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Abstract

Very small, altricial hadrosaur nestlings probably lived in open nests exposed to the weather. To survive and grow rapidly they needed to be insulated endothermic homeotherms. Altricial young of small ornithopods and small theropods needed similar adaptations unless they were brooded by their parents. If the parents did brood the hatchlings, they probably needed an elevated metabolism and soft insulation to insulate and warm their young.

Introduction

The dominant and most abundant dinosaurs in many Upper Cretaceous faunas are the large bodied duckbilled hadrosaurs. They grew from diminutive hatchlings with a body mass 5,000 to 10,000 times less than the adults (Fig. 18.1). These little creatures needed to thermoregulate, and how they managed this may have as much to tell us about dinosaur physiology as do studies of the adults. Until recently a lack of juvenile specimens, and the preferential interest shown for the adults have combined to keep the physiology of dinosaur babies from receiving much attention.

Thulborn (1973) and Reid (1978) have expressed the opinion that small size, naked skin, and endothermy would be a lethal combination for nonbrooded hatchling dinosaurs. Russell (1980) suggested that dinosaur hatchlings preferred densely vegetated, wet areas with minimal temperature fluctuations. In contrast, Hotton (1980) suggested that dinosaur hatchlings were large enough to be incipient inertial homeotherms. While McGowan (1979, 1984) believed that juvenile dinosaurs should have been well protected in their nests and good thermoregulators. Horner and Makela (1979) and Horner and Gorman (1988) suggested that juvenile ornithopods were endothermic, and Lambert (1991) argued that the altricial nature of some ornithopod nestlings is suggestive of endothermy.

Studies on dinosaur nesting habits and growth rates provide the basis for examining the thermal envi-

ronment in hadrosaur, hypsilophodont and small theropod nests (Horner & Makela, 1979; Horner, 1982, 1984, 1987, 1988; Horner & Gorman, 1988; Horner & Weishampel, 1988; Coombs, 1989; Kurzanov & Mikhailov, 1989; Russell, 1989; Winkler & Murry, 1989; Currie, 1990; Lambert, 1991; Horner & Currie, Chapter 21). Conditions within the open nests of these dinosaurs were probably often harsh. If this is correct, then the hatchlings that inhabited these nests may have needed "sophisticated" nonreptilian physiologies in order to thrive. Alternately, if small ornithopod and theropod adults were endothermic, then they could have used their warm bodies to brood their young.

Thermal strategies of modern juvenile vertebrates**Reptiles**

Reptilian hatchlings are precocial ectothermic heterotherms. They are not brooded by their parents, and immediately disperse from the nest (Bellairs, 1970). Thermoregulation occurs by behavioral modification and the use of refuges. Reptiles have a narrow preferred body temperature range (30°–39°C in most species, Bellairs, 1970) and a broader tolerance range (up to 45°–47°C in desert forms; Bellairs, 1970). When the upper or lower limits of the tolerance range is reached, reptiles seek refuge in shade, burrow, or water, for death may result from exposure. In addition, at extreme body temperatures growth stops.

Birds

Bird chicks practice a wide variety of metabolic and thermoregulation strategies to achieve ideal conditions for survival and growth. There are, however, some generalized patterns. Many altricial nestlings begin life as poikilotherms, and metabolism slows with falling ambient temperatures (Dawson & Hudson, 1970; O'Connor, 1975; Whittow, 1976a; Steen et al., 1989). They are

naked upon hatching and have lower resting metabolic rates than adult birds of the same mass. Consequently, the very survival of the altricial chicks depends upon the shelter provided by the nest and/or brooding by their parents. Brooding adults provide feathery insulation and warmth at night, and shade and insulation against excessive heat during the day.

Most altricial chicks experience difficulty thermoregulating outside a narrow body temperature range of 30°–40°C. Growth in this temperature range is rapid, but it slows or stops when this range is exceeded (Whittow, 1976b). Some species become torpid and stop growing when their parents leave the nest on long foraging trips (Steen et al., 1989). Air temperatures that drop much below 10°C can be lethal to an unprotected chick (Steen et al., 1989). At high temperatures, a few taxa can use evaporative cooling (Whittow, 1976a), but they remain vulnerable to direct sunlight as long as they are naked. As the chick grows, metabolic rates rise to adult levels, and downy insulation appears. Thermoregulation improves (Whittow, 1976b) and growth slows down, but it is still fast.

Precocial chicks are tachymetabolic while still in the egg, and hatchlings are good thermoregulators (Whittow 1976a, 1976b; Dawson & Hudson 1970; Dawson, Hudson, & Hill, 1972; Freeman, 1971). The body has an insulation of down feathers to maintain a high, constant temperature. Furthermore, the metabolism rises in response to declining external temperatures, and temperatures below freezing can be tolerated for a short time. Heat production in the cold includes both shivering and nonshivering thermogenesis. In addition, elevated temperatures up to 47°C can be tolerated for brief periods (Whittow, 1976a, 1976b; Dawson & Hudson, 1970; Dawson et al., 1972). Growth, however, slows or stops when body temperatures exceed 40°C or drop below 30°–35°C (Whittow, 1976b). Nidifugous chicks

may leave the nest immediately or soon after hatching. They seek optimal thermal microenvironments in the landscape for refuge.

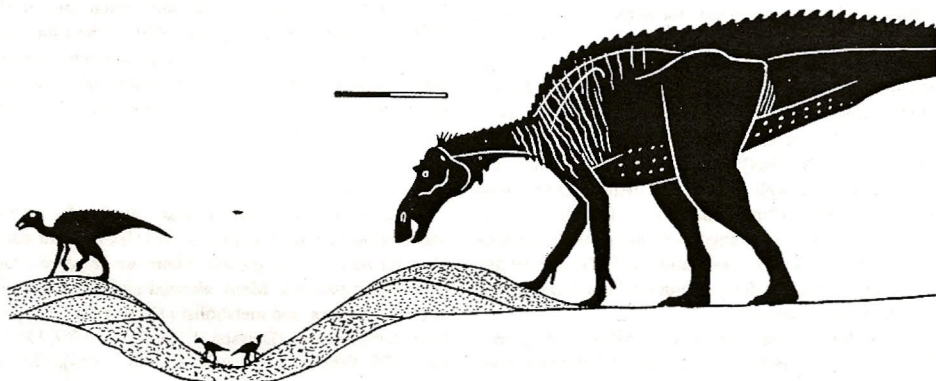
Some birds form nesting colonies in open areas having little or no vegetation to screen the nests from the sun or rain (Dawson & Hudson 1970, 1972; Whittow, 1976a; Perrins & Middleton, 1985). Thermal conditions can become severe due to sunlight, darkness, or storms. Most chicks in such habitats are brooded. One exception is the ridiculous chicks of some gulls. They remain in or near the nests and, because they are not brooded, seek shelter in the surrounding terrain when the nests become too hot (Dawson & Hudson 1970; Dawson et al., 1972).

Among all bird chicks, there is a general, positive correlation between metabolic rate and growth rate (Whittow, 1976b). On the other hand, growth of poikilothermic altricial nestlings is very energy efficient because most of the energy is devoted to growth; metabolic heat is obtained from the brooding parents. As a result, altricial chicks often grow more rapidly than precocial chicks (Case, 1978). Both altricial and precocial nestlings benefit from a steady and abundant supply of food from their parents. This allows them to convert energy into growth rather than use it for foraging.

Mammals

Mammalian young also exhibit diverse thermal strategies. In addition, when they are about one-quarter grown, their metabolic rates are about one third higher than those of adults of equal size (Brody, 1974). The young of most ungulates are precocial, have fairly large bodies, are endothermic, and are insulated with fur. These ungulates are thus able to cope with a wide range of thermal extremes. *Sus* piglets, with a mass of 0.4 kg, have an insulation of light

Figure 18.1. Comparison of a 2.5 metric ton adult *Maiasaura peeblesorum*, 0.3-kg hatchling, and 20-kg juvenile. Adult stands next to a schematic cross section of an open-mound nest containing two hatchlings, while a juvenile only a few weeks old leaves the nest. Nest restored after data in Horner and Makela (1979) and Coombs (1989). Scale bar = 1 m.



body fat and fur. They are able to cope with still, dry air temperatures as low as 5°C (Hull, 1973). Other mammals have altricial young. These are often naked and with underdeveloped endothermy. Consequently, the young receive close attention and warmth from their parents.

Growth

Modern vertebrates

Juvenile reptiles in the wild grow only about one tenth to one thirtieth as rapidly as mammals and birds (Case, 1978). Even in captivity where food is more abundant, they grow much more slowly than poikilothermic altricial bird chicks (Case, 1978; Coulson, Coulson, & Hernandez, 1973). These facts suggest that fast-growing animals must either have high metabolic rates and high, stable body temperatures or else be brooded by warm-bodied parents.

Speculations by Dunham et al. (1989), Houck, Gauthier, and Strauss (1989), and Reid (1990) that unbrooded juvenile vertebrates with reptilian or "intermediate" physiologies could grow as rapidly as birds and mammals remain unproven. For unbrooded juveniles to grow rapidly in a nest they need adaptations to cope with thermal extremes. To cope with high ambient temperatures, the ability to tolerate an elevated body temperature would be advantageous. An insulation of pelage would also protect the skin from absorbing heat. Fat is not a suitable insulation because it does not protect the skin.

Mechanisms for active cooling, such as sweating or panting, are also needed to keep the body temperatures within tolerable limits. On the other extreme, if the ambient temperature is too low, the body temperature can be kept elevated by having a high resting metabolic rate supplemented by nonshivering thermogenesis and shivering. Again, insulation is important because it allows as much energy as possible to be dedicated to growth rather than to keeping warm. Fat insulates well in cold, dry conditions. Fur or feathers insulate in cold, wet conditions because they shed rain and protect the skin from heat loss by evaporation.

Dinosaur nestlings

Maiaasaura nestlings grew rapidly and were able to increase their mass forty- to sixtyfold in 8 weeks or less (Horner & Makela, 1979; Horner & Gorman, 1988; Russell, 1989). Such rapid growth is similar to that observed in altricial bird chicks (see Paul, Chapter 15, Fig. 15.5). Rapid growth is also supported by histological studies of hadrosaurs, hypsilophodonts and small theropod bones (see references in Paul, Chapter 15). The capacity for rapid growth was probably made possible by parental care that allowed the nestling to devote its energy to growth.

Structure of dinosaur breeding colonies and nests

Hadrosaurs and hypsilophodonts apparently nested in colonies consisting of a half dozen to perhaps hundreds of nests (Horner & Makela, 1979; Horner, 1982, 1984, 1987; Horner & Gorman 1988; Horner & Weishampel, 1988; Coombs, 1989; Russell, 1989; Winkler & Murry, 1989; Currie, 1990; Horner & Currie, Chapter 21). These nesting sites appear to have been used repeatedly for many years. The colonies may have resembled those of ground nesting birds being devoid of shade trees (Horner & Makela, 1979; Horner, 1982, 1984, 1987, 1988; Horner & Gorman, 1988; Winkler & Murry, 1989; Currie, 1990; Horner, Chapter 8). Such an interpretation is supported by the apparent absence of large plant roots in the colony sites. The presence of plant material within nest structures suggests that the lack of fossilized plant material between the nests is not an artifact of preservation. The close spacing of the nests, about one adult body length apart, suggests that the nests were placed in open areas.

Without the protection of plants, the nests were exposed to the weather. Some protection, however, might have been provided by the nests themselves. The hadrosaur nest appears to have been a conical depression with a raised rim about 3.0 m across and 1.0 m deep; the sides were about ~30° (Figs. 18.1, 18.2; Horner & Makela, 1979; Horner, 1984; Horner & Gorman, 1988; Coombs, 1989).

Hypsilophodont nests appear to have been smaller and shallower, and therefore more exposed to the weather than those of hadrosaurs (Horner, 1984, 1987; Horner & Gorman, 1988; Coombs, 1989; Winkler & Murry, 1989). A possible theropod nest described by Kurzanov and Mikhailov (1989) appears to have been shallow.

Environmental conditions in open dinosaur nests

The raised rims of the open dinosaur nests partially screened the interior from breezes and low-angle solar radiation. Otherwise, the nests probably provided little protection for their inhabitants. The bottom of the nest was further subjected to infrared radiation reflected and radiating from the walls, creating an ovenlike effect. At night heat loss would be high. Precipitation would have dropped directly into the nest at any time. The exposed dinosaur nests parallels the situation observed in many bird colonies, contradicting McGowan's (1979) assertion that the dinosaur nest provided important thermal protection.

In the nesting grounds, the daytime near surface air temperatures may have exceeded 45°C during the dry season of the temperate and tropical summers (Dunham et al., 1989). Unshaded ground can be up to 30°C hotter than the air (Finch, 1972), so the temperature within the nest could have been as high as or higher than 70°C.

Figure 18.2. Restoration of a breeding season in a *Hypacrosaurus* nesting colony (based on Devil's Coulee egg site, Alberta, in Currie, 1990). The central depressions of the nests are exposed to the elements. Nestlings shown restored with a downlike body insulation to protect against thermal extremes (see text).



Direct sunlight could have also heated the surface of an animal to similarly high levels as observed by Schmidt-Nielsen et al. (1957). At night, when exposed to the open sky, nest temperatures could have dropped dramatically. Temperatures may have dipped as low as 10–15°C when the night was clear and dry and the overhead weather system was cool. Any breezes swirling into the pit would have added a wind-chill factor.

The worst cooling conditions would have occurred during rainstorms, when wind chill and evaporative cooling would have caused a severe heat drain in the nestlings and driven effective skin temperatures to 0°C or less (data from National Weather Service wind chill tables). Nocturnal temperatures during the Cretaceous would have been lowest in high-latitude nests during the winter night, when occasional frosts and storms were possible (Paul, 1988; Spicer & Parrish, 1990). The actual daily fluctuations would have been dependent on cloud cover and humidity. In general, the lesser the cloud cover and the lower the humidity, the higher the daily fluctuations would have been. Dunham et al. (1989) calculated that daily temperature fluctuations for the Campanian in northern Montana exceeded 20°C.

The geographic locale of the nesting sites also had an effect on the thermal extremes inflicted on the nestlings. The *Maiasaura* and *Orodromeus* nesting colonies were located in a dry upland habitat (Horner, 1984, 1987; Wolfe et al., 1987; Horner & Gorman, 1988) that probably experienced wide fluctuations in daily temperatures (Dunham et al., 1989). The *Hypacrosaurus* nesting sites (Horner & Currie, Chapter 21) in Montana and Alberta were closer to the coastline and thus probably under a more moderate maritime influence (Wolfe & Upchurch, 1987). The Proctor Lake nests in central Texas reported by Winkler and Murry (1989) were located in a semiarid environment. Finally, the small theropod nest described by Kurzanov and Mikhailov (1989) was located in the interior of Asia in an area subject to temperature extremes (Barron & Washington, 1982).

The Alberta and Montana nesting sites were probably at higher latitudes during the Upper Cretaceous (Paul, 1988; Russell, 1989). At noon the winter sun rose as little as 6°–12° above the horizon. Winter temperatures were cool, with a mean of 15°C and lows occasionally below 10°C (Paul, 1988 and references therein; Spicer & Parrish, 1990). The coolness was accentuated by the long nights, and chilling storms may have been frequent. The low angle of the sun would probably have suppressed floral growth, so it would have been difficult to feed the nestlings. The low light would also probably have been insufficient to heat the interior of the nests directly. Given these conditions, it is unlikely that ornithopod eggs were hatched at this time of year.

At the opposite extreme, the summer day was long and the sun high in the sky (up to 52°–58° above the horizon). With the nests exposed to the sun for long

periods and under such intensity, the heat loads in the nests would have been high. This effect would have been abetted by the subtropical conditions prevalent: the time and with mean summer temperatures of approximately 30°C (Russell, 1989; Dunham et al., 1989). Floral growth was reduced due to the dry condition. The combination of heat and reduced plant production suggests that the ornithopods did not nest at this time of year.

Russell (1989) suggested that hadrosaurs tried to time incubation of eggs to coincide with the end of the dry season and hatching to coincide with the floral flush at the beginning of the wet season. Horner (1987) suggested that the rainy season in Montana occurred during the spring. He thought that *Orodromeus* nested at this time, but if true, then their nests were often exposed to rain and storms. The noonday sun at this time would have been 29°–35° high at the solstice and higher afterward. On sunny days the interior of the nests could have received high levels of solar energy. Thermal fluctuations could have been very high at this time as weather conditions changed in 24 hours from a chilly and rainy spring night to a hot sunny day. The Proctor Lake and Mongolian nesting sites were farther south than the Alberta and Montana colonies. The nests would have received more warmth in the winter but might have become unbearable between late spring and early autumn.

Based on the above discussions of the various nesting locales and their thermal extremes, certain climatic conditions could be ameliorated by the choice of nesting season. Spring probably offered the best weather conditions for raising nestlings. However, there was no way for nesting dinosaurs to ensure that their young would not experience one or more episodes of severe weather at this time.

Thermal adaptations and strategies of dinosaur nestlings

Hadrosaurs

Hadrosaurs, such as *Maiasaura* and *Hypacrosaurus*, laid between 18–24 eggs in a nest (Horner & Makela, 1979; Horner, 1982, 1984; Horner & Gorman, 1988; Coombs 1989; Russell, 1989; Currie, 1990; Horner & Currie, Chapter 21). Upon hatching, *Maiasaura* chicks weighed only 0.3–0.5 kg and *Hypacrosaurus* 3–4 kg, judging from the volumes of the eggs and hatchling specimens (Fig. 18.1). Hadrosaur hatchlings, like those of most birds, were nidicolous, in that they were bound to the nest for an extended period of time (Horner & Makela, 1979; Horner, 1982, 1984, 1987, 1988; Horner & Gorman, 1988; Horner & Weishampel, 1988; Coombs, 1989; Russell, 1989; Currie, 1990). Evidence for this includes the relatively poor ossification of the limb joints; the apparent trampling of eggshells in small bits and shards, indicating that the nest was inhabited after the eggs hatched; the discovery of juveni-

remains, which would have had a mass of about 20 kg, in a few of the nests; and the extremely rapid rates of growth discussed above.

The underdeveloped joints of nestlings indicate that locomotor performance may have been too poor for the altricial chicks to leave the nest until they weighed over 20 kg. Remains of chicks that size have been found near to but outside the nests, suggesting that a degree of freedom from the nest began at that growth stage. This weight is believed to have been reached at about 8 weeks or less (Horner & Makela, 1979; Horner, 1984; Horner & Gorman, 1988; Horner & Weishampel, 1988; Coombs, 1989; Russell, 1989; Lambert, 1991). The depletion of the flora surrounding nesting colonies by foraging adults, and the need for the adults to cover increasingly larger areas in search of food, makes it doubtful that a longer nesting season could have been possible (Horner & Gorman, 1988; Russell, 1989).

Hadrosaur parents probably carried food to their young within their anterior digestive tracts, and regurgitated it into the nest (Horner, 1984; Horner & Gorman, 1988; Coombs, 1989; Russell, 1989). This would have been more efficient than carrying leafy browse in the mouth. In addition, at present there is no fossil evidence of twigs that may have supported leafy greens within the sediments filling the central pits (that this absence is not due to adverse soil chemistry is implied by the presence of woody material within a nest, Horner & Makela, 1979).

Being restricted to the nest for up to 8 weeks would have exposed the nestlings to potential thermal stress. The options for avoiding this stress appear to have been very limited. If altricial, then they could not leave the nests when conditions became too difficult. The locomotor performance of the nestlings would have been inadequate for them travel to and from vegetation shelter. Restricted to the nest, the nestlings could have burrowed into the soil of the nest; however, the poor ossification of their joints indicates this was probably not possible. Another alternative is for the hadrosaur parents to brood the nestlings. But at 2–3 tons, the adults were far too big and heavy to brood their young safely. In addition, the adults lacked the soft insulation needed for such a task.

Russell (1989) suggested that adult hadrosaurs screened nestlings from the elements, but how this was accomplished is not stated. I am not aware of any modern examples in which adults deliberately screen their young; instead the young seek the shade of their parents or other large objects (Langman, 1982). Nest-bound hadrosaur chicks were probably unable to seek shade in this manner. Instead, they were adapted to tolerate harsh conditions, and this reveals something of their physiology.

Lacking insulation and a cooling system, nestling hadrosaurs operating with a reptilian or intermediate physiology, would have been in danger of succumbing

to the direct rays of the sun. Furthermore, evaporative cooling by wind and rain would have been threatening to bradymetabolic chicks by suddenly driving body temperatures well below ambient air levels. Chilled, torpid hadrosaur chicks would also have been in danger of drowning if the nest flooded. Inertial homeothermy was probably not possible in newly hatched *Maiasaura* or *Hypacrosaurus* because their individual mass would have been considerably less than the 10 kg threshold value suggested by Hotton (1980). Not until body masses of 500 to 1,000 kg were reached after a few weeks was the inertial homeothermy adequate to protect against very high air temperatures and direct sunlight (Spotila et al., 1973; Dunham et al., 1989).

On the other hand, an endothermic physiology and outer surface insulation would have given the hadrosaur nestlings a much greater chance of surviving temperature extremes. Heat flow analyses (Dunham et al., 1989) of an uninsulated hadrosaur chick with a low metabolic rate showed that the body temperature could vary from 20°–45°C on a summer day. Under winter conditions, body temperature fluctuations could be 2°–20°C. The body temperature of an insulated endothermic nestling would have been much more stable, between 38°–45°C under the same conditions.

At present, there is no direct evidence for the integument of small juveniles. Nevertheless, as argued here some form of superficial insulation is needed for protection against solar radiation (including ultraviolet) and high external heat loads. This insulation may have been in the form of down feathers that were later shed (see comments in Paul, 1988). Other possible juvenile integuments are elongated scales with soft bristled edges or a hairlike pelage. A light colored downy plumage is typical of nonbrooded bird chicks in hot nesting colonies, and a similar pelage is advocated for hadrosaur chicks. Preening with glandular oils may have enhanced water shedding by the insulation.

Hadrosaur chicks may have cooled themselves by resonant frequency panting and/or gular fluttering. Water might have been obtained from the regurgitation by the parents of moist, predigested plant material. As long as this water was available, the thermoregulatory adaptations detailed above should have allowed the unshaded hadrosaur nestlings to survive daily peak temperatures as high as 70°C on the surface of their insulatory coats. Periods in which wind chill and rain drove the temperatures close to or below freezing could have also been tolerated as long as the chicks were well fed.

Hypsilophodonts

At Proctor Lake, Texas, 40-kg adult hypsilophodonts appear to have laid one or two dozen eggs per nest. The mass of the hatchlings was about 0.07–0.15 kg (Winkler & Murry, 1989). The presence of ~1.5 kg chicks in some of the nests suggest that they were either altricial, or semiprecocial in that they periodically re-

turned to the nest. At what point they permanently left the nest is not known. Some form of parental care is suggested by the altricial nature of the juveniles, their presence in the nests, and the presence of adult skeletons near the nests (Winkler & Murry, 1989).

In contrast, the young of the Montana hypsilophodont *Orodromeus* appear to have had a more mobile life-style (Horner, 1982, 1984, 1987; Horner & Gorman, 1988; Horner & Weishampel, 1988; Coombs, 1989). Intact eggshell bases, well-ossified limb joints in the hatchlings, and an absence of posthatchling juveniles in the nests are indicative of precocial chicks that left the nest soon after hatching – a pattern similar to most reptiles and various birds (Perrins & Middleton, 1985). The presence of half grown juveniles within the nest horizon sediments suggests that *Orodromeus* chicks remained in the area for a few weeks. A lack of adult skeletons near the nests implies, but does not demonstrate, that the precocial young were independent immediately upon hatching (Horner & Gorman, 1988). Lambert (1991), however, argues that the parents fed their young in the colony area.

Because *Orodromeus* chicks were apparently able to leave the nest to seek shade and other thermal microhabitat refuges, then their thermodynamic performance need not have been as well developed as that of hadrosaur chicks. However, the chicks could have grown rapidly only if they were tachymetabolic and insulated, or if they were brooded. The shallowness of the Proctor Lake hypsilophodont nests and the evidence for parental care are compatible with parental brooding, but do not prove that this occurred.

Brooding would have reduced or eliminated the need for well-developed thermoregulation in the nestlings. However, brooding makes sense only if the adults were themselves insulated endothermic homeotherms. A pelage would be necessary to keep the adults warm on cool nights and dry during storms, and to protect them from the sun. They may have also had a naked brood patch to facilitate warming the eggs and chicks. Insulation surrounding the patch would help screen the brood from the elements and trap heat when conditions were cool. The compact bodies of hypsilophodonts were probably not suited for brooding with their bodies in the manner of some pythons (Bellairs, 1970).

Small theropods

A nestlike structure, tentatively assigned to a small theropod by Kurzanov and Mikhailov (1989), contained the remains of many eggs. The size of the nestlings is unknown because they had evidently vacated the nest. However, they were probably similar in mass to hypsilophodont nestlings. Well-crushed eggshells and numerous small bones of possible prey suggest that the young were fed at the nest for a period of time. This care within the nest suggests that the chicks were either altricial or semiprecocial, and had little or no life outside the nest.

It is not known whether or not the theropod nest was shaded during the day or protected during storms. Regardless, if the chicks were either altricial or semiprecocial, they would have had the same need for well-developed endothermy and insulation as in hypsilophodonts. The close relationship of the theropods to birds reinforces the possibility that they had elevated metabolisms. It also suggests that, if the juveniles had insulation, it was true feathers.

Other dinosaurs

Nests of prosauropods, protoceratopsids, and iguanodonts have been reported, but not enough information is yet available to assess whether the babies in these cases were altricial or precocial. It is unlikely that sauropods gave live birth to large inertial homeothermic young (Paul, Chapter 15). The eggs of some dinosaurs assigned to sauropods and troodont theropods are laid in unstructured nests that suggest the young were fully precocial upon hatching and could retreat to thermal refuges (Horner 1987; Cousin et al., 1989).

Conclusion

All dinosaur nestlings, regardless of whether they were altricial, precocial, or semiprecocial, probably lived in exposed nests. The physiological model that best explains their rapid growth is tachymetabolic, endothermic homeothermy with an insulating pelage. Those hatchlings, such as hypsilophodonts and small theropods in which this physiology may not have been fully developed, may have been brooded by insulated, endothermic homeotherm adults.

This insulated endothermic model for the hatchlings is conservative in that it applies a standard physiological type to the subjects. There is no evidence that contradicts this conclusion, but it cannot be proven with the current data. The alternatives are that hadrosaur nestlings did not live in exposed nests, or that they managed to tolerate exposure with naked skin and a reptilian or some other physiology.

The first alternative would require a revision in our current understanding of the nest environment or the behavior of the nestlings. There might have been shade plants over the nests; the nests might have been filled with vegetation screens; or the juveniles might have been able to leave the nests when conditions were poor. Supportive evidence, however, is lacking for any of these alternatives. The second alternative would require an uninsulated nestling with a low metabolic rate to survive and grow rapidly without a refuge from weather extremes. This would require invoking a new type of physiology that would be difficult to test. That this alternative may be improbable is suggested by the fact that no reptile or altricial bird chicks live in open nests. We are left to conclude that the hypothesis of hadrosaur nestlings being insulated and endothermic best fits Ock-

ham's razor and is therefore most probable (Jefferys & Berger, 1992).

As the young dinosaurs grew, they may have gradually shifted from an endothermic to a more reptilian physiology in response to having a more thermally stable body mass (Lambert, 1991). It may have taken 1 or 2 years for the larger species of dinosaurs to reach the mass needed for thermal stability, and about 4 to 6 years to reach the higher thermal stabilities of masses over 1 ton (Paul, Chapter 15). Rapid growth may have continued for several years or decades after this stage in some of the largest dinosaurs.

It is doubtful, however, that once adult size was reached the metabolic rates dropped significantly. A moderate decline is seen in large mammals and birds (about 30 percent relative to mass^{0.75}; Brody, 1974). More dramatic declines in metabolic rates do not occur because heart rates would drop, as would blood pressure. This would seriously degrade the aerobic capacity of the animal. Tachymetabolic endothermy, combined with insulation provided by either a large size or a pelage, would have also improved the ability of adult dinosaurs to stand by and guard their nesting young in shadeless colonies by day and in the cold of the night.

Acknowledgments

I thank J. Horner, P. Currie, and K. Carpenter for discussions and information on the subjects of dinosaur nesting and skin, and L. Huxthall for the same on ostriches.

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