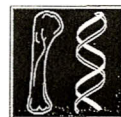


# Reproductive Behavior and Rates

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Despite the finding of dinosaur eggs in the year *On the Origin of Species* was published, and the famed Gobi Desert finds in the 1920s, little scientific attention was paid to dinosaur reproduction until the discovery of dinosaur nesting complexes starting in the 1970s. Since then our knowledge of dinosaur reproduction has expanded enormously, although it remains fragmentary (Coombs, 1989, 1990; Carpenter *et al.*, 1994). Past views that dinosaur reproduction was "reptilian" in nature and included little parental care have been replaced to a certain extent by an "avian-mammalian" view that may in some cases overemphasize their parenting skills.

The sexual aspect of dinosaur reproduction is preserved via the presence of sexual dimorphism and potential display and combat characters. A repeated pattern of two morphs, gracile and robust, has been recognized in many theropods. It has been argued that the gracile morphs are males, in part because of the configuration of bones at the base of the tail. Females are larger than males in a number of tetrapods (including birds of prey and whales), and species with robust females tend to be nonsocial and frequently predaceous. Herd-forming herbivores in which males fight for territory and/or females often exhibit male size-strength superiority, and this may have been true of most plant-eating dinosaurs. Many dinosaurs exhibited potential sexual skeletal features, some of which may be developed dimorphically between the sexes. The features include cranial tusks, hornlets, large horns, crests, and nasal diverticula, as well as erect body armor plates, spines, and tail clubs. Well-developed caniniform teeth of heterodontosaurs have been both suggested and denied as a male character. Hadrosaur head crests appear to have been better developed in one sex, probably males, in at least some examples. Ceratopsid crests and especially horns also exhibit signs of dimorphic development. Visual displays to establish male dominance, increase species identity, and enhance breeding success are

possible functions of prominent dental, cranial, and skeletal features. The hollow crests and nasal diverticula of hadrosaurs may have served similar purposes as sound-generating auditory display features. The crests of lambeosaurine dinosaurs and some theropods appear too delicate for physical use. The more solidly constructed nasal ridges of some large ornithomorphs, tail clubs of ankylosaurids and a few saurophids, lateral body spikes of armored dinosaurs, and especially the horns of large ceratopsids were potential weapons for establishing breeding dominance among males. Possible horn wounds in ceratopsid skulls may record combat of this nature. Sharp teeth, sharp beaks, and large claws could also be used for the same purposes. Even kicking may be an important way of establishing breeding rights, and broken ribs in predaceous and herbivorous dinosaurs may record such combat.

Intraspecific weaponry often evolves in order to minimize the potential for injury and death. The interlocking nature of large ceratopsid brow and crest horns, the nasal boss of pachyrhinosaurids, the flat-topped or horn-rimmed heads of some pachycephalosaurs, and the low, ridge-shaped nasal crests of some large ornithomorphs appear to have been adapted to minimize damage. However, this principle should not be exaggerated. Serious injury and mortality are often significant among extant large mammals fighting over breeding rights: Male lions and hippos are notable examples of this phenomenon. The same may have been the case among some dinosaurs, especially ceratopsids with large parrot-like beaks and long nasal horns. The full development of potential sexual display features in hadrosaurs (head crests) and ceratopsians (horns and head frills) suggests that these dinosaurs at least did not become sexually active until nearly fully grown—an attribute reminiscent of birds and mammals rather than of reptiles, which often become fertile when they are a fraction of adult size.

Little attention has been paid to the mating posture



of dinosaurs, which poses interesting problems in terms of the great size of many examples, and the erect dorsal armor of a few species. All dinosaurs had large tails and bore most of their mass on their hindlimbs (whose bones are always stronger than those of the forelimbs), so it was probably easier for even the most gigantic males to bipedally mount females than it may appear. In living diapsid reptiles and birds the male copulatory organs are internal except when needed, and the same was probably true of dinosaurs.

Our understanding of dinosaur nesting and parenting behavior is limited by a lack of data for the great majority of skeletal taxa and by the uncertain identity of most dinosaur egg nests (the origins of many of the long-known famous Cretaceous nests in France and central Asia are either in dispute or have only recently been resolved). What is known of dinosaurian nesting and parenting suggests that it was highly diverse, perhaps more so than within any extant major tetrapod groups (Table I). The reproductive flexibility of dinosaurs can be attributed to their combination of oviparity (which allowed the production of few or many young), often rapid growth (allowed care of young to be nil or to be provided until fully grown within a reasonable period of time), the absence of lactation (which allowed parental feeding to range from nil to substantial), and high locomotory capacity (which allowed but did not require extensive social-parenting activities, including long-range foraging trips by parents feeding nestlings). In these attributes dinosaurs were arguably most like their larger avian relatives. No dinosaur is known to have been viviparous in the manner of mammals and some reptiles. The well-calcified shells of dinosaur eggs may not have been compatible with live birth.

Many if not all dinosaurs were like most reptiles and large birds in being oviparous *r*-strategists (producing large numbers of eggs). A notable feature of many dinosaur nests is the careful placement of the eggs both individually and relative to one another in distinctive patterns (see EGGS, EGGSHELLS, AND NESTS). The organization is greater than that observed in most extant egg-laying amniotes. It has been argued that dinosaurs used their hands to make the final arrangement of the eggs before burying them. It has been countered that the eggs were deposited directly into their final positions. Among herbivores, nest building and egg laying may have been timed so that emer-

gence of hatchlings coincided with maximal seasonal floral growth, whether this was spring at higher latitudes or the beginning of the wet season at lower latitudes. Predatory dinosaurs may have timed the same event to coincide with maximum prey availability. Some herbivorous dinosaurs nested in colonies. Optimal local soil conditions could have encouraged egg-burying dinosaurs to nest in the same location. In addition, colonial nesting reduced but did not eliminate predation—whether by large theropods attacking large adults or by small predators hunting adults, juveniles, and eggs—by providing group protection and/or by overwhelming the feeding capacity of the local predator population. The nests of some small dinosaurs regularly appear to contain more eggs than could be laid by one female. This implies communal nesting, which is practiced by some large birds.

After egg deposition, dinosaurian care of eggs and young may have ranged from none at one extreme to the feeding and guarding of nestlings at the other. Eggs broadcast in simple hole nests were the most likely to be abandoned after burial: mound and open nests were the most likely to be guarded. The incubation temperatures of fermenting mound nests may or may not have been regulated by adults in a manner similar to megapode fowl, adding or removing nest material as needed. Recent and remarkable discoveries have included the discovery of small advanced theropods lying directly atop their eggs. The nests and eggs show a combination of the reptilian and the avian (Norell et al., 1995; Varricchio et al., 1997). The eggs are larger than expected in reptiles, but were deposited in pairs, and they were partly buried, which indicates a degree of environmental heating. The eggs were also partly exposed, and the position of some of the adults—with the forelimbs carefully draped over eggs—was like that of brooding ratites (Fig. 1). Although brooding may include shading exposed eggs, the ultimate reason to leave eggs exposed is to incubate them with body heat. The near avian brooding of these theropods appears to have been very different from the brooding observed in some snakes (Table I). Indeed, because the narrow body and slender arms of brooding theropods could not entirely cover the eggs, it is possible that some form of insulating pelage more completely covered the eggs.

The long snouts and large teeth of young tyrannosaurs are unusual for dinosaurs and suggest that they



TABLE 1 Nesting and Parenting Behavior in Cenozoic Amniotes and Dinosaurs

**Reptiles**

General—Oviparous and viviparous. Because eggs can be small relative to females, reproductive output can be low to very high. Eggs usually buried in soil. Because low aerobic exercise abilities prevent extensive social interaction and parental foraging, young are precocial and abandoned upon deposition. Slow growth also hinders parenting over extended periods.

Python—Brooks exposed eggs with sinuous body warmed by muscular contractions.

Crocodylians—Females of some examples build and maintain fermenting vegetation mound nest incubators. Nests usually guarded, to the point adults may lay atop nest (but eggs are not exposed and brooded). May assist hatchlings. Young often gregarious, sometimes herded and strongly defended by parent, which can socialize with young because they are energy efficient swimmers.

**Mammals**

Monotremes oviparous; the rest viviparous. Some small examples nest, often in dens. Reproductive output low to high in small examples, large size of calves limits large examples to low output. High aerobic exercise capacity and rapid growth allows extensive parenting over most of juvenile period. All juveniles nurse, rendering them highly dependent on parents. Juveniles altricial to precocial.

**Birds**

General—Oviparous. Reproductive output low. Nests from simple to complex usually constructed, sometimes in colonies. Because parents have high aerobic metabolisms and are warm-bodied, eggs are usually exposed and brooded, and juveniles receive extensive care including feeding in or near nest. Rapid growth facilitates parental care.

Juvenile altricial to precocial. Megapode fowl build and maintain fermenting vegetation mound nest incubators. Juveniles precocial and independent upon hatching.

Ratites (living and recent)—Reproductive output low in island examples, high in continental examples. Multiple females may deposit eggs in one nest. Precocial young leave nest soon after hatching and are largely self-feeding although minor parental assistance may occur. Gregarious young are herded and protected by adults; sometimes many broods are combined into a large crèche under care of one adult pair.

**Dinosaurs**

General—Probably all oviparous. Reproductive output high, with some low rate examples possible. Growth moderately to very rapid.

Simple hole nests (many unassigned eggs)—Nests may be isolated or in groups. Either abandoned immediately or guarded. In some cases semi-intact hatched eggs suggest young left nest soon after hatching.

Tyrannosaur juveniles—long snouts of juveniles suggest independence.

Hypsilophodont and other dinosaur nests with eggs laid vertically and in complex patterns—Careful placement of eggs in vertical position suggests burial rather than brooding. Nests often in colonies, spacing of nests by one adult body length indicates nests were guarded. In some cases semi-intact hatched eggs suggest young left nest soon after hatching. In some cases the presence of fast-growing, short-snouted juveniles with well-ossified limb joints near nest suggests that precocial chicks remained in nesting colony for an extended period, perhaps cared for and fed by parents.

Small theropod nests—Ratite-like posture of adult *Oviraptor* skeletons atop exposed eggs strongly suggests incubation via brooding. Trampled eggshells and damaged bones of small vertebrates in a nest tentatively assigned to small theropods suggest altricial nestlings fed by parents.

Hadrosaur mound nest colonies, bone beds, and trackways—Eggs incubated in fermenting vegetation mounds, built and probably maintained by parents in large colonies; spacing of nests by one adult body length suggests the latter. Trampled eggshells, and the presence of short-snouted juveniles in nest, suggest altricial chicks remained in open-pit nest and were fed by parents. Trackways and skeletal associations suggest that postnestling juveniles were gregarious and perhaps independent. Calves joined large herds when about one-half adult dimensions.

Ceratopsid bone beds—Sudden death assemblages suggest juveniles moved with adults when one-fifth adult dimensions.

Sauropod trackways—Young too small to join adult herds until they were one-third adult dimensions (about 1 ton).



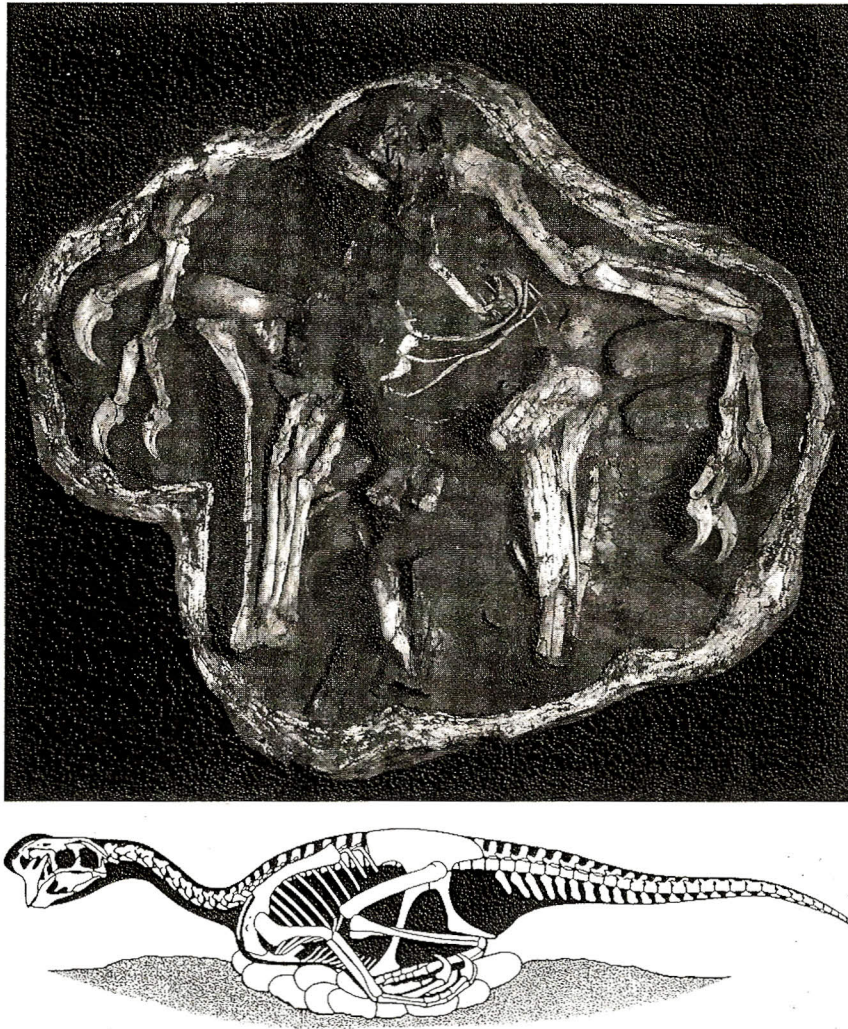


FIGURE 1 (Top) The preserved nest of an *Oviraptor* lying atop a spiral of eggs, viewed from above, with left side of the animal on the left. (Bottom) A restoration of the dinosaur brooding the eggs. Note that in both images the deep pelvis fits into the hollow circle formed by the eggs, and that the arms are draped over the eggs. No living reptile broods its eggs in this manner (contrary to Geist and Jones, 1996). Images courtesy M. Norell, American Museum of Natural History.

may have been independent hunters immediately or soon after hatching. As for those dinosaurs that cared for their offspring, the production of large numbers of young would have tended to reduce the parental attention received by each baby dinosaur. Also, most dinosaurs had small, simple brains, so their parent-offspring relationships were probably more stereotyped and limited than that observed in larger brained tetrapods. Therefore, most dinosaurs probably did not provide the intense one-on-one parenting observed in mammals and most birds. The short

snouts characteristic of most if not all herbivorous and some predaceous dinosaurs may have acted as visual cues to incite parental attention and care (Horner and Gorman, 1988). If any adults fed their young, they may have done so with regurgitants, which may have been an important means of transferring the gut bacteria needed to digest fodder from one generation to the next. It is not known whether any small dinosaurs brooded their nestlings, but it is plausible considering the evidence for egg brooding. Arguments that the tiny hatchlings of some small



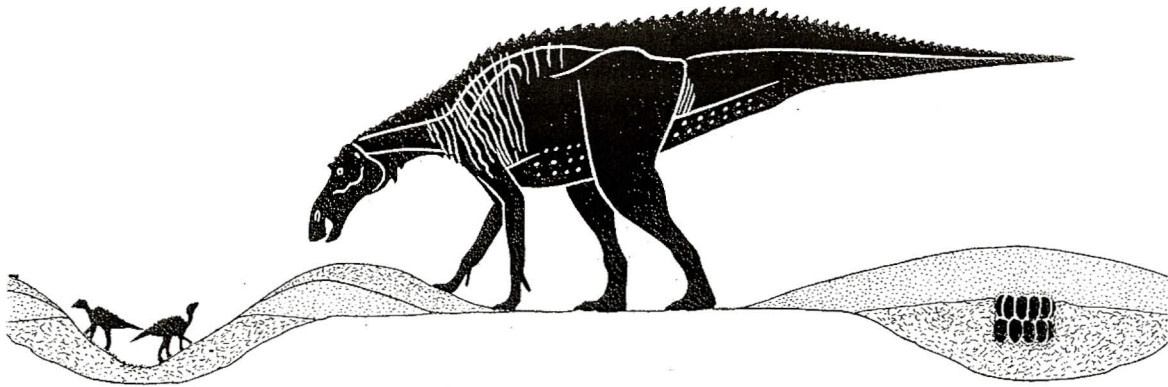


FIGURE 2 Restored nesting behavior in the 2.5-ton hadrosaur *Maiasaura*. Eggs were incubated in large, fermenting vegetation mound nests, spaced one adult's body length from other nests in large colonies. As eggs hatched, the nest was converted into a pit in which the nestlings lived.

dinosaurs were too small to be parented are countered by the extreme size disparity between newly hatched and adult ratites. Some of the largest-brained small theropods may have practiced the most comprehensive parenting among dinosaurs—but note that some hole nest eggs, probably abandoned immediately upon deposition, have been tentatively attributed to troodontids. Large dinosaurs were too heavy to brood their offspring. The extreme size disparity between adults and young of the largest dinosaurs may have rendered parental care impractical. The young juveniles of large dinosaurs were probably too small to join herds of adults, where they could have been trampled. Postnestling juveniles that were not independent were probably under the guardianship of only their parents, or perhaps in a multibrood crèche under the care of one pair of adults, until they were large enough to join herds. There is some evidence that independent and parented juveniles were gregarious. Suggestions that trackway patterns show juvenile sauropods within a protective ring of adults have been discounted, but it remains possible that the calves received active or passive protection by associating with larger individuals.

Hadrosaurs built mound nests in colonies, and the hatchlings weighed a few kilograms (Fig. 2; Horner and Gorman, 1988; Horner, 1996). Geist and Jones (1996) argued that the ossified pelvises of baby hadrosaurs indicate well-developed locomotory abilities associated with precocial habits, but Horner (1996) countered that the leg bone shafts were so poorly ossified that the babies should have been immobile

and therefore altricial. Trampling of the eggshells into small bits also suggests that the nests were inhabited for an extended period, as does the finding of individuals a few times larger than the hatchlings in or near the nests. Usually, fully immobile nestlings are limited to more isolated predator-free areas. It is possible that hadrosaur nestlings were semialtricial, with just enough locomotory ability to flee the nest if a predator penetrated the parental defenses. Some juvenile crocodilians, which are fully precocial and can wait for prey to move into their range, remain near their nest for months or years. However, the bone microstructure of hadrosaur chicks indicates that they grew much more rapidly than reptiles, which take years to grow the amount observed in hadrosaur nestlings. Such fast-growing herbivores would be under pressure to range far and wide if they fed themselves. The most logical explanation of why young hadrosaurs remained in and/or near their nests is because their parents fed them there. This would have been highly advantageous to the chicks; at no cost to themselves they received large quantities of food that dramatically boosted the pace of growth over that which can be achieved without parental feeding. If, for example, parent-fed nestlings grew about 15 kg in 1 or 2 months, then their growth rates matched those of the fastest growing birds (ostrich chicks take about 70 days to grow a similar amount). In this view, parental feedings of altricial nestlings were a means by which giant adults boosted the growth rates of tiny juveniles, until they were large enough to move in the company of adults without being trampled. Hadro-



saur nestlings apparently lived exposed to the elements in open-pit nests. Temperatures may have ranged from low during cool rain storms to very high under sunlight. Bird nestlings that live in similarly harsh nesting colonies, and are not shielded by their parents, have well-developed thermoregulatory controls. The same may have been true of hadrosaur nestlings, a possibility supported by bone isotope analysis (Barrick and Showers, 1995). The browsing pressure placed on the flora surrounding a nesting colony by hadrosaurs foraging for food for their charges may have been very high, and the parents may have had to range out a dozen or more kilometers each day toward the end of the nesting period. Lack of sufficient food due to drought and/or overpopulation, thermal stress due to extreme weather, flooding, and disease vectors were common potential sources of mass mortality that could wipe out most of a year's production of offspring in a hadrosaur nesting colony.

Some dinosaurs may have been no more parental than other reptiles, but the level of egg care and parenting exhibited in some dinosaurs appears to have been above that practiced by any living reptile, including crocodilians. Conversely, dinosaurian parenting was probably not at the very sophisticated and intense levels practiced by most mammals. The descendants of terrestrial dinosaurs, birds, have both retained and modified a set of reproductive strategies patterned after their ancestral group.

Because gigantic dinosaurs laid small eggs, they had the highest adult to juvenile mass ratios observed among tetrapods—many tens of thousands in the case of the largest sauropods (the ratio is about 30 in elephants). Such extreme initial-final size ratios required very fast juvenile growth in order to reach sexual maturity within two or three decades. Animals must start breeding within that time frame in order to ensure that enough juveniles survive to reproduce. The size superiority of dinosaurs vis-à-vis land mammals cannot be attributed to the indeterminate adult growth of the former. Termination of growth and life is nearly coincident in bull elephants, and incremental growth cannot account for the size disparity of 20–100 tons (like other animals, dinosaurs could not live and grow for more than 100–150 years because death becomes a statistical certainty). Consider a 100-ton sauropod that started reproducing at one-third adult mass at age 20 or 30. Its peak growth rate would

approach or exceed 5 kg per day, a rate otherwise observed only in whales. Even adult growth would have been about 2 kg per day, a rate far in excess of that of which living terrestrial reptiles are capable.

The reproductive strategies of large dinosaurs, birds, and mammals share the characteristic of rapid growth, which boosts rates of population expansion. The reproductive strategies of large dinosaurs and large birds differs from that of large mammals in two key regards: lactation or its absence, and rate of reproduction (Table II). Regarding the latter, large dinosaurs were not slow-breeding *K*-strategists like mammals of equal size. Instead, they were fast-breeding *r*-strategists with annual reproductive outputs similar to those of many smaller reptiles and mammals and large birds (Fig. 3). The annual and lifetime

TABLE II

Observed and Predicted Population Dynamics for Large Land Tetrapods

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<b><i>K</i>-strategist megamammals</b> —Birth rates low. Growth fast; generational turnover fairly rapid. Juvenile mortality moderate. Adult populations of megamammals must be high in order to raise the few highly dependent, nursing young they produce. If adult populations drop too low, not enough juveniles survive to mature and slowly produce enough new young to reestablish the population. Because the available resource base must be divided among a large number of adults, the size of individuals is limited to about 20 tons. Populations skewed toward adults; adult population densities relatively low.
<b><i>r</i>-Strategist reptiles</b> —Egg deposition rates high. Growth slow; generational turnover slow. Juvenile mortality high; nonnursing young fully or partly independent of adults. Growth is too slow to take full advantage of the size potential associated with rapid reproduction, so adult masses limited to 1 ton. Populations skewed toward adults; adult population densities very high.
<b><i>r</i>-Strategist megadinosaur</b> —Egg deposition rates high. Growth fast; so generational turnover probably fairly rapid. Juvenile mortality probably high; nonnursing young fully or partly independent of adults. Combination of <i>r</i> -strategy reproduction and independent young allowed whale-sized adults because even if small adult populations were lost, only a small population of nonnursing juveniles needed to reach sexual maturity and start repopulating the habitat. Populations skewed toward juveniles; adult population densities somewhat lower than those of megamammals of similar size, extremely low over 30 tons.

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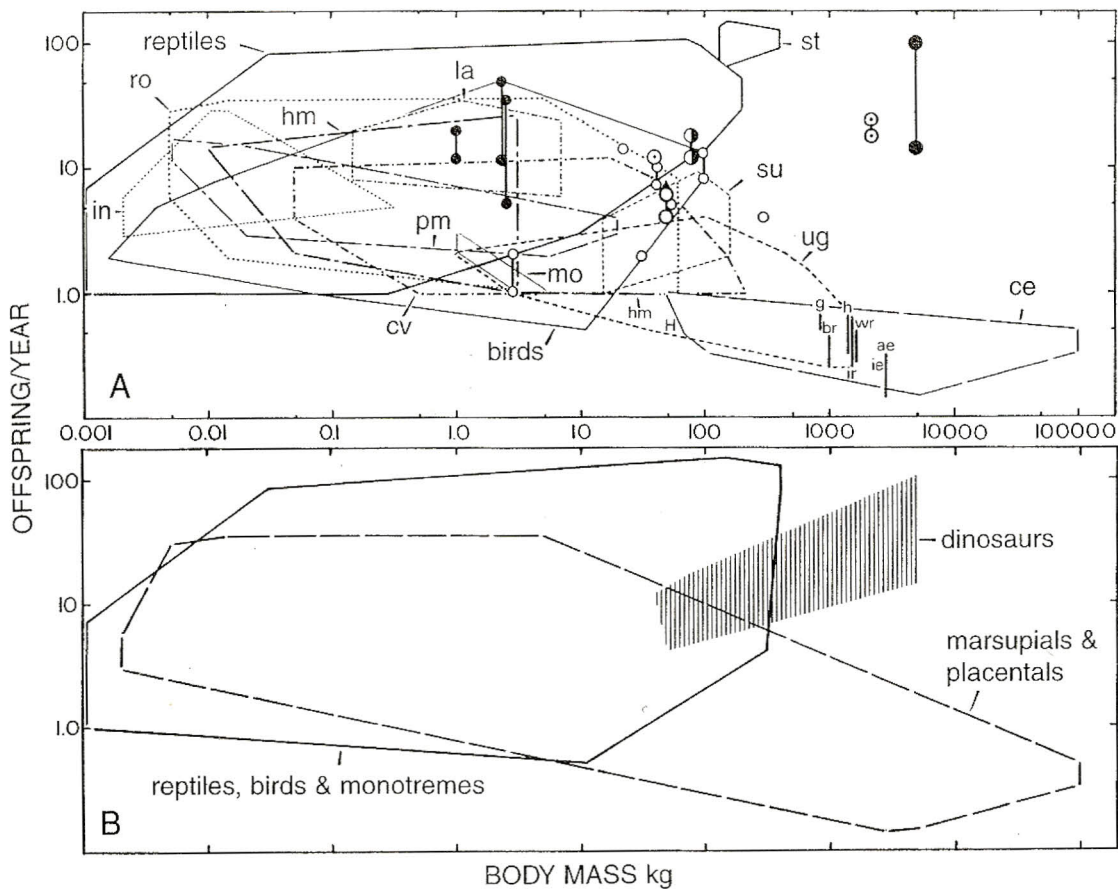


FIGURE 3 (A) Annual reproductive potential as a function of the body mass of breeding females in living and recent amniotes and dinosaurs. (B) The same data reorganized to compare oviparous versus viviparous taxa and dinosaurs. Reproductive potential is total egg or newborn production. Most living groups are enclosed in least-area polygons; nonpredaceous marsupials from 3 to 40 kg fall upon the single line indicated; marine turtles (st), megapodes (small solid circles), continental ratites (rhea, emu, cassowary, and ostrich; small open circles), island ratites (kiwi and moas; small circles with dots), elephants (African, ae; Asian, ie), giraffes (g), black rhinos (br), hippos (h), Indian rhinos (ir), white rhinos (wr), humans (H). The major mammalian groups plotted are cetaceans (ce), ungulates (ug), suids (su), carnivores (cv), rodents (ro), lagomorphs (la), insectivores (in), herbivorous marsupials (hm), predaceous marsupials (pm), and monotremes (mo). Dinosaurs plotted are the sauropod *Hypselosaurus* (tentative; large solid circles), hadrosaurs *Maiasaura* and *Hypacrosaurus* (large bold circles with dots), hypsilophodonts (large circle with dot), and the theropods *Oviraptor* (large half-solid circles) and *Troodon* (tentative; large open circles). From Paul in Carpenter *et al.* (1994).

reproductive output of a sauropod was at least 50 times higher than that of an elephant. Large ornithischians outbred rhinos of similar size by almost as much. Also, female dinosaurs could breed every year or more often, whereas extended gestation periods force big female mammals to space births by at least 2 years. Juvenile mortality was presumably much higher in dinosaurs than in mammals. Also, compared to smaller birds and mammals with similar annual reproductive rates, slower generational turn-

over limited large dinosaur reproductive output. Even after these factors are taken into account, the potential population growth rates of large dinosaurs under optimal realistic conditions were probably many times higher than the 6–12% expansion rates observed in large mammals.

In ecological terms, large dinosaurs may have been "weed species" with rates of population recovery and dispersal well above those seen in large mammals (Janis and Carrano, 1992; Farlow, 1993; Paul as cited



in Carpenter *et al.*, 1994). Because periodic loss of the adult portion of the population had to be tolerable, it was possible for species to evolve oversized adults whose populations were too low to ensure their stability—the extreme scarcity of extremely large, 50- to 150-ton sauropods suggests that this view is correct. A single large sauropod was the rough equivalent—in terms of energy intake, population density, and reproductive output—of an entire elephant herd. As a consequence, dinosaurs should have been able to achieve far larger adult masses than mammals living on similar resource bases. For example, South America supported 50- to 100-ton sauropods in the Cretaceous compared to 5-ton proboscideans in the Neogene. High recovery and dispersal rates also rendered large dinosaurs highly resistant to extinction, which may explain the long-term stability of most major large dinosaur groups. In comparison, slow-breeding large mammals are much more sensitive to disruption, and most major terrestrial groups (uinkatheres, arsinotheres, brontotheres, and indricotheres) have been geologically short-lived. The greater resistance of fast-breeding large dinosaurs to extinction vis-à-vis similar-sized mammals complicates attempts to explain their loss at the K-T boundary. It has been suggested that temperature fluctuations at the K-T boundary catastrophically distorted male-female sex ratios in dinosaurs because the ratio may have been dependent on the temperature of the incubating eggs. The closest reptilian relatives of dinosaurs, crocodilians, have temperature-dependent ratios, but the more closely related birds have genetically determined sex ratios. It is therefore possible that most or all dinosaurs had the latter system, and this hypothesis of dinosaur extinction cannot be falsified or supported.

#### See also the following related entries:

BEHAVIOR • EGG MOUNTAIN • EGGS, EGGSHELLS, AND NESTS • GROWTH AND EMBRYOLOGY

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