

# Dinosaur reproduction in the fast lane: Implications for size, success, and extinction

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## Abstract

Large dinosaurs were apparently r-strategy egg layers with reproductive outputs much higher than those of K-strategy large mammals. Dinosaur populations may have consisted mostly of posthatchling juveniles that were not dependent upon their parents for survival. That dinosaurs grew as rapidly as mammals suggests similarly elevated metabolic rates. Dinosaur population recovery and dispersal potentials were probably much higher than those observed in giant mammals. Low population levels of adult dinosaurs enabled individual adults to consume relatively large portions of the available resource base, thereby becoming larger than mammals. The r-strategy-based survival potential of the dinosaurs helps explain their long period of success, and exacerbates the problem of explaining their final extinction. Some of the problems inherent in modeling the population dynamics of r-strategy dinosaurs are examined.

## Introduction

Most investigations of the evolutionary forces behind the gigantism of some dinosaurs have focused upon the great size of the adults (Figs. 15.1 and 15.2; see also Weishampel & Horner, Chapter 14). Little attention has been paid to the fact that even the most colossal dinosaurs began life as nidifugous hatchlings no bigger than the chicken. Can hatchling dinosaurs provide clues toward understanding why they so often grew so large?

Large terrestrial mammals are K-strategists that emphasize low juvenile mortality, starvation resistance, and high dispersal to maintain population levels. As shown below, dinosaurs, on the other hand, were fast breeding r-strategists. The dramatic difference between these two reproductive strategies was briefly mentioned by Kurten (1953), but was only recently examined in detail by Carrano and Janis (1990), Janis and Carrano (1992), and Farlow (1993).

Many studies of dinosaur extinction tacitly as-

sume that dinosaurs were broadly similar to large mammals in population dynamics, genetic information processing, and vulnerability to disruptive events. For example, Jablonski (1991) lists large size as a possible factor in the extinction of the dinosaurs, but also acknowledges that juveniles and small adult forms also vanished. The apparent fecundity of dinosaurs suggests that in some ways their reproductive strategies were more like those of small mammals rather than large mammals. The production of many nidifugous juveniles may help explain how and why dinosaurs often grew to gigantic dimensions and why they were such a stable and successful group for such a long time, and also makes it more difficult to explain their ultimate extinction.

Much of the data, discussion, and conclusions presented must be considered tentative, and are offered in the hope of encouraging further consideration on dinosaur size and reproduction. The prefix "mega-" refers to animals with a body mass of one or more tons. Dinosaurs are not considered to be reptiles in the typical sense, and birds are treated as a separate group to better examine reproductive differences. I also assume that dinosaurs reproduced on an annual basis, although multi-annual and semi-annual breeding cannot be discounted. Because dinosaurs probably grew at rates similar to those of birds and mammals (see below), it is assumed that their life and reproductive spans were also broadly similar to those of birds and mammals of similar mass.

## Reproduction, growth, and recovery potential of dinosaurs

### Reproductive method and potential

Recently, Bakker (1986) has suggested that sauropods gave birth to live young. This hypothesis runs contrary to the fossil evidence of sauropod nests, eggs,

Figure 15.1. Size comparisons of giant continental dinosaurs, mammals, and reptiles drawn to the same scale. Extinct taxa based on largest known specimens, and masses from volumetric models. Extant and recent taxa based on large adult males. A. 60- to 80-ton titanosaur (Bonaparte, 1989). B. 55-ton *Supersaurus*. C. 45-ton *Brachiosaurus* (= *Ultrasaurus*). D. 13-ton *Shantungosaurus*. E. 6-ton *Triceratops*. F. 7-ton *Tyrannosaurus*. G. 16-ton *Indricotherium*. H. 2-ton *Rhinoceros*. I. 5-ton *Megacerops*. J. 10-ton *Mammuthus*. K. 6-ton *Loxodonta*. L. 0.3-ton *Panthera*. M. 1-ton *Scutosaurus*. N. 1-ton *Megalania*. Human figure 1.62 m tall. Scale bar = 4 m.

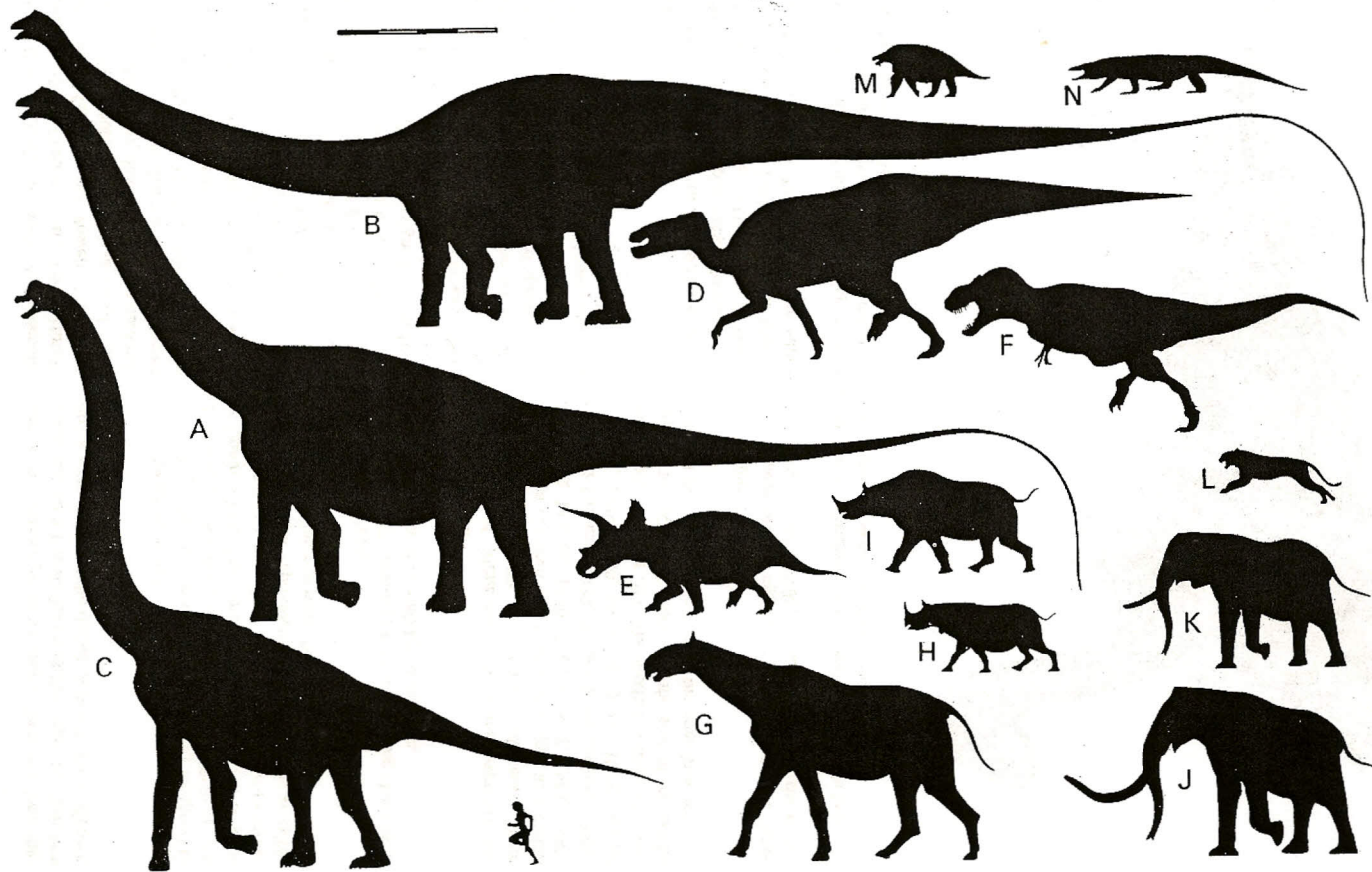
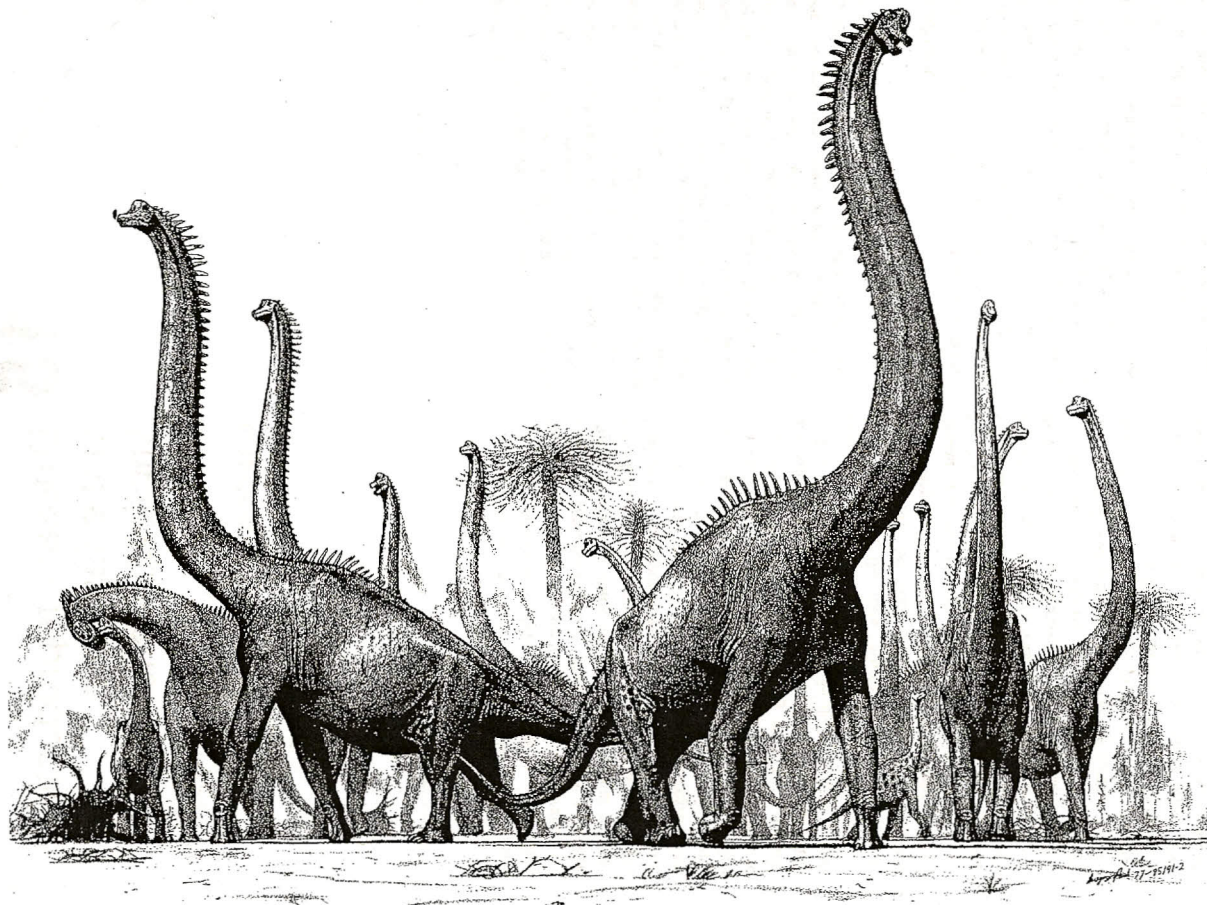


Figure 15.2. *Brachiosaurus brancai* as a representative of large dinosaurs. Size distribution based on associated parallel sauropod trackways, and includes a few large adults, some subadults, and juveniles. Size of juveniles is believed to be the minimum size able to keep up with the herd.





and hatchlings (Fig. 15.3; Erben, Hoefs, & Wedepohl, 1979; Mohabey, 1987; Cousin et al., 1989; Hirsch, 1989; Paul, 1991; Moratalla and Powell, Chapter 3; however Jain, 1989, disputes Mohabey's report of a sauropod hatchling). All known dinosaur eggs had hard calcified shells, and it is possible that this adaptation barred a shift to live birth (Packard, 1977). If this is true, then dinosaurs must have been oviparous.

Prosauropods, small to large theropods, small ornithopods, some hadrosaurs (such as *Maiasaura*), and small ceratopsians had egg volumes of 0.1 to 0.5 L (Case, 1978b; Horner & Makela, 1979; Horner, 1987; Horner & Gorman, 1988; Horner & Weishampel, 1988; Winkler & Murry, 1989). Eggs of the hadrosaur *Hypacrosaurus* were more voluminous at 4 liters (Horner and Currie, Chapter 21), while those assigned variously to iguanodonts and to sauropods were 2 to 3 liters in volume (Case, 1978b; Cousin et al., 1989; Dodson, 1990).

Reproductive rates for five types of Late Cretaceous dinosaurs can be determined. These are hypsilophodontid (*Orodromeus* and an unnamed species from Proctor Lake, Texas), small theropod (?*Troodon*), ceratopsian (*Protoceratops*), hadrosaur (*Maiasaura* and *Hypacrosaurus*), and sauropod (*Hypselosaurus*).

#### *Hypsilophodontid*

Nests are known for the small ~40-kg *Orodromeus* and Proctor Lake hypsilophodontid (Horner, 1982, 1984, 1987; Horner & Gorman 1988; Horner & Weishampel 1988; Coombs, 1989, 1990; Winkler & Murry, 1989; Hirsch & Quinn, 1990). The nests contain either

one or two dozen eggs or nestlings. These numbers suggest that each female laid a dozen eggs, and that two dozen eggs represent the output of two females (Horner, 1987).

#### *Small theropod*

Egg clutches have been questionably assigned to *Troodon*, a small 50-kg theropod (Horner, 1987; Hirsch & Quinn, 1990). The clutches contain two to three pairs of eggs a linear row. Four eggs is considered to represent the minimal reproductive potential. It is possible that multiple clutches were deposited.

#### *Protoceratops*

I follow Thulborn (1991) in assigning clutches of about 18 eggs to this ~80-kg ceratopsian.

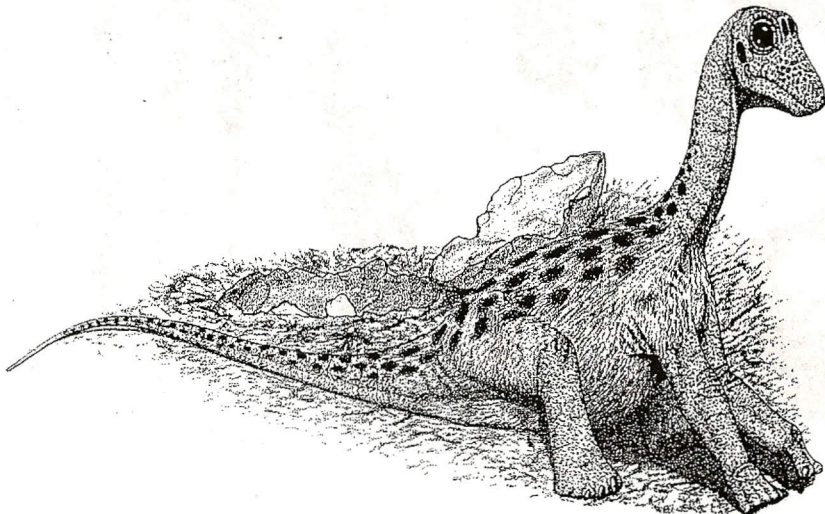
#### *Hadrosaur*

Nests of *Maiasaura* and *Hypacrosaurus* are known for these 2,000 to 2,500-kg hadrosaurs. There are between eighteen and twenty-four eggs in a clutch (Horner & Makela, 1979; Horner, 1982, 1984, 1987; Horner & Gorman, 1988; Horner & Weishampel, 1988; Coombs, 1989, 1990; Hirsch & Quinn, 1990; Horner and Currie, Chapter 21). The modest volume of these eggs (5 to 100 liters) relative to the size of the adults suggests that one female laid all the eggs in a nest.

#### *Sauropod*

Large arcs of eggs have been identified as *Hypselosaurus* (Case, 1978b; Hirsch, 1989; Cousin et al.,

Figure 15.3. Small size of dinosaur hatchlings (3 kg titanosaur sauropod hatchling shown here) made possible large clutch sizes and high reproductive rates that rendered even the largest dinosaurs r-strategists with exceptional population recovery and dispersal potential.



1989, Chapter 5; Dodson 1990; Vianey et al., Chapter 11). This sauropod is poorly known, but the adult mass is believed to be about 5000 kg. The arcs contain up to fourteen eggs, and this is taken as the minimum potential reproductive output of the sauropod. Case (1978b) suggested a maximum of 100 eggs per individual, a number that is reasonable for an animal of this size.

In Figure 15.4 the estimated breeding rates for the dinosaurs just discussed is compared to the known rates of extant female vertebrates. In extant taxa with an adult mass of 1 g to 10 kg, the annual number of young produced is broadly similar in both egg layers and live bearers. Above 10 kg the number of young of the two types diverge significantly, with many oviparous taxa being much more prolific than mammals. This divergence is mainly due to a decline in fecundity in mammals with a mass of over 5 tons.

Dinosaur reproduction is essentially an extension of the reptilian-avian pattern, with many eggs produced as part of an r-strategy mode of reproduction. Small dinosaurs had reproductive potentials overlapping those of both viviparous and oviparous animals. The annual reproductive output of herbivorous dinosaurs equals or exceeds that of rodents, lagomorphs, and other small mammals, and was much higher than that of large herbivorous mammals.

Reproductive potential over a lifetime can also be compared. For example, female elephants between age ten to fifty produce about a dozen young (Owen-Smith, 1988). During the same 40-year interval, a sauropod could have produced 500–4,000 eggs. Reproductive rates for dinosaurs and mammals also scale differently. Large mammals breed less rapidly than small mammals (Western, 1979; Eisenberg, 1981; Owen-Smith, 1988). In dinosaurs, however, reproductive rates remain constant or increase with size. This conclusion is similar to that of Janis and Carrano (1993) that the reproductive output of large mammals diverges from that of large dinosaurs.

Dinosaurs could breed every year or two, replacing clutches that were destroyed. Female mammals with a mass over 10–100 kg are constrained by the long gestation period or time spent by the progeny in a pouch or nursing. Weaning takes 3–12 months in most ungulates, 2–3 years in megaungulates, and 3–18 months in large marsupials (Langman, 1982; Owen-Smith, 1988; Nowak, 1991). Therefore, most cannot reproduce faster than once every year; megamammals are limited to reproducing every 2 or more years.

#### Parental care and feeding of juveniles

The amount of parental care given by dinosaurs appears to have varied widely, from wholly dependent (precocial) nestlings to fully independent (altricial) hatchlings (see Paul, Chapter 18).

Horner (1988; Horner & Gorman, 1988) has suggested that the short, "cute" snouts of altricial dinosaur

hatchlings may have been display characters designed to invoke parental care. Certainly hadrosaur hatchlings appeared to have been nest bound and dependent upon their parents for 1 or 2 months (Horner & Makela, 1979; Horner, 1982, 1984; Horner & Gorman, 1988; Horner & Weishampel, 1988; Coombs, 1989; Lambert, 1991).

Trackway and bone-bed evidence indicate that young dinosaurs did not join herds with adults until they were sufficiently large enough to keep up. The minimal sizes of juveniles in mixed size herds are the following: sauropods, over one third adult size (Fig. 15.2, Bird, 1985; Farlow, Pittman, & Hawthorne, 1989); hadrosaurs, nearly one half adult size (Horner & Gorman, 1988); ceratopsids, one fifth adult size (Currie & Dodson 1984); hypsilophodonts, one quarter adult size (Thulborn & Wade, 1984). Before joining the herds, the young may have formed into pods that were either independent or under the care of one or more adults (Horner & Makela, 1979; Horner & Gorman, 1988; Forster, 1990; Lockley, 1991). Pod behavior in some theropods may be seen in juvenile trackways that are not in association with the tracks of larger adults, suggesting that the youngsters were independent (Bird, 1985; Lockley 1991).

As these young became less dependent upon the parents, they were able to meet their own food, thermoregulatory, and defensive requirements which may have differed significantly from those of the adults. In these respects dinosaurs were like typical reptiles in that by pursuing a distinctly different niche, the juveniles avoid competing with and being a burden upon their parents.

#### Rates of growth

Juvenile dinosaurs grew rapidly at rates comparable to those of birds and mammals (Ricqlès, 1980; Currie, 1981; Bakker, 1980, 1986; Currie & Dodson, 1984; Paul, 1988b; Reid, 1990; Dunham et al., 1989; Russell, 1989; Farlow, 1990; Lambert, 1991; Leahy & Paul, 1991; Chinsamy, 1992; Varricchio, 1992). Rates of growth are plotted in Figure 15.5. The very rapid growth of hadrosaur nestlings matches the highest rates in altricial bird nestlings. These rates, as well as those of extant birds, show that lactation is not a prerequisite for high rates of growth (contra Pond, 1983). Instead, high minimal and maximal metabolic rates are required (Case, 1978a; Leahy & Paul, 1991). The gap between the growth rates of terrestrial reptiles and mammals increases with increasing size! This fact contradicts the possibility that the growth rates of gigantic ectotherms converge with those giant endotherms.

#### Adult/juvenile population ratios and total populations

Richmond (1965) suggested that the scarcity of juvenile dinosaur fossils reflected a reptilian pattern of high juvenile mortality and slow growth. In point of



fact, juvenile dinosaurs are abundantly represented in the fossil record (Dodson, 1975; Carpenter, 1982). Up to 80 percent of the dinosaur skeletal remains in the Two Medicine Formation are of juveniles less than half adult size (Horner & Makela, 1979). The high percentage of young individuals in the Two Medicine Formation is not abnormal, based on the many eggs laid by female dinosaurs. In fact, adult/juvenile population ratios should be skewed towards younger age classes. Support for such a prediction is available from the abundant trackway data of Texas and Korea (Lockley, 1991, Chapter 23).

The adult/juvenile ratios of dinosaurs stand in marked contrast with those of K-strategy mammals. Mature adults make up 60–70 percent of stable populations

of modern megaherbivores, and 45–55 percent of growing populations (Owen-Smith, 1988). Among carnivores, adults form 40–85% of the populations (Kruuk, 1972; Schaller 1972).

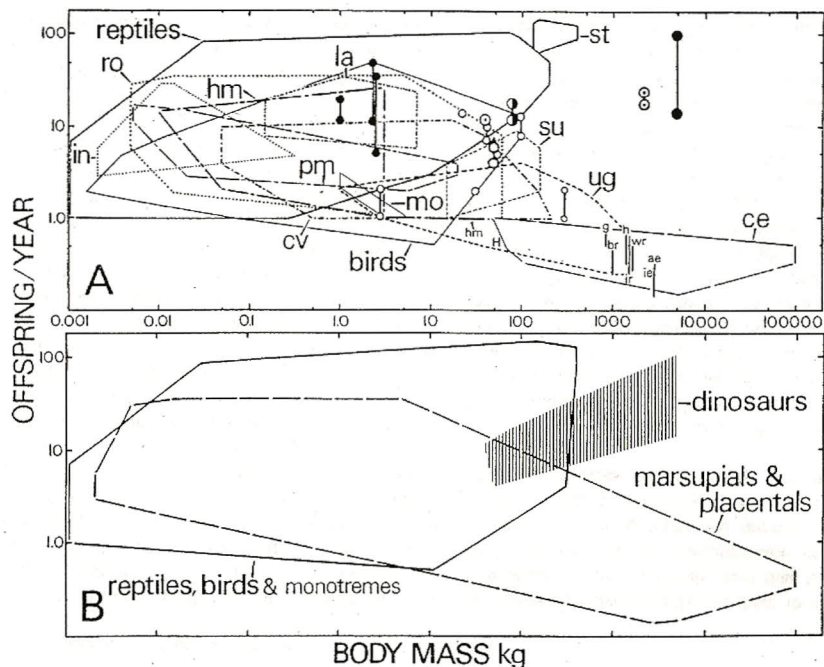
#### Population expansion, dispersal and recovery potential

In stable populations of r- and K-strategy animals, reproductive rates tend to be balanced by juvenile mortality (Colinaux, 1978). The differences between the two reproductive strategies become more apparent when the populations are less stable due to decreased competition (e.g., availability of a new habitat) or a population decrease of predators. K-strategists produce few offspring; therefore, maximum rates of population

Figure 15.4. A. Annual reproductive potential as a function of body mass in living and recent vertebrates and dinosaurs. B. Same data reorganized to compare oviparous and oviviparous taxa with viviparous taxa and dinosaurs. Reproductive potential is measured in terms of total egg or newborn production (marsupials newborn based on available number of teats). Ranges of reproductive potential are plotted except for unusually extreme values in mammals, and domestic and captive animals. Most living groups enclosed in least area polygons, except nonpredaceous 3- to 40-kg marsupials which all fall upon the single line indicated.

Symbols and abbreviations: small open circles, continental ratites (rhea, emu, cassowary, and ostrich); circles with dots, island ratites (kiwi and moas); small solid circles, megapodes; large solid circles, sauropod (*Hypselosaurus*); large heavy circles with dots, hadrosaurs (*Maiaasaura* and *Hypacrosaurus*); large half solid circles, *Protoceratops*; large light circle with heavy dot, hypsilophodonts and the theropod *Troodon*. ae, African elephants; br, black rhinoceros; ce, cetaceans; cv, carnivores; g, giraffes; H, humans; h, hippopotamus; hm, herbivorous marsupials; ie, Asian elephants; in, insectivores; ir, Indian rhinoceros; la, lagomorphs; mo, monotremes; pm, predaceous marsupials; reptiles, sphenodonts, turtles, lizards, snakes, and crocodilians; ro, rodents; st, marine turtles; su, suids; ug, ungulates; wr, white rhinoceros.

Data from Austin and Singer (1971), Grzimek (1972), Porter (1972), Ellis (1980), Nowak (1991), Campell and Lack (1985), Perrins and Middleton (1985), Seymour (1991), data for moas from Anderson (1989).



growth remain low even when juvenile mortality is reduced. In contrast, the population of r-strategists can grow much more rapidly when many juveniles survive. High rates of growth to sexual maturity increases the intrinsic rate of natural increase (McNab, 1980)

Megamammals (giraffes, rhinoceroses, hippopotomuses, and elephants), which are K-strategists, are limited to annual population expansions of only 6–12% by their maximum reproductive rates and minimal juvenile mortality rates (Owen-Smith, 1988). For this reason, at the beginning their population growth curves are rather shallow (Colinaux, 1978). Megadinosauurs, on the other hand, had steeper population growth curves because they produced many more young. How high the annual population growth of large dinosaurs might have been is unknown. Considering how many more potential, fast-growing young a megadinosaur could produce annually than a megamammal, dinosaurian population growth rates approaching or exceeding 100% per year

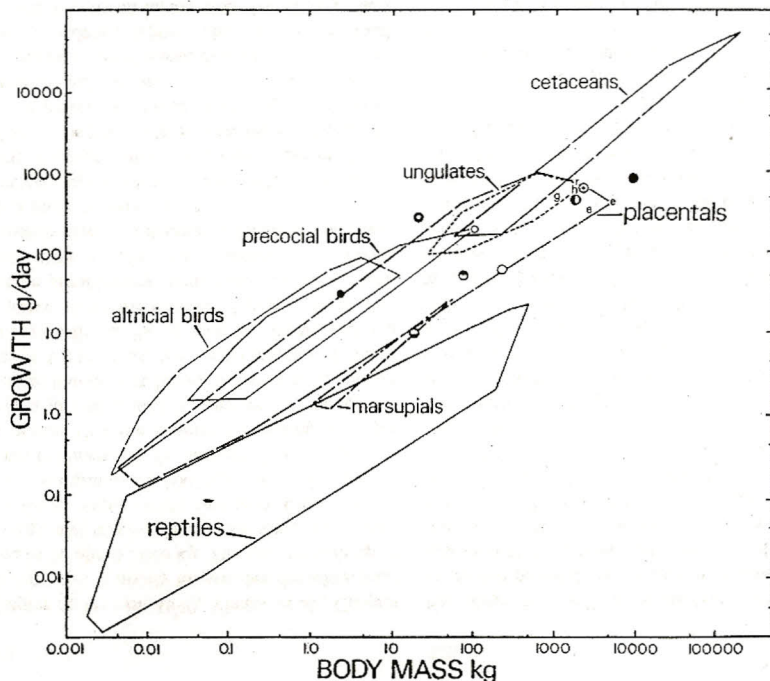
are hypothetically possible. In reality, high egg and juvenile mortality prevented this from happening.

The hypothetically high replacement rates of dinosaurs suggests that juvenile (post-nestling) dinosaurs could replenish decimated population levels to their former levels relatively fast, even if all the adults had been killed off! In this, megadinosauurs may have been better suited than megamammals to rebounding after devastation of their populations.

### Reproduction: key to the large size and success of dinosaurs

Evolving into a large size is a common feature among vertebrates (Stanley, 1973). The great size of dinosaurs was remarkable not only because many of them grew to body sizes unmatched by terrestrial mammals (Figs. 15.1 and 15.6), but also because they were a very successful group for ~150 Myr. About three-fifths of the dinosaur species were in the mega-size range (Hot-

Figure 15.5. Growth in grams per day as a function of adult body mass in living vertebrates and dinosaurs. Only terrestrial and freshwater, noncaptive reptiles are plotted. Placental data excludes primates and edentates. Symbols and abbreviations: small solid circle, megapode; small open circle, ratite; large solid circle, subadult sauropod; large solid left half circle, ceratopsian (*Monoclonius*); large circle with black dot, hadrosaur overall growth (*Maiaasaura*); large circle with white dot, hadrosaur nestling growth (*Maiaasaura*); large open circle, prosauropod (*Massospondylus*); large solid lower half circle, theropod (*Syntarsus*); large solid upper half circle, theropod (*Troodon*); e, African elephant cow and bull; g, giraffe; h, hippopotamus; r, white rhinoceros. Data from Ricklefs (1968, 1973), Case (1978a), Laws (1968), Dagg and Foster (1976), Webb et al. (1978), Chabreck and Joanen (1979), Hillman-Smith et al. (1986), Hurxthal (personal communication), Reid (1981, 1990), Currie (1981), Currie and Dodson (1984), Horner and Gorman (1988), Russell (1989), Chinsamy (1992), Varricchio (1992), and Paul (unpublished notes).



ton, 1980). Among ectotherms, the inability to grow rapidly to maturity may be one reason why they are limited to adult sizes of about 1 ton. As Dunham et al. (1989) have noted, giant animals must grow rapidly to reach sexual maturity in a reasonably short time (about two decades). Slow growth, slow generational turnover rates, and limited locomotion dispersal may inhibit even fast-breeding reptiles from exceeding 100 kg, and any reptiles from breaking the 1-ton barrier.

Dinosaurs were able to evolve large sizes because of their high metabolism and r-strategy reproductive system. Only a few adults are needed to produce the many juveniles needed to keep the population viable. With fewer adults in the population, each can claim an unusually large share of the resource base. This would allow the evolution of larger adult body sizes than could be reached by high metabolic, K-strategy giants living on the same resource base. Any serious depletion of the adult population is not critical to the survivability of the species as long as enough of the juveniles survive and mature to reproduction.

The predatory dinosaurs benefited from the increased size of their prey because their resource base was expanded. This expansion in combination with their

r-strategy reproduction allowed them to achieve larger biomass/area ratios and body sizes than they otherwise could. Nevertheless, the megapredators cannot become as large as the megaherbivores because of the latter's broader energy base (various plants). This restricts the predators to sizes not exceeding elephantine masses (Farlow, 1993).

The reproductive strategy of the dinosaurs also has implications for predator/prey ratios. Much of the herbivore mortality due to predation by megapredators probably occurred among one-third to half-grown juveniles. With a large portion of the herbivore biomass made up of juveniles, predators can cull a larger portion of the herbivore biomass. If true, it is possible (but not proven) that predator/prey ratios might be higher (~1.5–3.0 percent) than are observed in modern communities of large endotherms (~0.2–1.5 percent, Farlow, 1990).

An "arms race" may have occurred between prey and predator dinosaurs. Adult herbivores are under selective pressure to improve their defensive performance to enhance the ability of each adult to protect their own high reproductive value. This might entail developing better defensive weaponry or armor, to increasing size, or a combination of both. Predators would also increase

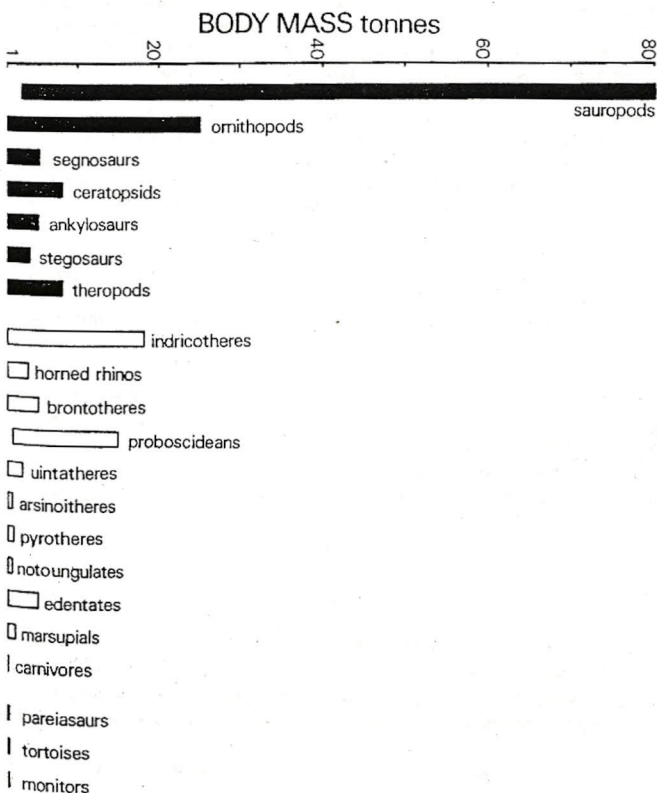


Figure 15.6. Mass ranges over 1 ton in continental tetrapod groups. Maximum values represent typical large adults for extant groups and for extinct groups of the largest known specimens (either skeletons or footprints). Data in part from Paul (1988a, 1992).



their size to better overcome the prey's defenses. The resulting feedback system could result in very large body sizes.

Another possible cause for large adult dinosaur sizes was the sheer numbers of juveniles. Small adult dinosaurs could have found themselves facing competitive or exclusionary pressures from large populations of juveniles their own size. Many small dinosaur niches may, therefore, have been filled by juveniles of larger species.

Janis and Carrano (1992) conclude that high rates of reproduction, population growth, and population recovery were important reasons that so many dinosaurs became so large. In addition, juvenile independence, genetic flexibility, high speciation rates, and the positive attributes that derive from fast growth and high metabolism also contributed to their great size and success.

### Dinosaur reproduction and extinction

During the Mesozoic several events occurred that were potentially lethal to the dinosaurs. Periods of low sea level and low topography may have suppressed speciation rates among the dinosaurs and heightened extinction rates via competitive interchange between faunas and increased disease vectors (Bakker, 1977, 1986). Dinosaurs survived some of these events because of the potentially high speciation rate of their r-strategy reproduction. High rates of genetic processing should have increased the ability of dinosaurs to evolve disease-resistant strains. Wildebeest, cape buffalo, and cattle had little trouble recovering after the devastating rinderpest epidemic of the 1890s (Sinclair, 1979). The faster-breeding dinosaurs should have been even better able to recover from similar events.

The high rate of genetic processing by the dinosaurs should also have enhanced the species' ability to adapt to changing climates and floras. The high reproduction and dispersal potential of those dinosaurs that could not adapt enabled them to shift their populations to more favorable climates and habitats during the many climatic shifts of the Mesozoic.

It is doubtful that changing climate affected the ability of dinosaur eggs to hatch or skewed the sex ratios of the embryos in a dysfunctional manner. Today, birds and reptiles living in a wide variety of temperature regimes are able to maintain the nest temperatures for proper egg viability and embryonic sex selection. There is no reason to suppose that dinosaurs could not also have kept the nest temperatures within tolerable limits, contrary to the arguments of Erben et al. (1979) and Paladino et al. (1989). After all, dinosaurs successfully nested in a variety of different and changing thermal conditions for over 150 Myr.

Competition by early ungulates and other small herbivorous mammals has been suggested by Van Valen and Sloan (1977) as a possible cause for the extinction

of the dinosaurs. However, large K-strategy mammals have endured well with the competition from small r-strategy mammals. In fact, fast reproduction should have given dinosaurian megaherbivores an even better ability to meet the challenge posed by the tiny herbivores.

Another hypothesis attributes the extinction of the dinosaurs at the end of the Cretaceous to the formation of extensive volcanic traps (Duncan & Pyle, 1988; Officer et al., 1987; McLean, 1988; Kerr, 1991b; Chatterjee, 1992). The intense volcanism produced extremely adverse climatic effects and pollution that caused periodic collapses of the global flora communities. However, small dinosaur species and the juveniles of larger dinosaur species might have survived to recover along with the flora. Again, the genetic flexibility of the dinosaurs improved the chances of their survival.

Finally, evidence has been growing for the impact of an asteroid coincident with the global termination of the dinosaurs globally (Melosh et al., 1990; Kerr 1991a, Izett, Dalrymple, & Snee, 1991; Pope, Ocampo, & Duller 1991; Sigurdsson et al., 1991; Smit 1991; Hildebrand et al. 1991; Chatterjee 1992). However, the effects of the impact on the dinosaurs needs to be examined in light of the reproductive system of dinosaurs.

In the worst case scenario, the impact resulted in a total collapse of the terrestrial ecosystem, resulting in the death of the dinosaurs (see discussions by Crutzen, 1987; Waldrop, 1988; Paul, 1989; Melosh et al., 1990; Kerr, 1991a; Sigurdsson et al., 1991; Smit, 1991; Wolfe, 1991; Hildebrand et al., 1991). Burrowing and freshwater vertebrates were the least affected, as were many birds (Olson, 1985).

The survival of the birds after the Cretaceous is important because they may hold a clue to the ways dinosaurs might have been able to resist extinction. Most birds lay fewer eggs than dinosaurs and are apparently more sensitive to environmental change than were dinosaurs. It is therefore difficult to understand how birds could have survived the impact but not the dinosaurs. If just a few dinosaurs survived the catastrophe, their rapid reproduction and genetic flexibility should have allowed them to reestablish themselves and adapt to a dramatically altered world. These surviving dinosaurs would have formed the basis of a new dinosaur radiation. That this did not happen is an unsolved puzzle.

The history of the dinosaurs is marked by remarkable success and stability during the Mesozoic. Far from being inherently vulnerable, the dinosaurs survived in spite of repeated changes in sea level and climate, enormous volcanic eruptions, and great impacts. Indeed, the dinosaurs' fecundity makes it hard to see how such resilient animals could ever have been killed off. The extinction of the dinosaurs was probably not part of the normal course of evolutionary fluctuations, nor was it just another result of random extraterrestrial disruptions.

Instead, it remains one of the most extraordinary and inexplicable events in Earth history.

### Conclusion

The last quarter of a century has seen the emergence of a revisionist view that sees dinosaurs as much more like birds and mammals than the typical reptile. Dinosaurs are now seen as having been highly active on a sustained basis, fast growing, and often possessing highly developed social and parental skills. A few researchers have taken this concept to the extreme, suggesting that the sauropods dropped live young like the giant ungulates. However, a combination of very high breeding rates, high genetic turnover, nonlactation, and fast growth shows that large dinosaurs were not K-strategist large mammals. But nor did they have the slow generational turnover rate and short travel range of ectothermic reptiles.

Instead, they enjoyed a remarkable, dualistic system combining features of both r- and K-strategist endotherms. They had an r-strategy type of reproduction, high population growth, rapid recovery rates, dispersal performance, and genetic processing usually found in much smaller mammals. But they also utilized the K-strategy of survival, high dispersal performance, rapid growth, and generational turnover rates found in large endothermic mammals.

Juvenile (post-nesting) dinosaur independence and the potential ability to survive the loss of all adults is a reptilian trait that is shared by a few birds and even insects. The juveniles may have congregated into large numbers, either fending for themselves or cared for by a few adults. Mass migrations may have brought partly grown juveniles together with many adults.

The reproductive biology of dinosaurs was probably most similar to that of large ground birds. This is not surprising since the latter have retained or replicated the system of their ancestors. The rapid growth of dinosaurs is strongly indicative of their having had high metabolic rates. The r-strategy reproduction of dinosaurs was an important factor in their ability to exploit new conditions and made their capacity exceptionally high to resist and recover rapidly from severe environmental disruptions – so much so that no hypothesis of dinosaur extinction fully explains their demise.

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