

ON THE RARENESS OF BIG, FIERCE ANIMALS: SPECULATIONS ABOUT THE BODY SIZES, POPULATION DENSITIES, AND GEOGRAPHIC RANGES OF PREDATORY MAMMALS AND LARGE CARNIVOROUS DINOSAURS

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ABSTRACT. Carnivorous dinosaurs reached larger body sizes than the predatory mammals that replaced them as the dominant big terrestrial meat-eaters. Although some workers have suggested that tyrannosaurs and other large theropods were able to achieve huge size only by becoming sluggish carrion-eaters, an alternative explanation is presented here.

The maximum body size attained by a predator species reflects a balance between two conflicting demands. Population densities of huge predators must be very low to prevent their over-exploiting their food base of prey species. At the same time, however, total population sizes must be large enough to prevent chance extinction of the predator species. Calculations based on predator food requirements, prey population turnover rates, and prey:predator population density ratios, and on observed natural population densities of mammalian carnivores, suggest that a dinosaur-sized predatory mammal might find it difficult or even impossible simultaneously to maintain low enough population densities and large enough population sizes.

Flesh-eating dinosaurs were able to get around this size constraint due to one, or more likely some combination, of the following factors: larger population densities and/or faster population turnover rates of their herbivorous dinosaur prey than expected for dinosaur-sized herbivorous mammals, oviparity in dinosaurs as opposed to viviparity in mammals, differences in diet between juvenile and adult theropods, and lower mass-specific food consumption rates of carnivorous dinosaurs than expected for equally large meat-eating mammals.

In a given area, the herbivorous mammals always outweigh the carnivorous. An ungulate population is much denser than that of a carnivore of comparable size. This leads . . . to a much greater concentration of ungulate species with very small [geographic] ranges. . . . When the number of individuals in a population is constantly held below a certain minimum, extinction is inevitable. For the ungulate population, with its high density, this limit size corresponds to a smaller range than for the carnivore. Björn Kurtén (1957; reprinted in Kurtén, 1988, p. 231).

[The] probability of extinction varies inversely with body size and hence with population density. Consequently, increasing land areas are required to support progressively larger mammals, and areas as large as the largest continents are necessary to maintain the largest living mammals over the time spans required for differentiation and radiation at the generic level. James H. Brown (1986, p. 243).

INTRODUCTION

Large meat-eating animals like lions, tigers, wolves, and bears are spectacular members of modern faunas, combining grace and beauty with deadliness of purpose. Many carnivorans are big animals by human

standards. Tigers (*Panthera tigris*) reach masses of 306 kg, brown bears (*Ursus arctos*) 780 kg, and polar bears (*U. maritimus*) 800 kg (Nowak and Paradiso, 1983). Gigantic races of lions, tigers, and other modern species are known from the Pleistocene, along with many extinct species of big cats, hyenas, dogs, and bears (Kurtén, 1968; Kurtén and Anderson, 1980; Anderson, 1984). The largest mammalian carnivore may have been the arctocyonid *Andrewsarchus* (Carroll, 1988) or the creodont *Megistotherium*, the latter of which may have weighed as much as 880 kg (Savage, 1977).

As big and dangerous as these creatures undoubtedly are or were, they are dwarfed by carnosaurs and other big theropod dinosaurs of the Mesozoic Era (fig. 1). A 900-kg carnosaur would be at best mid-sized; typical carnosaurs probably weighted 1500 to 3000 kg, and really big forms like *Tyrannosaurus* may have attained masses of 5000 kg or more (Paul, 1988; Alexander, 1989; Holtz, 1991). The size difference between carnosaurs and carnivorous mammals is even more striking when one considers that most of the largest flesh-eating mammals (brown bears, *Andrewsarchus*, *Megistotherium*) either are or likely were omnivorous; most of the largest strictly or primarily predatory mammals (some canids, and hyaenids and big cats) are very much smaller than large meat-eating dinosaurs.

The existence of such titanic predators during the age of reptiles poses an obvious question "Why . . . was there nothing like a tyrannosaur in the great age of mammals, that later part of the Tertiary epoch (sic) when all the plainslands of the Earth held herds of game that make the herds of modern Africa seem trivial by comparison" (Colinvaux, 1978:30)?

Colinvaux argued that loss of energy in the flow from one trophic level to the next—a condition imposed by the second law of thermodynamics—sets a limit to the size and abundance of what he called "big, fierce animals": "We can now understand why there are not fiercer dragons on the Earth than there are; it is because the energy supply will not stretch to the support of super-dragons. Great white sharks or killer whales in the sea and lions and tigers on the land are apparently the most formidable animals the contemporary Earth can support. Even these are very thinly spread. . . . Great white sharks and tigers represent the largest predators that the laws of physics allow the contemporary earth to support" (Colinvaux, 1978, p 27–28).

Colinvaux concluded that the immense size of tyrannosaurs reflected a bit of trophic-dynamic cheating on their part: "The tyrannosaur was not a ferociously active predator . . . most of its days were spent lying on its belly, a prostration that conserved energy and from which it periodically roused itself. . . . The tyrannosaur did indeed support a large mass by meat-eating, but it escaped the energy-consuming price of being active in order to overcome prime specimens of the giant prey it ate . . . Nothing like it has been seen since because the true active predators of the age of mammals were able to clean up the meat supplies before a sluggish beast such as a tyrannosaur could get to them. And "

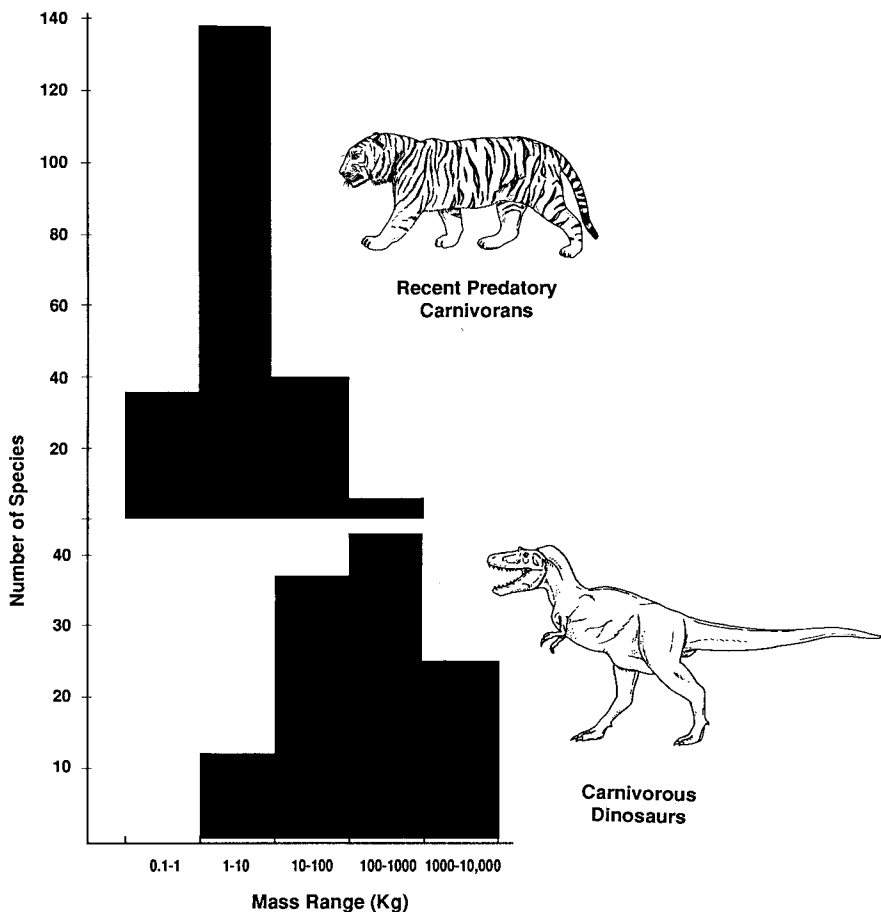


Fig. 1. A comparison of the body masses of modern carnivorans and carnivorous dinosaurs. Data for mammals are taken from Nowak and Paradiso (1983); primarily herbivorous species are excluded. The species taxonomy for dinosaurs is based on relevant papers in Weishampel, Dodson, and Osmólska (1990). Most dinosaur mass estimates are taken from Paul (1988); the remainder are guesses on my part, with help from R. Molnar (personal communication). Ornithomimosaurs and oviraptorosaurs are included in the dinosaur sample; some workers believe these dinosaurs to have been omnivores or herbivores. Excluding these groups shifts the dinosaur species number:body mass distribution toward larger body sizes by decreasing the number of species in the 1 to 10, 10 to 100, and 100 to 1000 kg categories. Comparing the number of species of living carnivorans—animals living during an instant of geologic time—with the number of species of predatory dinosaurs over more than 150 my may give a somewhat misleading picture of the number of species in different size categories in the two groups, if there is a significant difference in the evolutionary turnover rate of species of different body size. This will not, however, affect the main point of the comparison: that carnivorous dinosaurs routinely reached body sizes much greater than any seen in predatory mammals.

active predators might even have eaten the tyrannosaur itself" (Colinvaux, 1978, p. 31).

So unflattering a portrait of carnosaurs has been supported by some paleontologists, particularly for *Tyrannosaurus* (Lambe, 1917; Halstead and Halstead, 1981; Barsbold, 1983). However, there are reasons for thinking that characterization of big theropods as lethargic giants may be extreme. For one thing, the skeletal anatomy of these dinosaurs subjectively does not *look* like that of particularly sluggish creatures; they seem to have been fairly long-legged, erect, dynamic bipeds. This impression is bolstered by trackway evidence; large theropods seem to have walked at respectable speeds of 5 to 10 km/hr, as fast or faster than the walking speeds of modern mammals (Bakker, 1987; Molnar and Farlow, 1990), and medium-sized theropods, at least, may have been able to run at speeds as fast as 40 km/hr (Farlow, 1981). Furthermore, features of the skull, jaws, and teeth of these dinosaurs suggest that large theropods were more than mere scavengers (Paul, 1988; Molnar and Farlow, 1990; McGowan, 1991; Farlow and others, 1991).

The body size of an animal presumably is affected by many physiological and ecological variables, such as diet, foraging strategy, intraspecific and interspecific competition for food, digestive processes, thermoregulation, intraspecific rivalry for breeding rights, and reproductive dynamics. It is probably a mistake to single out any one of these as the most important factor influencing body size.

In considering the maximum body sizes attained by different kinds of predatory vertebrates, we must make a distinction between factors that might select *for*, as opposed to constraints that might *prevent*, the evolution of gigantic forms. Part of the reason for the larger size of carnosaurs than of carnivorans is surely the larger average size of the theropods' presumed prey—herbivorous dinosaurs—than of herbivorous mammals (Molnar and Farlow, 1990). The large size of plant-eating dinosaurs undoubtedly constituted a factor that prompted the evolution of big predatory dinosaurs. If this were the only relevant factor, then the question of the existence of huge flesh-eating dinosaurs could be pushed back a trophic level to consider the physiological or ecological features of plant-eating dinosaurs (compare Farlow, 1987; Tiffney, 1989; Janis and Carrano, in press; Spotila and others, 1991) that permitted/selected for gigantism in these herbivores. But as noted by Paul (1988), there *are* some groups of herbivorous mammals that have attained the size (1000 kg or larger) of many plant-eating dinosaurs. Colinvaux's question can be restated: What constraints might have prevented predatory mammals but not theropods from attaining correspondingly large body masses?

Janis and Carrano (in press) speculate that specialized flesh-eating mammals (like the big cats), unlike omnivores (such as most bears), need to have a flexed limb stance in order to be agile enough to use their forelimbs to bring down their prey. At body masses greater than about 200 kg, however, such a flexed stance becomes incompatible with biome-

chanical constraints associated with weight support. Janis and Carrano suggest that this prevented the evolution of tyrannosaur-sized predators among quadrupedal animals like carnivorans. Although large theropods presumably had to use a less flexed stance than their smaller kin (compare, Gatesy and Biewener, 1991), this may have presented less of a problem for bipedal carnivores whose jaws were more important than their forelimbs in prey handling.

Whatever the merits of the hypothesis of Janis and Carrano, in the present paper I will develop an alternative, perhaps complementary, explanation, relating the maximum body size attained by predatory mammals to the problem of simultaneously existing at low enough population densities to avoid over-exploiting their food base and also maintaining large enough total population sizes to ensure long-term species survival; although aspects of my hypothesis have been considered by previous workers (Kurtén, 1957; Brown, 1986; Brown and Maurer, 1989; Flannery, 1991; Diamond, 1991), to my knowledge the present paper is the first attempt to link these arguments into an explicit hypothesis about the maximum size attainable by mammalian predators. I will then try to identify those features of the biology of carnivorous dinosaurs that permitted them to avoid the body size constraints imposed on meat-eating mammals.

LIMITS TO THE MAXIMUM BODY SIZE OF PREDATORY MAMMALS

Prey:Predator Ratios and Predator Population Densities

We begin by expressing the food consumption rate of a predator population in the following terms:

Equation 1—Predator population food consumption rate = (predator population density) * (average predator mass) * (predator mass-specific food consumption rate)

where predator population consumption rate is in $\text{kg}/([\text{km}^2] * \text{yr})$;
 predator density is in number of animals/ km^2 ;
 average predator mass is in kg;
 mass-specific food consumption rate is in $\text{kg food}/(\text{kg predator} * \text{year})$, or $(\text{yr})^{(-1)}$

We then state that:

Equation 2—Prey productivity rate = (prey population density) * (average prey mass) * (prey turnover rate)

where prey productivity rate is in $\text{kg}/([\text{km}^2] * \text{yr})$;
 prey density is in number of animals/ km^2 ;
 average prey mass is in kg;
 prey turnover rate is in $(\text{yr})^{(-1)}$.

If we assume the *best-case scenario*, in which the predators consume all of their prey's productivity, with no wastage, then:

Equations 3.—Predator consumption rate = prey productivity rate and

Equation 4.—(Predator density) * (average predator mass) * (predator mass-specific food consumption rate) = (prey density) * (average prey mass) * (prey turnover rate)

We can then rearrange this equation to get:

Equation 5.—Average predator mass

$$= \frac{(\text{average prey mass})(\text{prey density})(\text{Prey turnover rate})}{(\text{predator density})(\text{predator mass-specific food intake rate})}$$

Both prey turnover rate and predator mass-specific food intake rate are related to body size in a predictable fashion; we will use eq 3 from Farlow (1990) to estimate prey turnover rate:

Equation 6.—Prey turnover rate = $0.94 * \text{mass}^{(-0.28)}$

where mass is in kg, and turnover rate is in $\text{yr}^{(-1)}$

Eq 2 of Farlow (1990) presents food consumption rates of “composite” tachymetabolic endotherms (birds and mammals) in terms of watts. This can be converted to kg/yr by assuming that the energy content of animal tissue approximates $7 * 10^6$ joules/kg live mass (Peters, 1983, p. 33). Thus

Equation 7.—Annual predator mass-specific food intake (kg/[kg * year]) = $48.87 * (\text{mass}^{(-0.30)})$

predator mass in kg

There is a bit of inelegance that must be addressed before proceeding further. We are trying to calculate predator mass, but to do this we need to know the predator’s mass-specific feeding rate—which is itself a function of mass. To break out of this circle, I assume that the predator’s mass-specific feeding rate is the same as that for an animal of the same average mass as the prey species. Because we are interested in ecological situations that permit the existence of predator and prey species that are about the same body size, this seems a reasonable approach.

The exponent of mass in eq 7 is close enough to that in eq 6, and both of these are close enough to the theoretical $-(1/4)$ (Peters, 1983; Calder, 1984) to suggest that we could eliminate prey mass^(-0.30) as a factor in eq 5. If we did this, eq 5 would reduce to predicting predator mass from prey mass, prey and predator density, and a ratio of about 1/50. In the following calculations, however, I will not do this and will instead use the empirical equations.

We can use the equations given above to generate a family of lines (fig. 2) in which the ratio of prey density to predator density ranges from 1 prey animal:1 predator to 300 prey animals:1 predator, and for which we calculate the average predator mass that could be supported by prey animals of a given mass. An endothermic predator can attain a body size comparable to that of its prey if the prey density:predator density ratio is

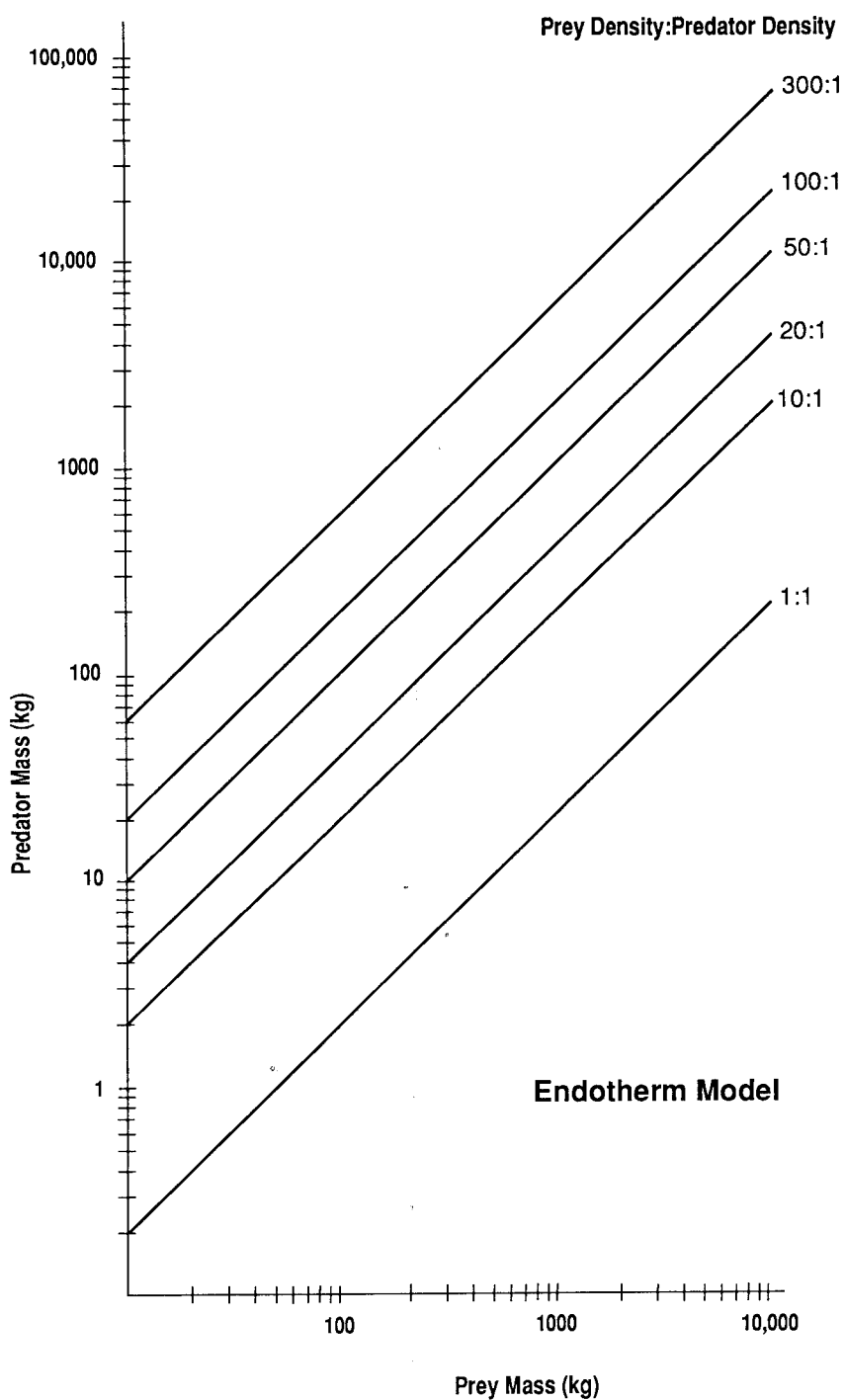


Fig. 2. Predictions of the maximum body mass attainable by an endothermic carnivore feeding on prey of a specified body mass, given a particular prey population density:predator population density ratio. Other assumptions are as stated in text.

at least 50:1 (fig. 1). This is not surprising, given the comments in the preceding paragraph; we can generalize and say that, if a predator is to attain the same body mass as its prey, the prey density:predator density ratio must be at least as large as the reciprocal of the ratio of prey turnover rate to predator mass-specific food consumption rate. In modern mammalian predator/prey systems the prey:predator ratio is usually considerably higher than 50:1, for reasons that I discuss below (compare Farlow, 1990).

A rough estimate of the average adult mass of a large herbivorous (ornithischian) dinosaur from the Campanian Judith River Formation of western North America would be 2000 kg and for an ornithischian from the Maastrichtian Hell Creek Formation of the same region, 5000 kg (Coe and others, 1987; Paul, 1988). Because we are interested in why mammalian carnivores did not attain the large sizes seen in big theropod dinosaurs, we will apply the results of my model to hypothetical mammalian predators feeding upon dinosaur-sized mammalian prey.

The largest herbivore biomasses seen in modern game parks run about 20,000 to 25,000 kg/km² (Farlow, 1976, 1980; East, 1984; Owen-Smith, 1988). If we assume a biomass of 20,000 kg/km² for dinosaur-sized prey and further assume that our herbivores average 2000 kg individual mass, we will have an average herbivore density of 10 animals/km²; with an herbivore:carnivore ratio of 50:1, this would give us a carnivore density of 0.2 animals/km². For 5000-kg animals, prey density would be 4/km² and predator density 0.08/km².

The calculated predator densities are rather low. As Colinvaux says, big, fierce animals really *are* rare; it is lonely at the top of food chains. The question then becomes whether it is *too* lonely for the predators to maintain viable breeding populations. That is, even though the model suggests that dinosaur-sized predatory mammals are energetically feasible, would the necessarily low population densities of such predators be demographically possible?

BODY SIZE, GEOGRAPHIC RANGE, AND POPULATION PERSISTENCE OF PREDATORS

Belovsky (1987) addressed the question of the long-term persistence of populations of mammals by modifying a more general extinction model developed by Goodman (1987). Belovsky's version of Goodman's model is based on three variables: (1) the population density of the species (estimated as a function of body size); (2) the population growth rate, r (the difference between birth rates and death rates), also estimated as a function of body size; (3) the variance in r , V , that is due to environmental changes. V is the most difficult parameter to obtain; Belovsky estimated the range of values of V likely to occur in natural populations of mammals by analyzing the variation seen in such environmental features as rainfall, stream flow, lake levels, and tree growth rings. From population density, r , and V , Belovsky calculated N_m , the population size needed for a species to maintain breeding populations with a 95 percent probability of persistence for 1000 yrs or an expected persistence

of 20,000 yrs. He presented two equations, one for a situation in which r is strongly affected by environmental variability, and another in which the effect of environmental variability on population growth rates is low:

$$\text{Minimum population size} = 409,540 * (\text{mass}^{(-0.36)})$$

[high variability of r]

$$\text{Minimum population size} = 19,018 * (\text{mass}^{(-0.40)})$$

[low variability of r]

Mass in both of these equations is in kilograms.

A population of dinosaur-sized mammals living under conditions that cause a high variability of r will remain viable if the total population size is at least 27,000 animals (2000 kg avg mass) or 19,000 animals (5000 kg avg mass). If the effects of environmental variability on population growth rates are low, viable populations can be smaller: 910 animals (2000 kg avg mass) or 630 animals (5000 kg avg mass). These population size estimates should not be viewed as extremely accurate predictions of what is needed for long-term survival of species but only as rough guides to the numbers required for persistence. Of particular importance to our discussion, Belovsky indicated that his extinction model may underestimate the likelihood of extinction of carnivore populations (compare Diamond, 1984; Shafer, 1990).

In order to translate our previously calculated dinosaur-sized predator densities into total population sizes, we need some idea of the geographic range occupied by any such species. We can start by assuming that the geographic range of our dinosaur-sized predator species is comparable to the area of the contiguous United States—(I pick this area for reasons that I will discuss later)—roughly 8,000,000 km².

With the densities previously calculated for 2000- and 5000-kg endothermic predators, we get total population sizes of 1,600,000 animals (2000-kg individual mass) and 640,000 animals (5000-kg individual mass). These numbers are 40 to 60 times larger than those needed for population viability in the worst-case, high variance of r , version of Belovsky's model, and so our initial conclusion might be that dinosaur-sized predatory mammals are completely feasible.

But we must make explicit and reexamine some of the assumptions that had to be made in getting these results: (1) all the herbivore productivity is being consumed by our carnivores; (2) all that productivity can be eaten (no problems with indigestibility of skeletons, for example); (3) herbivore biomass is uniformly high over our entire landmass; (4) our hypothetical predator species is distributed throughout the landmass.

Assumption (1) is where most problems with reality probably lie. Even if we suppose that carnivores of some kind did manage to eat all the productivity of dinosaur-sized herbivores, our calculations so far have assumed that all this productivity is being eaten only by dinosaur-sized carnivores of the kind that interests us. This was clearly not true, for

example, in the Late Cretaceous of western North America, where, in addition to tyrannosaurs, there were smaller carnivorous dinosaurs like elmsaurs, troodonts, and dromaeosaurs, along with crocodiles and varanid lizards (Baird and Horner, 1979; Dodson, 1983; Naylor, 1986), at least some of which presumably killed young (including eggs) or even adult ornithischians from time to time or at least scavenged carcasses that escaped the notice of tyrannosaurs. It is unrealistic to suppose that an ecological community that included dinosaur-sized carnivorous mammals would not also include smaller predators that could consume at least some of the prey productivity also sought by their larger predatory neighbors.

We can try to account for the probability that not all the dinosaur-sized prey species' productivity will be consumed by equally large predators. The calculations presented thus far assume a prey:predator density ratio of 50:1. In actuality, the prey:predator biomass ratio (which will be roughly comparable to the prey:predator density ratio when the prey and predators are about the same individual mass) in modern large-mammal communities is usually somewhere between 200:1 and 100:1 (East, 1984; Farlow, 1990) but can get as low as 45:1 (compare Prins and Reitsma, 1989, for a forest community—although in this case the situation is complicated by the larger body size of predators in comparison with that of some of the prey species). The higher values of observed prey:predator ratios than in our best-case scenario presumably reflect the difference between conditions prevailing in real ecological communities and the ideal conditions assumed in our best-case scenario.

If we substitute a prey:predator ratio of 100:1 for the 50:1 ratio used in the best-case scenario but leave all other values unchanged, we halve the expected number of predators on our hypothetical continent: 800,000 animals of 2000-kg mass and 320,000 animals of 5000-kg mass. These numbers are still 15 to 30 times the values needed for minimum population viability when the effects of environmental variability on r are great.

There is another aspect of the first assumption that remains troublesome, however. Our calculations so far assume that we are only dealing with one species of dinosaur-sized predator. In the Late Cretaceous of western North America, however, two (or even more?) different species of tyrannosaurs can occur in the same fauna (see below) and might even have coexisted in the same biological community. The larger the number of species of such super-dragons on our continent, the smaller the total population size of each.

Assumption (2) is also unrealistic; as a first approximation, the proportion of live mass composed of skeleton in a dinosaur-sized animal should be roughly that in an elephant, about 13 percent (Vogel, 1988). However, using a 100:1 or 200:1 prey:predator ratio probably provides a sufficient correction for this problem.

Assumption (4) does not seem unreasonable. We might expect a dinosaur-sized predatory vertebrate to be fairly mobile, and so individuals of that species should be present in all but the most hostile environments of its geographic range.

Assumption (3), like the first assumption, is much more serious. Herbivore biomass in modern large-mammal communities is strongly affected by such things as rainfall and soil nutrient quality, and carnivore biomass is in turn correlated, as one would expect, with herbivore biomass (East, 1984; van Orsdol, Hanby, and Bygott, 1985). If, on the average, herbivore density across our entire hypothetical continent were much less than it was in areas of prime habitat (where we might expect biomass to reach values of 20,000 kg/km²), we would be able to support much lower populations of dinosaur-sized endothermic carnivores.

Suppose that the average prey biomass across the entire continent is only 10,000 kg/km², that the prey:predator ratio is 100:1, and that the herbivores and predators have an average mass of 2000 kg. With an 8,000,000-km² continent, there will be 400,000 dinosaur-sized predators. If there are two species of these predators, each will be represented by 200,000 individuals. This is still about 10 times the number needed for viable populations under Belovsky's worst-case scenario. If we assume that the prey:predator ratio is 200:1, that there are four species of dinosaur-sized predators, and keep all the remaining variables the same as in the preceding calculation, we would have 50,000 individual predators of each species. We are now down to twice the minimum number of animals needed for population viability in Belovsky's worst-case scenario.

The assumption that the average biomass of our hypothetical fauna of dinosaur-sized herbivores across the continent would be half that in prime habitat (10,000 kg/km² versus 20,000 kg/km²) may be overly generous. In tropical savanna ecosystems, large herbivore biomass may vary by more than a ten-fold factor from one place to another (East, 1984), and the biomass of large herbivores in forest ecosystems is often much less than in savanna situations (Bodmer, 1989; Prins and Reitsma, 1989).

Comparison of the results of my model with the projections of minimum population sizes needed for long-term viability, based on Belovsky's model, suggests that dinosaur-sized predatory endotherms are in principle possible, particularly if environmental factors affecting population growth rates are not very variable. However, if r is variable enough, and if we make our assumptions about habitat area, absolute prey density, the prey:predator ratio, and the number of predator species restrictive enough, we can create situations in which the long-term survival of our endothermic super-dragons becomes questionable. It is worth repeating, too, that Belovsky (1987) thought that his model probably underestimates the chances of extinction of carnivore species.

We can take our analysis further by using a complementary approach. In a paper relating body size to population density in animals, Damuth (1987) presented an equation predicting population density from body mass for mammalian "vertebrate-consumers":

$$\text{carnivore density} = 3.89 * \text{mass}^{-0.96}$$

where density is in number of animals/km²; mass is in kilograms.

For a 2000-kg predator, Damuth's equation predicts a density of $0.003/\text{km}^2$ and for a 5000-kg predator, $0.001/\text{km}^2$. These numbers should be taken with caution, because 2000 and 5000 kg are an order of magnitude larger than the numbers used to generate Damuth's equation. Nonetheless they do represent projections from empirical data, rather than purely theoretical constructs like those presented above.

The density values predicted by Damuth's equation are about 70 to 80 times smaller than those generated by our best-case scenario. In part this is because they are projections of the density of a single species. If we once again assume that these densities are maintained uniformly across an 8-million-square kilometer area, we get population sizes of 24,000 animals (2000 kg individual mass) and 8000 animals (5000 kg individual mass). Comparing these numbers with Belovsky's projections, mammalian carnivores of this mass should be viable if environmental conditions affecting birth and death rates are not very variable, but in serious trouble if they are.

The assumption of uniform density, as in our earlier models, may be critical here. Presumably densities of dinosaur-sized mammalian carnivores would be higher than those predicted by Damuth's equation in some places and lower in others. However, because Damuth's regression is based, as far as possible, on ecological rather than crude densities (that is, on densities of the animals in the habitats actually used by them, rather than on densities within the boundaries of some artificial man-made park, political, or administrative unit), the actual densities of our carnivores over a broad geographic area would be more likely to be less than greater than those estimates predicted by Damuth's equation.

This suggests that while dinosaur-sized carnivores are not impossible, such species might be in danger of extinction unless they occupied large enough geographic ranges to permit good-sized populations. Belovsky calculated the size of geographic ranges big enough to permit a 95 percent probability of persistence over 1000 yrs for mammalian carnivores. In the best-case scenario (temperate habitats whose environmental variability has a low impact on birth and death rates), the minimum habitat area needed by a dinosaur-sized mammalian predator is about 10^5 km^2 ; in the worst-case scenario (tropical habitats of high variability) the minimum habitat area is between 10^6 and 10^7 km^2 . Smaller geographic ranges are possible if one specifies that the required 95 percent probability of survival be for only 100 instead of 1000 yrs, but this obviously introduces a much greater likelihood of extinction. This suggests that a dinosaur-sized mammalian carnivore would require a very large geographic range—maybe even larger than the contiguous United States—if environmental conditions and carnivore population densities were sufficiently variable.

If we now shift our attention from hypothetically huge to real carnivorous mammals, we find that the largest-bodied living species—animals much smaller than tyrannosaurs—have continent-wide or even intercontinental geographic ranges, or at least did so before human

TABLE 1

*Present and historical geographic ranges of some large mammalian carnivores
(data from Nowak and Paradiso, 1983)*

| | |
|--|--|
| Lion (<i>Panthera leo</i>) | Balkans and Arabia to central India, nearly all of Africa |
| Tiger (<i>P. tigris</i>) | Much of Eurasia |
| Leopard (<i>P. pardus</i>) | Much of Africa and Eurasia |
| Jaguar (<i>P. onca</i>) | Southern United States to northern Argentina |
| Snow Leopard (<i>P. uncia</i>) | Mountainous areas from Afghanistan to Lake Baikal and eastern Tibet |
| Cheetah (<i>Acinonyx jubatus</i>) | Middle East to central India, Africa except for the central Sahara and rainforests |
| Cougar (<i>Felis concolor</i>) | Most of North America to southern Chile and Patagonia |
| Spotted Hyena (<i>Crocuta crocuta</i>) | Sub-Saharan Africa except in rainforests |
| Coyote (<i>C. latrans</i>) | Most of North America |
| Gray Wolf (<i>Canis lupus</i>) | Most of Eurasia and North America |
| Hunting Dog (<i>Lycaon pictus</i>) | Most of Africa |
| Asiatic Black Bear (<i>Ursus thibetanus</i>) | Most of central and eastern Asia |
| American Black Bear (<i>U. americanus</i>) | Most of North America |
| Brown Bear (<i>U. arctos</i>) | Most of Eurasia (except tropical regions), northern Africa, most of North America |
| Polar Bear (<i>U. maritimus</i>) | Arctic Eurasia and North America |

persecution had too severe an effect (table 1). Kurtén (1957) showed that the geographic ranges of Eurasian felid, canid, and ursid species were roughly four times the size of the geographic ranges of bovid species and about twice the size of the ranges of cervid species.

Some living species of carnivorans had even larger geographic ranges during the Pleistocene than at present: the lion, for example, occurred in Europe and the Americas (Kurtén, 1968; Kurtén and Anderson, 1980; Guthrie, 1990—but some workers consider the American lion to be a different species, *P. atrox*). Both living and extinct carnivoran species were widespread during the Pleistocene. "Many Pleistocene taxa . . . were present in virtually every part of the United States. The most conspicuous of these are the large carnivores (for example, *Smilodon floridanus*, *Panthera atrox*, *Arctodus simus*, *Homotherium serum*, *Canis dirus*, *Canis latrans*, *Ursus americanus*, *Felis concolor*, and *Canis rufus*)" (Lundelius and others, 1983, p. 312). Whether this was also true for pre-Pleistocene mammalian carnivores is hard to say. Savage and Russell (1983) report geographic occurrences of Tertiary taxa but candidly admit that the taxonomy they use is over-split. However, Kurtén (1957) noted that similarities in the carnivoran species between Europe and China during the Pliocene suggested that the geographic ranges of carnivorans were as broad then as at present.

The large geographic ranges of big-bodied species of carnivorans are consistent with the results of my theoretical calculations. This suggests that while the existence of dinosaur-sized predatory mammals is at least possible, the population densities of such species would be so small, requiring geographic ranges so large, they they might face a significant threat of extinction over evolutionary, and maybe even ecological, time

(compare Brown, 1986; Brown and Maurer, 1989). Consequently the evolutionary risks involved in attaining huge body size may outweigh their benefits. This may be why terrestrial mammalian carnivores have been restricted to body sizes less than those reached by predatory dinosaurs.

If my hypothesis is true, then body size should have a significant impact on the extinction rate (excluding pseudoextinction due to phyletic evolution) of mammalian predators. We might expect to observe a decline in species longevities, shorter species half-lives (Kurtén, 1959), and higher rates of true species extinction with increasing carnivoran body size. In addition (or alternatively), we would expect to see a frequent shift from pure carnivory to omnivory among the largest-bodied mammalian flesh-eaters. Data on mammalian species extinction rates broken down by body size and trophic level are presently unavailable (but are potentially available for Pleistocene mammals), and so whether the first expectation is met is unknown. The second expectation, however, does seem to be met. As noted in the introduction, the biggest meat-eating mammals are usually omnivores; furthermore, some of the largest facultative mammalian flesh-eaters are members of clades most of whose species are herbivores or omnivores (compare Van Valkenburgh, 1988; Joeckel, 1990).

The limits to maximum body size seen in land-living carnivorous mammals do not apply to marine mammals: many cetaceans and some pinnipeds are of tyrannosaur size or considerably larger, and yet they are carnivores. This is presumably due in part to the fact that the larger forms have world-wide geographic distributions, which permitted very large pre-exploitation population sizes (Nowak and Paradiso, 1983; Ridgway and Harrison, 1985, 1989), but there is more to it than that. In most marine food chains there is a substantial increase in organism body size with increasing trophic level (Sumich, 1988, p. 276). As noted by Colinvau (1978), baleen whales feed upon zooplanktonic crustaceans and small fishes (see previously cited references), whose populations turn over very rapidly, permitting these filter-feeders to attain titanic sizes.

The big toothed whales and the larger pinnipeds do not feed as low on marine food chains as the baleen whales do but nevertheless often rely heavily on prey much smaller than themselves (Ronald, Selley, and Healey, 1982; Leatherwood and Reeves, 1982). Killer whales (*Orcinus orca*) feed on large whales but also consume fishes and pinnipeds (Leatherwood and Reeves, 1982). The most important prey of sperm whales (*Physeter macrocephalus*) are medium-sized mesopelagic squid and demersal fishes (Leatherwood and Reeves, 1982; Rice, 1989). The large standing crops and/or the presumably high biomass turnover rates of the relatively small-bodied prey of these whales permitted the evolution of huge size by their predators. In contrast, the gigantic body-size option may not be open to terrestrial carnivorans that feed on mammalian herbivores of about their own size.

If this is true, then how were tyrannosaurs and other large theropods able to escape this size-related energetic and demographic constraint?

BODY SIZE AND GEOGRAPHIC DISTRIBUTION OF TYRANNOSAUR SPECIES

Before proceeding further, a caveat must be stated. Large terrestrial carnivores are known among therapsids before the dinosaurs (Kemp, 1982), and ground-living birds (Andrews, 1901; Matthew and Granger, 1917; Witmer and Rose, 1991 [but see Andors, 1989]; Brodkorb, 1963) and varanid lizards (Auffenberg, 1981; Rich, 1985) after the dinosaurs' extinction. In mammals, large predatory forms are known among marsupials (Marshall, 1978; Murray, 1984; Churcher, 1985; Wells, 1985), arctocyonids, mesonychids, creodonts, and carnivorans (Carroll, 1988; Janis and Damuth, 1990). None of these creatures (apart from the cetacean descendants of mesonychids), however, attained the body size seen in large theropods.

I have presented an energetic/demographic hypothesis to account for the failure of mammals to evolve tyrannosaur-sized predators. This hypothesis might also explain the failure of flesh-eating birds to achieve the body size of dinosaurs. It does not account for the absence of dinosaur-sized predators among the therapsids, although the similar absence of dinosaur-sized herbivores among therapsids suggests that there was no ecological "need" for huge carnivores among mammal-like reptiles. This is not true for varanids, which share the Old-World tropics with a diversity of very large herbivorous mammals. However, even though varanids did not attain the body size of tyrannosaurs, Flannery (1991) and Diamond (1991) suggested that these and other large reptiles were able to take on the role of large carnivores in Australia, as marsupials generally did not, due to the reptiles' ability to maintain viable populations on a relatively low and unpredictable food supply.

We can think of the various adaptive radiations of terrestrial vertebrates as a series of "natural experiments" (Simpson, 1980). The difficulty in interpreting such evolutionary experiments, of course, is that they have no controls. Even if the hypothesis I have developed can explain the absence of tyrannosaur equivalents among mammals, the same body size constraints may not apply to other kinds of predators; as noted in the introduction, the sizes attained by animals are influenced by many biological variables, which are probably not of the same relative importance in all groups of terrestrial vertebrates. Furthermore, unless we adopt a rigidly deterministic outlook on evolution and argue that if an ecological opportunity for a particular mode of life exists, then, barring anatomical, physiological, or other constraints, some creature should have evolved to exploit it, we must also be open to the possibility that some groups of terrestrial predators might or might not have evolved gigantic species simply due to chance. In the speculations to follow, however, I will assume that the difference in maximum body size

between carnosaurs and predatory mammals does reflect some difference in their biology that permitted gigantism in dinosaurs, but not mammals, and I will try to identify what that or those difference(s) might have been.

My discussion will focus on tyrannosaurs, even though other clades of large carnivorous dinosaurs are known from Mesozoic faunas. In part this is because the fossil record of tyrannosaurs is better known than that of other big theropods. More important, however, is that tyrannosaurs, unlike earlier carnivorous dinosaurs, lived in a time when the break-up of Pangaea had proceeded to the point that the continents were beginning to move into positions relative to each other like those of the present day (Dott and Batten, 1988; Fastovsky, 1989; Sereno, 1991). Ceratosaurs and allosaurs had ruled a world in which movement from one landmass to another was relatively easy; tyrannosaurs lived in a world of fragmented continents. This continental separation may in fact have resulted in a Late Cretaceous biogeographic differentiation between the large theropods of northern and southern portions of what had been Pangaea, with tyrannosaurs dominant in eastern Asia and western North America and abelisaurs in the Gondwana continents (Molnar, 1990; Molnar and Farlow, 1990; Bonaparte, 1991). Consequently tyrannosaurs are among the large theropods most likely to have been confronted by the problem of occupying large enough geographic ranges to maintain viable populations.

Geographic Distribution of Tyrannosaurs

Lehman (1987, p. 191) and Russell (1989, p. 147) published maps of the paleogeography of North America in the Late Cretaceous (Campanian), about the time the sediments of the Judith River Formation were being deposited. The area of the western North American land mass, what Lehman termed the Asian-American Peninsula (excluding any extensions into what is today Asia proper), looks to have been roughly that of the present contiguous United States—hence my reason for choosing such an area in my previous calculations. Tyrannosaurs presumably occurred in all but the most mountainous regions, or areas that were environmentally very harsh for other reasons, of this landmass. Assuming that climate, soil conditions, and vegetation varied across the Asian-American Peninsula (Lehman, 1987; Sloan and Barron, 1990), however, ornithischian biomass (and thus tyrannosaur density) would probably not have been uniform across the landmass—and so the demographic problems raised for a dinosaur-sized mammalian predator in my theoretical calculations may have some relevance to tyrannosaurs. There are suggestions that regional differences in Campanian dinosaur faunas of western North America had developed (Lehman, 1987); of particular interest for the present discussion, there is a possibility that a non-tyrannosaurian carnosaur occurred in the Judith River fauna of Montana, but not Alberta (Fiorillo, 1989).

By the Late Maastrichtian the Western Interior Sea had largely drained away, and the Asian-American Peninsula joined the remainder of North America (Lehman, 1987). The potential living space for North American dinosaurs was greatly increased over what it had been in the Campanian. However, Late Cretaceous dinosaur faunas in western North America may have become rather provincial. Lehman (1987) proposed that during the Late Maastrichtian there were three major dinosaur faunas in the western interior: a southerly *Alamosaurus* fauna typical of seasonal, semi-arid environments in intermontane basins, a more northerly *Triceratops* fauna occurring in wetter coastal floodplains and swamps, and a *Leptoceratops* fauna found in cool piedmont situations adjacent to the Cordilleran mountains. These faunas were characterized by differences in the proportions of groups of herbivorous dinosaurs. Some dinosaur genera, however, did range throughout the western interior. One of these was *Tyrannosaurus*, but Lehman noted that *Tyrannosaurus* and other cosmopolitan dinosaur genera might actually be represented by different species in different areas (compare Carpenter, 1990).

The known geographic occurrences of tyrannosaurs and other large theropods (Haubold, 1990; Molnar, Kurzanov, and Dong, 1990; Jerzykiewicz and Russell, 1991) are rather limited. *Albertosaurus libratus*, for example, occurs in Late Campanian-Maastrichtian deposits from Canada into the southwestern United States. *A. sarcophagus* is reported from rocks of about the same age in Alberta, Wyoming, and Montana. *Daspletosaurus torosus* is presently limited to Late Campanian beds of Alberta. *Tarbosaurus bataar* (possibly *Tyrannosaurus bataar*) occurs in deposits of about the same age in Mongolia and China. *Tyrannosaurus rex* reportedly occurs in Late Maastrichtian units from Alberta to the southwestern United States, but one of the southern specimens may represent a different taxon (Carpenter, 1990). Some workers go even further, believing some of the Montana specimens presently attributed to *T. rex* belong to a second, equally large species of theropod (Archibald, 1989; Russell, 1989; Archibald and Bryant, 1990; Larson, 1991).

These seem like very small geographic ranges for such immense predators, particularly if we assume that tyrannosaurs were mammal-like or bird-like endotherms. Three possible interpretations come to mind:

1. The limited geographic occurrences are artifacts caused by the scarcity of large top predators in ecological communities and the incompleteness of the fossil record. If we had a good enough record, we would find the same species of carnosaurus or other big theropods at sites across many continents. At the very least, we would expect to find tyrannosaur species typical of the Asian-American Peninsula extending well into Asia proper. Currie (1989, p. 118) thought that "it is highly probable that at least some carnivorous dinosaur species [of the Late Cretaceous] had intercontinental distributions."

2. The limited geographic occurrences are artifacts caused by an over-split taxonomy. This might imply, for instance, that *T. bataar* belongs to the same species as *T. rex*.

3. Carnosaur species really did have limited geographic distributions, continent-wide or smaller. This would be interesting in itself, but as previously noted, there is a surprising diversity of large theropod species in the various Late Cretaceous faunas of western North America. In the Judith River Formation of Alberta, for example, we find *A. libratus*, *D. torosus*, *Aublysodon* sp., and an undescribed tyrannosaurid—not to mention several species of smaller theropods (Weishampel, 1991). In the Hell Creek Formation of Montana are *Aublysodon mirandus*, *Nanotyrannus lancensis*, and *T. rex* (and possibly another huge carnosaur species, if what is now called *T. rex* does in fact consist of more than one species), and once again several smaller forms (Archibald, 1989; Molnar, Kurzanov, and Dong, 1990; Archibald and Bryant, 1990; Weishampel, 1990). If there were as many sympatric species of tyrannosaurs and other medium-sized and large predators as occur together in fossil faunas, all of them tapping the productivity of herbivorous dinosaur populations, this would have exacerbated the problem of supporting large enough populations for long-term viability of any particular carnivore species.

Possible Explanations for the Gigantic Size of Tyrannosaurs

Mesozoic terrestrial communities were dominated by plants and animals rather different from those of the Cenozoic, and so we cannot assume that patterns of energy flow or other functional attributes of Mesozoic communities were very much like those of any modern terrestrial community (Tiffney, 1989; M. Brett-Surman, personal communication). We can consider ways in which tyrannosaur-ornithischian predator-prey systems might have differed from those of modern large mammals and thus have permitted larger body sizes of tyrannosaurs than of carnivorans by re-examining eq 5. For a given predator density, body size can be larger if: (A) herbivore body mass is larger, (B) prey density is higher, (C) prey turnover rate is higher, or (D) predator mass-specific food consumption rate is lower.

Tyrannosaurs in the Judith River and Hell Creek faunas were members of ecological communities in which the largest herbivores were animals of about their own size, and so the first possibility does not seem very helpful. It might, however, have some relevance to any carnosaurs that routinely attacked sauropods. However, it is also true that herbivore mass is inversely proportional to herbivore population density (Damuth, 1987) and also population turnover rate (Farlow, 1990), and so we probably do not gain anything by invoking a larger prey size.

We could in principle, however, increase herbivore density without an accompanying decrease in average herbivore body mass in several different ways. First of all, if the primary productivity of Mesozoic vegetations was greater than that of present-day plant communities, either due to features of the plants themselves (which seems unlikely, particularly for vegetations dominated by gymnosperms—Tiffney, 1989) or to extrinsic factors (such as a higher carbon dioxide concentration in the atmosphere (Berner, 1991; Cerling, 1991; Kerr, 1991), as suggested by Russell (1989), this might have permitted a greater biomass of ornithis-

chians than of modern large mammals. Alternatively, ornithischians might have been more efficient at extracting energy and nutrients from their fodder than herbivorous mammals are. Still another possibility is that the mass-specific food consumption rates of ornithischians were less than those of mammals, such that a given level of primary productivity could support a greater biomass of ornithischians than of mammals. Evaluating most of these possibilities requires data that are presently unavailable and perhaps even unknowable.

The histology of primary bone in ornithischians suggests fairly rapid growth rates (de Ricqlès, 1980; Reid, 1987). This interpretation is corroborated by circumstantial evidence about hadrosaur growth rates based on careful study of nest sites (Horner and Gorman, 1988; Horner and Weishampel, 1988). Russell (1989) concluded that the growth rate of the hadrosaur *Maiasaura* was about two-thirds that predicted for a comparably-sized "average" eutherian mammal. Although in theory ectothermic reptiles could grow at such rates (Dunham and others, 1989) there is some question as to whether this really happens under natural conditions (Farlow, 1990). Consequently we might tentatively conclude that ornithischians had faster metabolic rates than modern reptiles.

If growth rate is indeed tightly correlated with standard metabolic rate, and if the growth rate of hadrosaurs was two-thirds that of an average eutherian, we could suppose that the standard metabolic rate of hadrosaurs was roughly two-thirds the basal metabolic rate expected for a hadrosaur-sized, average eutherian mammal. If this were true, ornithischian populations might have been one and a half ($3/2$) times larger than herbivorous mammal populations for a given level of plant productivity. Such larger ornithischian populations might in turn have permitted a slightly larger body size for tyrannosaurs, at a given tyrannosaur population density, than would be possible for hypothetical gigantic carnivorans preying on elephant-sized herbivorous mammals. We could increase ornithischian density even further if we are willing to entertain more novel hypotheses about dinosaur energetics, such as the possibility that dinosaurs had mammal-like metabolic and growth rates as juveniles, but much lower, more reptile-like metabolic rates as adults (Farlow, 1990). Unfortunately, none of these possibilities can be evaluated, given the present state of our knowledge about dinosaur biology.

Janis and Carrano (in press) speculate that oviparity permitted big dinosaurs to have a larger potential reproductive output than is possible for viviparous mammals. In terrestrial mammals the frequency of reproduction and the number of young per litter both decline with increasing adult body mass. In large ground-living birds, in contrast, there is no such decline in either of these variables with increasing body size. Consequently birds have a greater total reproductive potential than mammals of similar size. Janis and Carrano suggest that the same may have been true for dinosaurs, in comparison with mammals.

If the hypothesis of Janis and Carrano is true, then in order for populations to remain reasonably constant in size, a given cohort of

herbivorous dinosaurs had to suffer greater mortality than does a cohort of herbivorous mammals of comparable adult body mass. If so, and if most mortality happened at fairly small body sizes (and thus young ages), such that many ornithischian victims (including victims of egg predators) were consumed by small-bodied carnivores instead of tyrannosaurs, the greater hypothetical reproductive potential of dinosaurs in comparison to that of large ungulates might have been of little benefit in supporting bigger tyrannosaurs than carnivorans at a specified predator density. On the other hand, if a large proportion of young ornithischians survived to reach sizes where tyrannosaurs would have been their main threat, then this might well have permitted tyrannosaurs to attain a larger body size than is possible for predatory mammals.

We can calculate how much the turnover rates of ornithischians would need to have been greater than those of equally large mammals in order for this parameter alone to have accounted for the greater size attained by tyrannosaurs than of carnivorans. Examination of eq 5 indicates that, given the assumptions of the best-case scenario previously described, the prey turnover rate will be inversely proportional to the prey:predator density ratio. If, in an extreme case, we assume the prey:predator ratio of Late Cretaceous dinosaur communities to have been 10:1 (see below), and that the mass-specific food consumption rate of endothermic tyrannosaurs was that predicted for a 2000-kg animal on the basis of eq 7, this means that the minimum ornithischian turnover rate would have to have been 0.5 yr^{-1} —an annual biomass turnover rate of 50 percent—about 5 times that expected for a 2000-kg mammal on the basis of eq 6.

Thus far I have implicitly assumed that tyrannosaurs usually preyed upon ornithischians of an adult size comparable to their own. If, however, this was not true, and tyrannosaurs concentrated on much smaller prey, such as ornithomimids or hypsilophodontids, then they would have tapped prey populations that presumably had much higher turnover rates than their own. This would have come at the expense, however, of ignoring the larger plant-eating dinosaurs that presumably dominated herbivore biomass in Cretaceous communities. Consequently it is unlikely that specializing on small-bodied prey would itself have made the evolution of gigantic predators like tyrannosaurs possible.

Baby carnivorans eat the same foods as their parents, albeit indirectly, via their mothers' milk. If hatchling and small juvenile tyrannosaurs foraged on their own and thus ate large insects and small mammals, lizards, frogs, turtles, adults of small-bodied dinosaurs, and juveniles of large dinosaurs (Farlow, 1976, 1980), then tyrannosaur populations would have had a larger food resource base than adult tyrannosaurs alone. This larger resource base would have compensated to some extent for losses of the productivity of hadrosaurs, ankylosaurs, and ceratopsians to small theropods and other modest-sized predators. This might in turn have contributed to the attainment of larger adult body sizes of tyrannosaurs than of carnivorans.

The final possibility suggested by eq 5 is that carnosaurs reached larger body sizes than terrestrial carnivorous mammals because they had lower mass-specific food consumption rates than predicted for dinosaur-sized endotherms by eq 7. As in the case of ornithischians, the histology of theropod primary bone makes me unwilling to suggest that these dinosaurs were typical bradymetabolic ectotherms (Chinsamy, 1990, 1991), but we can model a limiting, extreme case in which we assume that they had the mass-specific food consumption rates predicted for reptiles and amphibians. Using the same energy content-live mass conversion factor as before, I converted eq 1 of Farlow (1990) to:

$$\text{Equation 8.}—\text{Annual intake (kg/[kg * yr])} = 3.81 * (\text{mass}^{-0.16})$$

Once again, intake is in yr^{-1} ; mass is in kg.

As for the endotherm model, I constructed a family of lines in which the prey density:predator density varies, this time from 1:1 to 50:1. An ectothermic tyrannosaur comparable in body mass to its prey species is energetically feasible if the prey density:predator density ratio is at least 10:1 (fig. 3).

As before we will assume average individual herbivore masses of 2000 kg or 5000 kg and a total herbivore biomass of 20,000 kg/km^2 . For 2000-kg animals, this again yields an herbivore density of 10 animals/ km^2 ; with an herbivore:carnivore ratio of 10:1, this gives us a carnivore density of 1 animal/ km^2 . For 5000-kg animals, we have an herbivore density of 4/ km^2 and a carnivore density of 0.4 animals/ km^2 . Then if we once again assume that our carnivores roam a continent that has an area of 8,000,000 km^2 , we have total population sizes (as before, under ideal conditions) of 8,000,000 2000-kg carnivores or 3,200,000 5000-kg carnivores. Even if we now start stacking the ecological deck against our carnivores, we can nonetheless concentrate 5 times as many ectothermic carnivores into our landmass as we could endothermic carnivores.

Damuth (1987) does not report a regression of density against animal mass for reptiles and amphibians, but he does provide some data that can be used for this (I have modified his data, however, by substituting Auffenberg's 1981 density and mass data for Komodo dragons for the older numbers Damuth quotes):

$$\text{density} = 66.07 * \text{mass}^{-1.01}$$

Again density is in animals/ km^2 , and mass is in kilograms.

We must now proceed with considerable caution, because the largest reptile in Damuth's data sample has a mass more than 2 orders of magnitude less than our hypothetical tyrannosaur-sized predators. But plunging ahead anyway, for a 2000-kg animal the regression predicts a density of 0.03 animals/ km^2 , and for a 5000-kg animal a density of 0.01 animals/ km^2 , or 10 times the densities predicted for mammalian vertebrate-consumers of the same mass. For an 8,000,000 km^2 continent, this gives us 240,000 2000-kg predators and 80,000 5000-kg predators.

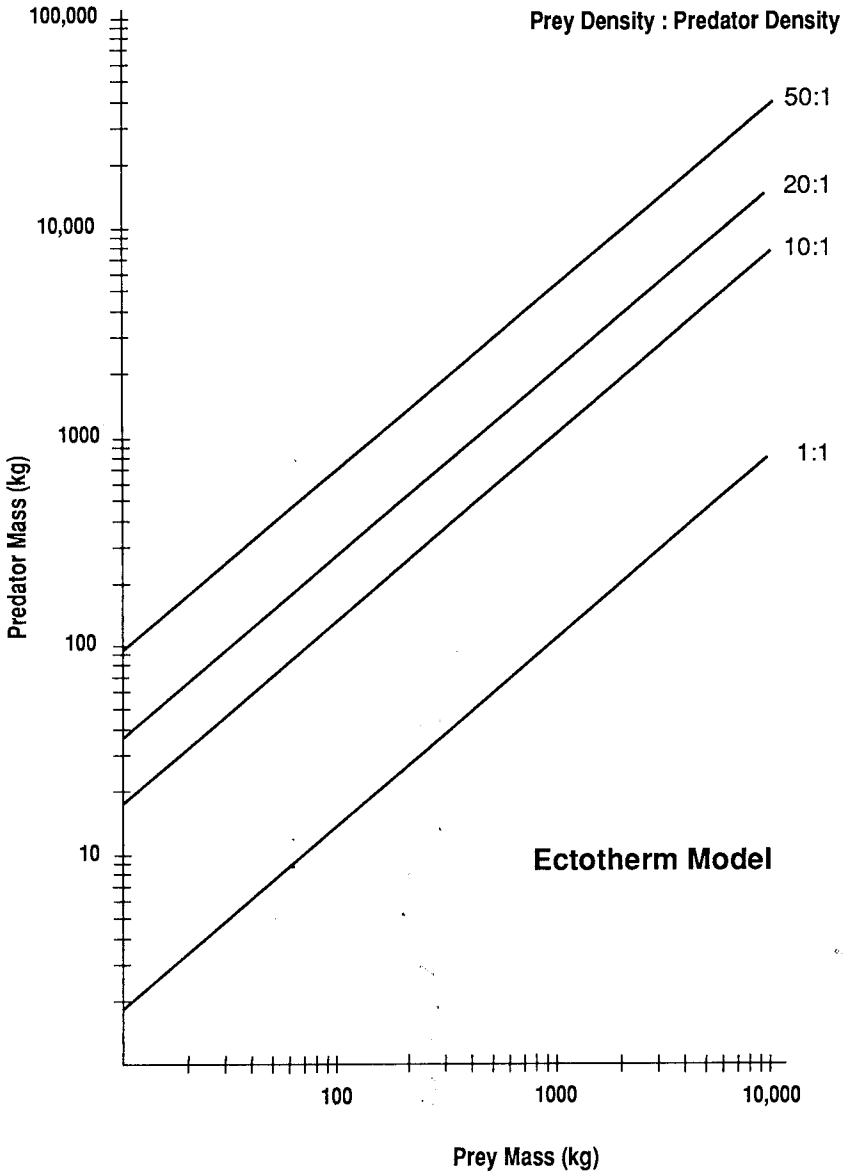


Fig. 3. Predictions of the maximum body mass attainable by an ectothermic carnivore feeding on prey of a specified body mass, given a particular prey population density: predator population density ratio. Other assumptions are as stated in the text.

We have now gone far beyond the limits of real data. Even so, both our models of dinosaur-sized ectothermic carnivores suggest that there would be less problem in maintaining viable populations of such creatures than of endothermic dinosaur-sized predators, assuming that the densities of our ectothermic super-dragons are as high as the models indicate is possible. Differences in the likelihood of extinction of this kind can be seen in comparisons of lizards with birds (Diamond, 1984a, p. 831).

The ornithischian:tyrannosaur ratio for "articulated" dinosaur specimens in the Judith River Formation is roughly 10:1 to 13:1 (Béland and Russell, 1978; Dodson, 1983, 1987; Russell, 1989), which, interestingly enough, is close to the minimum prey:predator ratio predicted in my best-case ectothermic tyrannosaur model. The articulated ornithischian:tyrannosaur ratio is, furthermore, much less than the 50:1 ratio required for endothermic predators in my best-case endotherm model. (The lowest herbivorous dinosaur:tyrannosaur ratio occurs in the fauna of the Nemegt Formation of Mongolia, where tyrannosaur specimens are about as abundant as those of their presumed prey [Osmólska, 1980], but this ratio is so low as to suggest some unusual taphonomic circumstance.)

The Judith River ornithischian:tyrannosaur ratio based on surface-collected isolated bones and teeth in "microfaunal" samples is also rather low—about 6:1 (Dodson, 1983, 1987). Similarly, for a more southerly, specimen-rich Judith River locality, Fiorillo (1991) found an ornithischian:carosaur surface scrap ratio of roughly 5:1. In the Hell Creek Formation, the ornithischian:tyrannosaur ratio of surface-collected bones (based on minimum number of individuals) is rather higher, about 23:1 (P. Sheehan, personal communication). Taken at face value, these numbers suggest that tyrannosaurs were more like ectotherms than endotherms in their food requirements.

However, Brinkman (1990) screen washed samples of the Judith River formation in Dinosaur Provincial Park and found ornithischian:large theropod ratios (based on the number of identifiable elements of each taxon) ranging from 22:1 to as high as 511:1, with a mean ratio of 115:1. Furthermore, in some of his samples there were no identifiable large theropod elements. A cumulative count of ornithischians and large theropods across all his sites gives a ratio of 97:1, which is considerably higher than the ratio based on articulated specimens or surface-collected skeletal elements.

Brinkman's data suggest the possibility that the ornithischian:tyrannosaur ratio based on articulated specimens or surface collected bones underestimates the true value. This might result from large, showy elements like tyrannosaur teeth being more obvious to surface collectors than the much smaller teeth or ornithischians. In addition, small pieces of ornithischian scrap may weather such that exposed surfaces would be difficult to distinguish from ordinary pebbles; during screen washing such pieces would be turned over, and their unweathered surfaces exposed (Brinkman, personal communication). Dodson (personal com-

munication), however, doubts that surface-collected samples are biased in either of these ways.

Employing either surface-collected or screen-washed microfaunal samples to estimate the relative abundance of tyrannosaurs and large ornithischians in Late Cretaceous faunas requires the assumption that the rate at which skeletal elements were contributed to sedimentary systems by their erstwhile dinosaurian owners did not create biased samples. Microfaunal assemblages of large-dinosaur material are usually dominated by teeth. Tyrannosaurs obviously shed old and worn teeth and also lost relatively unworn teeth during fighting or feeding; an isolated tyrannosaur tooth found in a Cretaceous formation does not necessarily mean that the tooth's owner had died in the process of losing that tooth. Hadrosaurs, on the other hand, may have worn individual teeth so thoroughly during mastication that those teeth were completely ground away before they could be shed; isolated teeth of hadrosaurs presumably represent disaggregations from the dental batteries of dead hadrosaurs (D. Weishampel, personal communication). Is it reasonable to assume that the marked differences between large ornithischians and tyrannosaurs in the number of individual teeth per animal and in the method (tooth replacement versus animal death) by which isolated teeth entered the sedimentary record could nonetheless result in microfaunas in which the relative abundance of isolated teeth of different dinosaurian groups approximates the relative abundance of individual animals in the living faunas? It seems a lot to ask, and suggests that "articulated" skeletal censuses of dinosaur faunas may provide a better picture of the composition of those faunas than do microfaunal censuses.

In any event, the possibility that the ornithischian:tyrannosaur ratio could have been as low as 10:1 or as high as 100:1 means that at present we cannot confidently conclude much about the food requirements of tyrannosaurs from such ratios; furthermore, there are reasons for thinking that predator species may frequently be over-represented in fossil vertebrate faunas (Farlow, 1990). If the ornithischian:tyrannosaur ratio was high as suggested by Brinkman's (1990) study, and if we want to argue that tyrannosaurs were more reptile-like than mammal-like or bird-like in their food requirements, we must then conclude that tyrannosaur populations were regulated by some factor(s) that kept them considerably smaller than their food requirements alone would have dictated. Low-density populations of ectothermic tyrannosaurs might have faced the same threat of extinction as endothermic tyrannosaurs, if tyrannosaur geographic ranges were as small as the presently available data suggest.

The already-described speculations of Janis and Carrano (in press) may again be relevant here. We have previously considered the implications of their work for the biomass production rate of tyrannosaur prey, but it also has some bearing on the reproductive dynamics of the carnivorous dinosaurs themselves. If, as seems plausible on the basis of

Janis and Carrano's study, the reproductive potential of tyrannosaurs was greater than that of hypothetical dinosaur-sized carnivorans, this would have made it much easier for low-density tyrannosaur than carnivoran populations to have survived on a long-term basis in a geographically restricted area—but even so, this factor in itself does not seem sufficient to have guaranteed the survival of small populations of such large predators.

If we postulate that tyrannosaurs had mass-specific food consumption rates less than those of very large mammals, it would seem reasonable to suppose that the same might have been true of their ornithischian prey. As previously discussed, this would have permitted larger absolute prey densities, and this in turn would have allowed larger absolute tyrannosaur densities, even if the herbivore:carnivore density ratio was no greater than seen in mammalian faunas.

If the large ornithischian:tyrannosaur ratio was as low as suggested by the articulated skeletal census or the surface-collected microfaunal census, the problem of maintaining viable populations of tyrannosaur species in relatively confined geographic settings becomes much easier, as already discussed. In that case, the factors considered in the preceding two paragraphs may have contributed to making tyrannosaur populations viable but would not have been as critical to the survival of these animals as in the scenario in which the ornithischian:tyrannosaur ratio was as high as suggested by Brinkman's count of screen-washed specimens.

CONCLUSIONS

Colinvaux's (1978) basic premise, that the second law of thermodynamics sets an upper limit to the body size of predatory animals, seems unquestionably true. However, the factors involved in this limitation are more complicated than in Colinvaux's statement of the problem. Terrestrial carnivores must simultaneously have small enough population densities to avoid over-eating their food resources but also large enough total population sizes to avoid chance extinction. A dinosaur-sized carnivorous mammal would require so large a geographic distribution that this seems to be difficult, or even impossible, to do.

Tyrannosaurs and other large theropods were somehow able to get around this problem. I would argue, however, that being pitifully sluggish behemoths, as in Colinvaux's interpretation, was not the way they did it. I have outlined several possible ecological escape hatches through which tyrannosaurs might have avoided the problem predatory mammals were unable to solve. I cannot with assurance say which one, or combination of, these factors was (were) the one(s) that actually permitted the evolution of huge body size in carnivorous dinosaurs, but it is possible to suggest a series of scenarios of tyrannosaur biology in which these factors might have operated in tandem. It is also possible to indicate

which combinations of hypothetical features of tyrannosaur biology are mutually exclusive.

The most obvious of the mutually exclusive features are low population density and small geographic range. I think it unlikely—probably impossible—for tyrannosaurs to have had the low population densities predicted for mammalian carnivores of comparable size by Damuth's (1987) equation and also the rather small geographic ranges suggested by their presently-known fossil record. If their population densities were as low as predicted for gigantic predatory mammals, then the actual geographic range of tyrannosaur species had to have been considerably larger than indicated by the known occurrences of these dinosaurs. If, on the other hand, the present geographic distribution of fossil sites containing tyrannosaur species does reflect the geographic ranges of those species, then the population densities of tyrannosaur species had to have been much higher than those predicted for tyrannosaur-sized flesh-eating mammals.

Any features of the biology of plant-eating dinosaurs that caused the productivity of these herbivores to have been greater than that of elephant-sized mammals could have resulted in higher population densities for their tyrannosaur predators than expected for gigantic carnivorans feeding on elephantine prey. It is hard to say which of the various factors that might have so stimulated ornithischian productivity were the most important. I consider it very likely, however, that oviparity in ornithischians, as opposed to the viviparity seen in most mammals, contributed to at least some such enhancement of ornithischian productivity. To the extent that ornithischian food requirements were less than those of similar-sized mammals, this might have resulted in higher ornithischian biomasses than expected for mammalian megaherbivores and thus higher biomass production rates—unless, of course, relatively low ornithischian metabolic rates were associated with substantially slower growth rates than seen in mammals.

Features of the biology of tyrannosaurs themselves might also have permitted higher population densities of these carnosaurs than expected for huge carnivorans. Tyrannosaurian oviparity and possible differences in diet between young and adult tyrannosaurs are two likely candidates.

If the ornithischian:tyrannosaur ratio was as high as suggested by screen-washed microfaunal collections from the Judith River Formation, it is quite possible that tyrannosaurs had food requirements comparable to those expected for dinosaur-sized carnivorans. This implies low population densities and necessarily large geographic ranges. Indeed, the hypothesis of tyrannosaurian tachymetabolic endothermy is probably incompatible with a highly split taxonomy of these dinosaurs, either within faunas or between contemporaneous faunas.

On the other hand, if the prey:predator ratio was as low as suggested by the Judith River articulated skeleton census or even lower in other regions occupied by tyrannosaurs, it is likely that the food requirements

of tyrannosaurs were enough less than those expected for dinosaur-sized predatory mammals to have been a major factor in permitting viable tyrannosaur populations. This is a particularly important point if the geographic ranges of tyrannosaur species were as small, and the number of co-existing theropod species as high, as suggested by our present understanding of Late Cretaceous dinosaur faunas.

It may be significant that the only continental predators that overlap (and perhaps even exceed) the body sizes of large carnivorous dinosaurs are crocodilians, such as the Late Cretaceous *Deinosuchus* (which may have been a competitor of tyrannosaurs; Baird and Horner, 1979) and the Tertiary *Purussaurus* (Campbell and Frailey, 1991). As I have argued here, and is implicit in the arguments of Flannery (1991) and Diamond (1991), the presumably lower food requirements of such monsters as compared with those expected for mammalian super-dragons would permit the establishment of much larger populations of enormous cold-blooded than warm-blooded predators. Even among marine predators, the largest known form that is likely to have specialized on big-bodied prey was a shark (*Carcharodon megalodon*; compare Randall, 1973), the food requirements of which were presumably less than those of large toothed whales.

Even if tyrannosaurs were not tachymetabolic endotherms in the usual sense, however, this does not necessarily mean that they had to have been true ectotherms or even gigantotherms (Paladino and others, 1990). Biologists agree that birds are derived from archosaurian reptiles, even though there is still disagreement as to which archosaurian group was the immediate avian ancestor (Hecht and others, 1985; Chatterjee, 1991). Just when tachymetabolism was achieved in archosaurian and/or avian evolution is also debated. Most paleontologists believe that the presence of feathers in *Archaeopteryx* indicates that true endothermy had been achieved in this bird, but this interpretation is not universally accepted (Regal, 1975; Ruben, 1991).

At some point in the reptilian ancestry of birds, however, there must have been animals with low metabolic rates, and at some later point in the evolution of birds or their ancestors a shift to rapid metabolic rates occurred. At the same time, other physiological and anatomical features today associated with tachymetabolic endothermy in birds were also evolving. It may well be that all these features evolved in lock-step with each other, but it also seems possible that some might have evolved sooner or at different rates than others; some of these features might even have been preadaptations that made the evolution of others possible. We might ask ourselves, for example, which came first: elevated standard metabolic rates, or a double pump heart, or erect posture, or cursorial adaptations?

Given that mosaic evolution seems to be common in the phylogeny of anatomical features, it does not seem radical to suppose that the same might have been true in the evolution of the complex of characters that

are today associated with tachymetabolic endothermy. If this is true, we might speculate that in various archosaurian (including dinosaurian) lineages there may have been novel combinations of anatomical and physiological features that are not exactly like those seen in living reptiles or birds (compare Regal and Gans, 1980; Reid, 1987; Farlow, 1990).

I would be hard-pressed to say just where tyrannosaurs were on a continuum between bradymetabolic ectothermy and tachymetabolic endothermy, but the results of my admittedly crude models suggest that one of the reasons for the greater body size of tyrannosaurs than of terrestrial carnivorans might have been lower mass-specific food requirements of the dinosaurs than of the mammals. Whether this was because tyrannosaurs had metabolic rates that were consistently less than those of modern tachymetabolic endotherms or whether they were able temporarily (on an ontogenetic, seasonal, or even shorter time scale) to shift their metabolic rates from levels similar to those of modern reptiles to levels more like those of living birds and mammals, I cannot say.

To summarize, I suspect that the most likely factors involved in permitting the evolution of immense size in tyrannosaurs and other theropods were larger population densities of herbivorous dinosaurs than of elephant-sized mammals, somewhat higher population turnover rates of plant-eating dinosaur than of large-mammal populations, at least somewhat lower mass-specific food consumption rates of carnivorous dinosaurs than expected for tyrannosaur-sized carnivorans, differences in diet between young and adult tyrannosaurs, and a higher reproductive potential for theropods than carnivorans. If I have correctly identified the relevant parameters, the gigantism seen in tyrannosaurs and other theropods was the result of a fortuitous concatenation of physiological and ecological features in which dinosaurs differed from the mammals that replaced them.

Even though theropods were able to attain larger sizes than predatory mammals for one or more of the reasons given above, carnivorous dinosaurs must themselves have had some ecological upper limit to body size. City-smashing monsters like Godzilla and Gorgo may make for amusing movies, but they had no counterparts among real flesh-eating dinosaurs. Could it be that the absence of sauropod-sized predators among theropods was the dinosaurian equivalent of the lack of elephant-sized carnivores among mammals?

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