Biogeography

Big thinking

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Since the demise of the dinosaurs, no land vertebrate has matched them for size. Why? The answer may lie in the particular conditions prevailing in the Cretaceous period.

How does evolution produce giant land vertebrates? One of the prerequisites for making such creatures appears to be the existence of big continents[1–3]. Writing in *Proceedings of the National Academy of Sciences*, however, Burness *et al.*[4] demonstrate that the largest animals also eat plants and are cold-blooded.

The authors have analysed data on the largest vertebrate herbivores and carnivores from 30 islands and continents. For each land mass, the authors identified either the largest living species of vertebrate land animal or the largest species that became extinct within the past 65,000 years. They show that, for a land mass of a given size, the largest warm-blooded herbivore was bigger than the largest warm-blooded carnivore. Data for cold-blooded land vertebrates are sparse, because so few of them are the largest vertebrate on a land mass. But, for a given land mass, the authors show that cold-blooded carnivores were larger than warm-blooded carnivores. Similarly, the three data points on cold-blooded herbivores suggest that they are larger than warm-blooded herbivores. Burness and colleagues then go on to evaluate the factors that may have been responsible for the evolution of large dinosaurs.

Like many ecological relationships, that between maximum body mass and land area is a power function[4]. That is, if M is the maximum body size of a group of terrestrial vertebrates on a particular continent, and A is the area of that continent, then $M = kA^b$. Burness *et al.* found that the exponent b effectively equals 0.5, but that the constant k varies among warm- and cold-blooded herbivores and carnivores. The largest warm-blooded herbivore on any given land mass is roughly an order of magnitude larger than the biggest warm-blooded carnivore, if there is one. The few data that are available suggest a similar relationship for cold-blooded vertebrates.

Why should the largest carnivores be smaller than the largest herbivores? It is well established in ecology that the energy available to organisms declines by about 90% for each step up the food chain. So it is reasonable to expect that the largest size a carnivore can reach will be about 10% of the size of the largest herbivore on the same land mass.

Given a specific power function that describes the relationship between maximum body size and continental area for a given group of organisms, how does such a relationship arise? If maximum body mass is controlled in some manner by continent size, then continent size must be related to the minimum number of individuals in the geographical population of a large-bodied species. Each individual of a species of a given size requires a certain minimum amount of space within which to obtain resources and mates. This space, the organism's 'home range', is larger for animals of larger body size[5]. The relationship between home range size, H, and body size is also a power function: $H = aM^z$. The total number of home ranges available for a species of a given size on a given continent will be the continent size divided by the size of that species' home range. After a little algebra, one can deduce that b (the exponent for the power function relating maximum body mass to continent size) should be the inverse of z (the exponent for the power function relating home range to body mass).

Testing whether $b = 1/z$ is true for the largest animals on islands and continents isn't entirely straightforward. Data to test this idea are currently available only for mammals, not reptiles or amphibians. There are no instances where the largest mammal on an isolated island or continent is less than about 100 g in mass[2]. So although many mammals are smaller than 100 g, the test will be valid only for those greater than 100 g. Given these restrictions, Burness *et al.* analysed some previously published data[5]. When they fitted a power function to the sizes of large mammals as a function of their territory size, the resulting exponent was very close to 0.5, confirming the prediction. So large mammals are found only on large continents because small continents don't have enough space to maintain adequate populations of them.

Where do dinosaurs fit into the relationship between maximum body size and continent size? If dinosaurs were warm-blooded

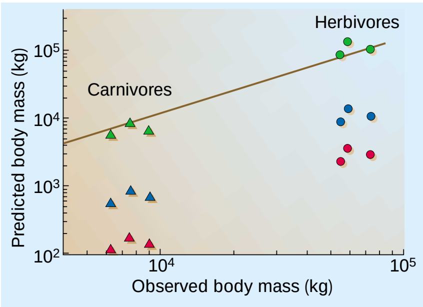

Figure 1 **Why were the biggest dinosaurs so huge? Shown in red and blue are estimates of the sizes of several of the largest herbivorous (circles) and carnivorous (triangles) dinosaurs derived from modern relationships between continent size and maximum body size[4]. It is still not known whether dinosaurs were warm- or cold-blooded. Estimates made using relationships for warm-blooded modern vertebrates (red) are two orders of magnitude lower than the actual sizes (solid line); but those using relationships for cold-blooded vertebrates (blue) are still an order of magnitude lower. A possible explanation for the failure of these estimates, proposed by Burness *et al.*[4], is that the productivity of terrestrial vegetation was ten times higher in the Cretaceous period, between 144 million and 65 million years ago, when dinosaurs reached their largest sizes. That vast extra productivity allowed animals to evolve that were an order of magnitude larger than those that modern continents can support (green symbols).**

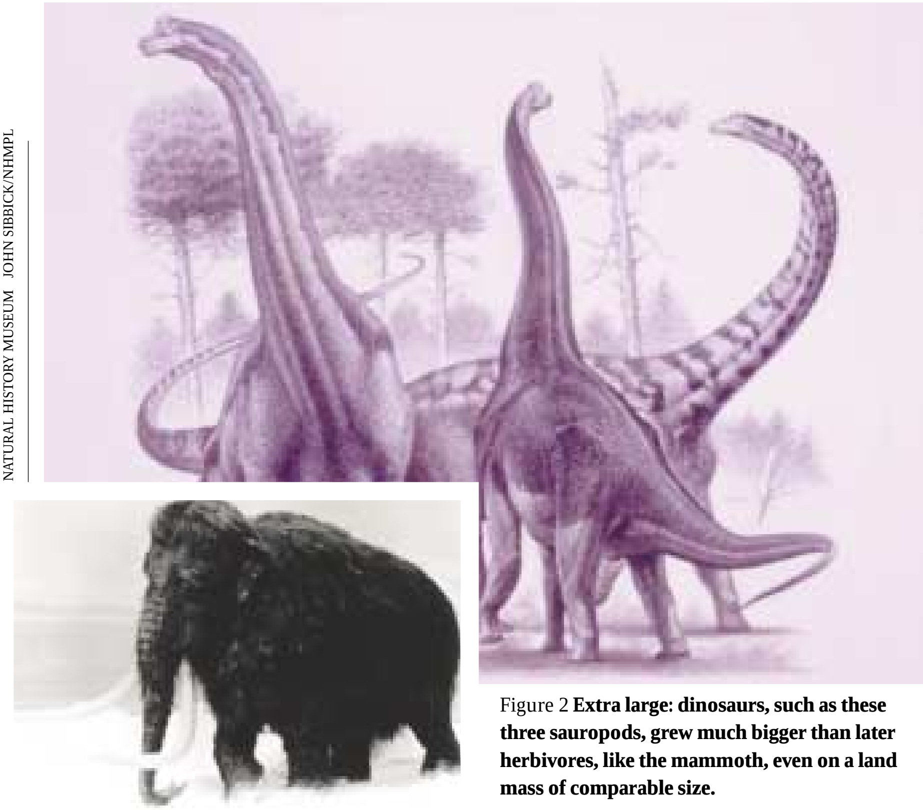

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Figure 2 **Extra large: dinosaurs, such as these three sauropods, grew much bigger than later herbivores, like the mammoth, even on a land mass of comparable size.**

they should more or less follow the relationship for warm-blooded organisms. But Burness *et al*. show that six species of dinosaurs for which estimates of body masses are available — three carnivores and three herbivores — were nearly two orders of magnitude larger than they should have been if they had been warm-blooded (Fig. 1). Using relationships for modern cold-blooded animals improved the prediction, but dinosaurs were still nearly an order of magnitude larger than predicted. The largest herbivorous and carnivorous dinosaurs lived in South America around 100 million years ago. The herbivore *Argentinosaurus huincluensis* weighed in at a massive 73,000 kg. The largest predator that may have fed upon this giant was *Giganotosaurus carolinii*, which tipped the scales at 9,000 kg.

So why were dinosaurs so much bigger than they would be if they had been alive more recently (Fig. 2)? The answer cannot be found by appealing to continent sizes. True, in the past, most of the continents were connected to form a megacontinent called Pangaea. But this land mass started breaking up nearly 180 million years ago, some 80 million years before the largest dinosaurs appeared[6]. By the time dinosaurs had achieved their largest sizes, the continents had separated and were roughly the same size as they are today.

Burness *et al.*[4] suggest a possible explanation: during the Cretaceous period (about 144 million to 65 million years ago), concentrations of CO_2 in the atmosphere were up to ten times higher than they are today. An additional point, not made by the authors, is that the Cretaceous was also notable for the relatively small portion of the Earth's land mass that had cool temperate climates[6]. So during this time a larger proportion of the Earth's terrestrial environment was covered by warm temperate and tropical ecosystems than is the case today.

The higher atmospheric CO_2 and greater land mass in warm climates suggests that the amount of terrestrial vegetation available to support large animals was much greater during the Cretaceous, when the largest dinosaurs lived, than it is now. So it could have been this greater 'ecological size' of continents that allowed large dinosaurs to evolve. This idea might be tested by examining the sizes of modern large animals living in the tropical and temperate land masses of comparable size to see whether those in the tropics are bigger.

Dinosaurs present us with a puzzle. In many respects they seemed to be constructed like warm-blooded animals. Their posture indicated they were more active than living cold-blooded vertebrates. They apparently had extended parental care and complex mating rituals. Yet, ecologically, they filled continents as if they were cold-blooded. So what on the surface appears to be a case of convergent evolution between dinosaurs and modern vertebrates may in fact be the result of unique evolutionary events occurring in different ways at different times. Dinosaurs lived in a very different world to any modern animal, and may have interacted with their environment in ways that have no clear parallels among living land vertebrates. The more we study them, the more we get a glimpse into the complex workings of the evolutionary engine. ■

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