors for a transition from brooding to flight. While tail feather evidence is rare, the trait of forelimb lengthening is seen clearly among those theropods related to *Archaeopteryx*'s ancestors. Thus, forelimbs lengthened more or less continuously in going from *Coelophysis* to *Ornitholestes*, to dromaeosaurs, and to *Archaeopteryx* (Dingus and Rowe 1998). In our view, brooding may have been the primary driving force behind both forelimb and feather lengthening among pre-avian theropods.

Among the oviraptorid ancestors, the need for egg and chick coverage behind the forearm and manus could have led to the exact pattern of forelimb feathers commonly found in modern birds. Coverage of the exposed oviraptorid eggs would have required the longest feathers on the animal's manus, whereas shorter feathers would have sufficed along the ulna. The greater length of primary versus secondary feathers has been cited as proof that wing feathers are optimized for flight (Feduccia 1996). However, it would appear that the wing feather lengths of modern birds are equally fine-tuned for brooding. Note again how a mallard (fig. 11.1) uses its longest primary feathers to cover chicks at its rear quarter.

Evolution of Feather Form

In proposing brooding as the driving force behind flight feather evolution, it is necessary to explain why these feathers developed into flat, aerodynamically useful structures rather than downy or plumaceous forms seen in modern flightless birds. Some authors believe that the flattened pennaceous type of feather was the first to evolve, based on morphological grounds (Dyck 1985); and Parkes (1966) and Feduccia (1996) consider the flight feather itself as the primordial type, with body contour feathers and downy or plumaceous feathers being derived from it. This contention is not universally accepted, and the recent discovery of filamentous featherlike structures on the theropod *Sinosauropteryx* casts further uncertainty on the timing of the origins of various feather types (Chen et al. 1998). We consider it likely that the requirements of brooding would have led to the present form of the flight feather, whether starting from scales or from a pre-existing downy, filamentous, or contour feather type.

We envision that the feathered brooding forelimb evolved as an integrated unit, shaped by the need to shelter chicks and to carry the sheltering structure compactly when not in use. The "flight" feather is a lightweight, easily manipulated component of this overall structure, and is highly optimized for its brooding-related purposes. For example, the stout quill (rachis) is required for directing each feather to its unique position, and modern birds exhibit a remarkable range of feather orientations while brooding (cf. figs. 11.1-11.3). Feathers may be either fanned out or compactly folded back against the body, depending on the particular need. The flattened, bladelike form of the feather vane facilitates smooth sliding back and forth during fanning or folding adjustments of the wing shelter, and the barbule-and-hooklet vane microstructure adds rigidity that helps the feather resist the rigors of nestling care, where feathers are trodden upon and come in contact with a variety of nest-building materials. Thus, resistance to damage and reparability, functions of the barbule-and-hooklet system, are required not only for flight, but also for allowing the adult bird to maintain an adequate umbrella-like cover for its chicks.

Feduccia and Tordoff (1979) have made much of the asymmetrical vanes in the feathers of *Archaeopteryx*, arguing that the narrow leading edge is a flight-related condition that favors an arboreal, gliding history among the ancestors of *Archaeopteryx*. However, we note that these authors cited exceptions to their own rule; for example, the retention of asymmetry in the wing feathers of the flightless grebe, *Centropelma micropterum*. Furthermore, there may be non-flight origins of such an asymmetry. The narrow-vaned, leading feather edges are nearest the ground

during brooding (note fig. 11.1), suggesting that feather asymmetry could have arisen in a brooding ground-dwelling theropod in order to keep the edges from fraying through contact with soil or vegetation.

Viewed as an integrated unit, the feathered wing offers a highly adaptable shelter that is useful either for warming or shading the young, yet which can be tucked away tightly when not needed for these purposes. The value of such an adaptable, foldable shelter may have influenced the evolution of the bones of the wing and the flight stroke as well.

Evolution of the Folded Wing

In the evolution of bird flight, an important anatomical development is the folded forelimb posture found among modern birds (fig. 11.7, top). While this is the normal resting posture for most birds, it also approximates the up (or recovery) stroke used in flight (Ostrom 1997). We propose that a need to manipulate brooding feathers may have led to the folding anatomical adaptations of the forelimb before flight arose, and that a brooding-adapted forelimb may have dictated aspects of the anatomy and geometry of the forelimb's use in flight. That is, brooding may have pre-adapted the forelimb for the motions seen in the modern flight stroke, rather than the reverse, where brooding is considered secondary to flight.

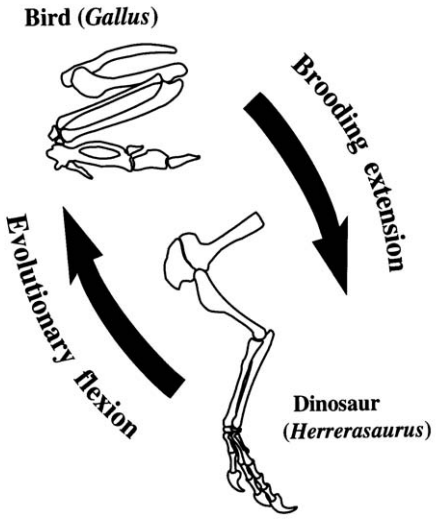

Figure 11.7, Folded vs. extended forelimb (wing). The folded wing of modern birds (top) is an advanced derived condition that is needed to keep the long flight feathers off the ground. However, even modern birds lower their wings to a more primitive posture similar to that of Citipati *while covering chicks (bottom). The relatively inflexible forelimbs of* Herrerasaurus *could attain the postures used by brooding birds (compare to figs. 11.1B, 11.2, and 11.3).*

Among the theropod ancestors of birds, the evolution of longer brooding feathers on the forelimbs eventually would have led to problems—the feathers might be stepped on by the hind feet, seized by a predator, or damaged by contact with the ground or vegetation. The solution to this problem is to hold them close to the body, which in turn requires the joints of the forelimb to be flexed sharply. We suggest that a tightly folded forelimb structure is the consequence of the need to manage the evolving set of brooding forelimb feathers, and that this fold was not, at its outset, dictated in any way by flight requirements. The widespread occurrence of a tightly folding wing, found among many flightless birds, confirms that the way a wing folds, of itself, represents a critical function.

Therefore, most of the anatomical adaptations that occurred during the progression from the forelimbs of theropods to those of early birds may have taken place without any contribution from flight requirements, being driven solely by the need to lift the forelimb feathers. These adaptations include the elevation of the glenoid fossa, development of the uniquely shaped articular surfaces of the elbow that allow its tight folding, and the semilunate carpal bone and wrist architecture that allows acute sideways flexion of the wrist. Most importantly, our concept reverses the order of things: long brooding feathers came first, necessitating the evolution of the elevated, folded forelimb and semilunate carpal, which in turn were co-opted (exapted) for flight.

Although the wrist and elbow joints of the Triassic dinosaur *Herrerasaurus* were far less

flexible than those of the maniraptors and *Archaeopteryx*, they nevertheless suggest the beginnings of the folding characteristics of birds' wings (Paul 1988). Sereno (1993) noted moderate flexion capacity in the forelimb of *Herrerasaurus*, including some sideways wrist flexion (eversion). In particular, we note that the ulnare of *Herrerasaurus* and its wide articulation surface on the ulna (Sereno 1993) suggest a primitive form of birdlike wrist eversion. To us, this implies that this early dinosaur might already have possessed lengthened primary feathers, because this eversion is required for folding such feathers. Novas and Puerta (1997) noted that the extremely birdlike Cretaceous theropod *Unenlagia* could fold its forelimb tightly even though it appears to have been a nonflying species. Thus, forelimb feather lengthening and forelimb folding may have been interrelated processes that started in the Triassic Period and continued among theropods into the Cretaceous.

We note that, while modern birds are capable of assuming tightly folded forelimb postures, many of the orientations used in brooding are reminiscent of those available to their ancestors (fig. 11.7, bottom). Thus, when an adult bird covers a large nest of eggs or a brood of partially grown chicks, it unflexes the wing and extends it outward, downward, and sometimes backward. While the degree to which the wing is extended varies considerably, it is nevertheless true that all brooding uses of the wing move the bones of the forelimb into postures that are more like those that were attainable by primitive dinosaurs such as *Herrerasaurus* (Sereno 1993) and *Coelophysis* (Paul 1988). Some brooding postures represent nearly complete extension of the forelimb into an orientation that should have been available even to theropods with relatively inflexible forelimbs (fig. 11.8). This behavior of modern birds leaves open the possibility of a truly ancient origin for wing feather brooding, because it defines a function for which no flexion capacity in bone structure is required, in contrast to flight, which requires both feathers and forelimb flexion.

Figure 11.8. Brooding gray gull Larus modestus *with one wing extended above its chick. Brooding encompasses many postural variations, and forelimb extension and fanning of wing feathers over the young is important in the hostile environment where these birds nest. Gray gull chicks may die if left unshaded through the heat of a single afternoon in their dry, high desert habitat. (Photograph from Howell et al. 1974, plate 13. The original caption reads, "Gray gull shading chick." Used with permission)*

Brooding and the Origin of Flight

In over 100 years of theorizing about bird evolution, the concept of *Archaeopteryx* as a brooding parent has not to our knowledge been discussed. However, although it is still debated whether *Archaeopteryx* was a good or a poor flier, there can be little doubt that it was a good parent, or it

would not have survived long enough to leave fossils at Solnhofen. Whether or not it engaged in brooding behavior as portrayed (fig. 11.9) remains speculative, but is worth bearing in mind when considering the transition from brooding to flight that probably occurred shortly before the appearance of *Archaeopteryx*.

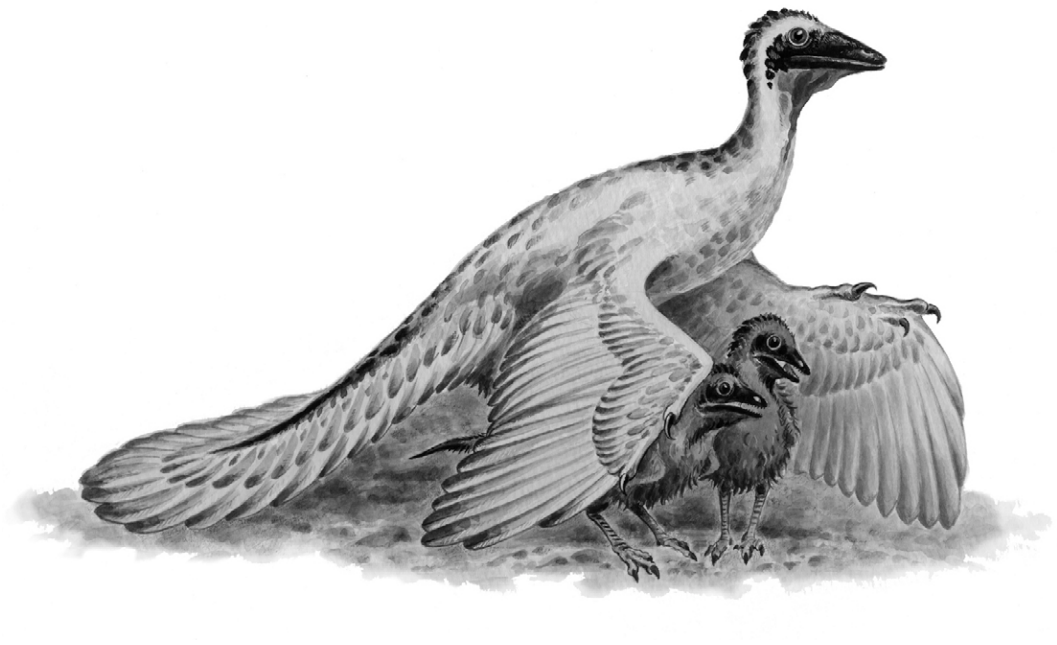

Figure 11.9. Archaeopteryx *parent brooding its chicks. In this restoration, the adult has lowered its forelimbs and spread its wing feathers to provide shelter for its young. Only two chicks are shown for clarity, but we make no assumption regarding the actual brood size for* Archaeopteryx. *(Painting by Mark Orsen)*

Assuming that *Archaeopteryx* arose from a small, nonflying, cursorial theropod ancestor, it is instructive to use the roadrunner *Geococcyx californianus* (fig. 11.10) as a model for the transition to flight. Although roadrunners differ from theropods in that they can fly, they are good models because they spend most of their time on the ground and are cursorial hunters of lizards and snakes (Meinzer 1993). While moving through brush or attacking prey with its beak, a roadrunner keeps its wings tightly folded, only opening them momentarily to confuse its victims or to augment its leaps away from prey counterstrikes. In the latter maneuver, flapping increases the duration of the leap, keeping the roadrunner off the ground for a longer period.

Figure 11.10. Roadrunner Geococcyx californianus *at full stride. This cursorial hunter is a good model for a feathered, brooding theropod. In the theropod ancestors of birds, the shapes of brooding forelimb feathers and the tight folding of the forelimbs may have been dictated by the requirements of this type of foraging, where the feathers would have been subject to trampling or entanglement in vegetation. (Photograph from Meinzer 1993; used with permission)*

In preceding sections of this paper, we have explained how a creature very much like *Archaeopteryx* could have evolved long feathers on its forelimbs for brooding purposes, and developed the bone structure necessary to manage the orientation of these feathers. This leads to an animal closely similar to *Archaeopteryx* in bone and feather structure, from which a roadrunner-like lifestyle could, in turn, lead to the transition to flight. As is true for the roadrunner, the cursorial nonflying theropod could have benefited from brief flapping of the forelimbs to lengthen the distance or to increase the duration of leaps while hunting or escaping predators. Note that such brief flight maneuvers start from the folded wing position and return to it after landing, providing an explanation for the unique geometry of the flight stroke, which includes a close approach to the folded position during recovery before the next stroke begins (Ostrom 1997).

Based on the above rationale, we propose a revised sequence of events in the evolution of bird flight:

1. Long quill feathers with modern flight-feather architecture developed on the forelimbs of nonflying theropod dinosaurs for brooding purposes.
2. The ability to fold the forelimb arose next, or concurrently, to streamline the animal and protect the feathers.
3. Flapping maneuvers developed next, starting from the folded posture, and evolved into the flight stroke.

In our view, the folding geometry of the theropod forelimb, which developed for brooding-feather management, subsequently influenced the mechanism and pattern of the flight stroke. Features of the stroke, such as the simultaneous flexion-extension movements of the wrist and elbow (Ostrom 1997) and the ability to spread the primary feathers into an airtight foil, arose first for brooding and were subsequently exapted for flight. Furthermore, the seemingly prescient development among early dinosaurs of anatomical features used in flight (clavicles, folded forelimbs, elevated glenoids, robust sterna) may instead represent a progression of refinements for handling the ever-lengthening sets of forelimb feathers whose primary purpose was, and is, brooding.

Evolutionary Timing Considerations

In previous models of flight evolution, the development of wing feathers and flight are assumed to be tightly coupled because they are causally related. However, in our model, long forelimb feathers exist independently of flight (or gliding). This allows the possibility that such feathers may have arisen much earlier in time, much more gradually, or both. Given that wings are used for brooding among all the major phylogenetic groups of modern birds, it is most parsimonious to consider wing-brooding a basal rather than a repeatedly derived trait. Therefore it must have existed in the common ancestor of paleognaths and neognaths, whose divergence occurred some time in the Late Cretaceous (Chiappe 1995) or earliest Tertiary (Feduccia 1996). This pushes back the origin of wing feather brooding to a time nearly contemporaneous with *Oviraptor*. Furthermore, if oviraptorids did indeed possess brooding feathers, then the divergence point would revert to an even earlier common ancestor with *Archaeopteryx*, one that must have predated the Jurassic appearance of the latter.

It is not possible to extrapolate further back based on modern birds or oviraptorids, but it is interesting to speculate on how early the forelimb feather brooding trait might have arisen. No

definite feather fossils have been found before *Archaeopteryx*, but just as the posture of the oviraptorid forelimbs (fig. 11.4) suggests the presence of brooding feathers, other bone evidence may be relevant as well. As mentioned, the wrist and elbow joints of *Herrerasaurus* suggest the beginnings of the folding that is characteristic of birds' wings, which in our view may relate to an already existing need in *Herrerasaurus* to lift brooding feathers away from the ground. This suggests that even primitive theropods assumed postures conducive to the kind of feather lengthening portrayed in fig. 11.6.

Based on the points just mentioned, fig. 11.11 portrays graphically the timing of events involved in our "brooding came first" scenario for wing and flight evolution. In this scenario, forelimb feathers arose among the early theropods, and then underwent a substantial period of selection for brooding throughout the Late Triassic and into the Early and Middle Jurassic. Once large forelimb feathers were present, they were eventually exapted for flight as a secondary use at around the time Archaeopteryx appeared in the Late Jurassic.

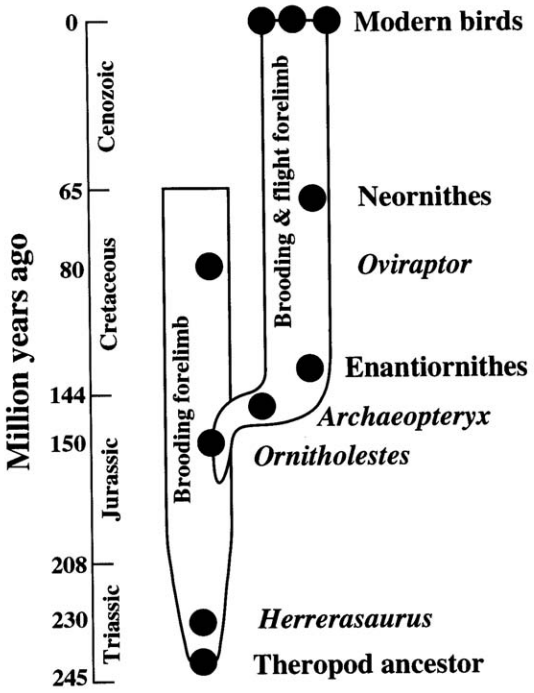

Figure 11.11. Time diagram for feather evolution. The two most critical uses of wing feathers are brooding and flight. If brooding preceded flight as we propose, then the use of a feathered forelimb for this purpose may extend much farther back in time than flight does. Even the basal theropod Herrerasaurus *shows a moderate degree of forelimb flexibility, implying that feathered brooding forelimbs may have existed throughout the history of the theropods from their origins in the Triassic to their demise at the end of the Cretaceous Period (left-hand bar). Bird flight arose secondarily as an exaptation of the already large brooding forelimb feathers (right-hand bar). Brooding remains to this day a major use for wing feathers.*

Conclusions

Recent descriptions of the feathered theropods *Caudipteryx* and *Protarchaeopteryx* (Ji et al. 1998), *Microraptor* (Xu et al. 2000), *Sinornithosaurus* (Xu et al. 1999; Xu et al. 2001), and the unnamed dromaeosaur NGMC 91 (Ji et al. 2001), which appeared in the literature after our presentation of this concept,* are consistent with what we proposed. The forelimb feathers of all these creatures are insufficient for flight, but are large enough and distributed appropriately along the forelimb to have functioned in brooding. Prum (1999) recently proposed a model of feather evolution based on the ontogeny of feather forms. His model is entirely consistent with our concept, and in fact, brooding may have been the primary driving force for the evolution of increased feather complexity that Prum described. Ostrom recently published a discussion of limb-bone flexibility in the evolution of the flight stroke (Ostrom et al. 1999) that is also consistent with our proposal. Recent suggestions that oviraptorosaurs may be secondarily flightless birds (Lu 2000; Maryanska et al. 2002) do not negate our arguments regarding nesting in theropods, because similar nest arrangements are found widely among dinosaurs.

We propose that the need to provide better cover for eggs and chicks was a powerful selective pressure that drove much of the early evolution of flight feathers. In addition, the development of folded wings may be explained by the need to manage the forelimb feathers during different activities ranging from brooding to cursorial hunting. Fossils of nesting oviraptorids provide a snapshot of a primitive, extended-forelimb posture in which forelimb feathers would have been useful for covering either eggs or a brood of chicks. Given that the forelimbs of basal theropods were capable of attaining similar brooding positions, it is possible that forelimb feather lengthening might have begun as much as 80 million years before *Archaeopteryx*. Modern birds retain brooding postures related to those of theropods, suggesting that flight may represent a later secondary adaptation of long feathers that have been used over a much longer period of time for brooding.

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