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Megaherbivores as pacemakers of carnivore diversity and biomass: distributing or sinking trophic energy?

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ABSTRACT

Question: What is the trophic role of megaherbivores?

Hypothesis: Depending on their life histories, megaherbivores can either act as sinks or distributors of trophic energy.

Methods: Comparative review of mammal and dinosaur faunas, and aspects of their reproductive biology.

Conclusion: Extant (mammalian) megaherbivore populations represent trophic sinks that potentially limit carnivore diversity and productivity, because they are immune to predation and follow a reproductive strategy of very few, well-protected offspring. In contrast, in dinosaur faunas, the particularities of reproductive biology such as a larger number of offspring and limited parental care made a major part of megaherbivore biomass available to carnivores. Consequently, this increase in available trophic energy allowed for larger body masses and higher species diversity of dinosaur carnivores.

Keywords: dinosaurs, mammals, parental care, reproductive biology.

INTRODUCTION

Among the most noticeable differences between dinosaur and mammal faunas are the astonishingly high body masses, the high species diversity, and the comparatively low degree of trophic diversity attained by the dinosaur (theropod) megacarnivore fauna (Farlow and Pianka, 2002; Van Valkenburgh and Molnar, 2002). Animal biomass, diversity, and maximum body size are governed by the available resources, as exemplified, for example, by the correlation between herbivore and carnivore maximum body mass and land mass area (Burness *et al.*, 2001). Comparisons with mammals have led to the conclusion that the primary productivity of the dinosaur ecosystems was higher, offering more resources to primary and hence also secondary consumers (Burness *et al.*, 2001). In contrast, a comparison with home range requirements of mammalian carnivores, without accounting for differences in habitat productivity,

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leads to the conclusion that animals of the body size of theropods could not have been endotherms (Farlow, 1976; Farlow and Pianka, 2002). Here, we propose an additional cause for the characteristics of the theropod megafauna, which is independent of the question of whether a higher primary productivity of the dinosaur ecosystem or a lower energy requirement of dinosaur organisms, or both, led to a general shift in maximum body sizes – primary productivity, and hence the resources of herbivores, are mainly influenced by geoclimatic factors. Secondary productivity – that is, the resources of carnivores – while also depending on these factors, can be drastically influenced by the life history of the primary consumers. We propose that the life-history attributes of megaherbivores will dramatically influence their trophic effect on (mega)carnivore diversity and the productivity of the carnivore guild. This variable megaherbivore effect can be best explained by contrasting dinosaur and mammalian megaherbivore life histories.

EXTANT MEGAHERBIVORES AS TROPHIC ENERGY SINKS

Extant mammalian megaherbivores are comparatively immune to predation (Sinclair *et al.*, 2003; Owen-Smith and Mills, 2008); here, we define 'megaherbivores' as species that are, at their adult body size, not affected by predation in their respective ecosystem. In fact, immunity to predation is an oft-cited, assumed selective advantage driving evolutionary increase in body size (e.g. Hone and Benton, 2005). This means that the trophic energy these animals use for maintenance is unavailable to secondary consumers. Energy used for reproduction is directed at a single offspring that receives intensive parental care and protection, usually resulting in very low mortalities due to predation (Loveridge *et al.*, 2006), and hence is also mostly unavailable for secondary consumers. As long as this offspring is suckling (i.e. consuming milk), it is a secondary consumer itself that uses the energy of the primary production consumed by its mother at a lower trophic level – that is, with the corresponding tropho-dynamic energetic losses (Pond, 1977). Because energy used by mammalian herbivore populations increases with the average body mass of the species (du Toit and Owen-Smith, 1989), megaherbivores thus represent sinks for trophic energy that is then not available for other fauna (Owen-Smith, 1988; Fritz *et al.*, 2002; Cristoffer and Peres, 2003). Megaherbivores typically make up 40–70% of the total large herbivore biomass of African ecoystems (Owen-Smith, 1988), which underlines the significance of these facts. In theory, mammalian megaherbivore abundance should therefore limit, not enhance, mammalian carnivore density and diversity.

Tests of this hypothesis are rare. During experimental removal of megaherbivores from ecosystems (e.g. Eltringham, 1974; Waldram *et al.*, 2008), carnivore populations were not monitored, but the duration of such experiments might anyway have been too short to notice an effect. However, the palaeontological record provides some corroboration of our hypothesis. Across the European late Miocene, mammalian carnivore diversity decreased with increasing megaherbivore diversity (Fortelius *et al.*, 1996). In mammalian Mediterranean palaeocommunities, trends of increasing body size were found for herbivores, but not for carnivores (Rodriguez *et al.*, 2004; Raia *et al.*, 2007), and in Italian communities, the predator to non-predator species ratio decreased with an increasing proportion of megaherbivores in the overall fauna (Raia *et al.*, 2007). In North American mammal palaeocommunities (Van Valkenburgh and Janis, 1993) as well as globally (Croft, 2006), the predator to non-predator species ratio decreased with increasing overall species diversity; the latter parameter could be interpreted as an indication for an increasing body size range (Gillman, 2007). More tests in mammals are warranted.

COMPARISON WITH DINOSAUR MEGAHERBIVORES

There are numerous indications in the palaeontological literature that dinosaur carnivores occurred at higher density, and with apparently less trophic differentiation, than mammalian carnivores, as extensively elaborated by James Farlow over years of research (Farlow, 1993; Farlow *et al.*, 1995; Farlow and Pianka, 2002; Farlow and Holtz, 2003). A detailed comparison of Cretaceous and extant ecosystems modelled a 2–5 times higher population density for herbivorous dinosaurs, and a 25–100 times higher density for dinosaur carnivores, compared with the Serengeti ecosystem (Matsukawa *et al.*, 2006). From a carnivore point of view, in particular, the dinosaur ecosystem differed in some fundamental aspects from the mammal-dominated ecosystems of today, linked to the reproductive biology of dinosaurs. Dinosaurs produced much greater numbers of young per lifetime than mammals of similar size, and in contrast to mammals, their reproductive output most likely did not decrease with increasing body size (Janis and Carrano, 1992; Paul, 1994). This results in a hypothetical drastic shift of dinosaur populations towards juvenile individuals. The few sauropod herds for which data are available in fact seem to have been composed of a much higher proportion of juvenile animals than is observed in aggregations of mammalian herbivores (Paul, 1998). Although a certain degree of parental care is assumed for dinosaurs (Horner, 2000), one can only speculate whether sauropods would have actively defended their offspring; anyway, simply due to the higher number of dinosaur offspring present at any one stage, one would assume that dinosaurs would have lost a higher proportion of their offspring to predation than large mammals. Consequently, in contrast to extant ecosystems, juveniles of Mesozoic megaherbivores most likely represented a major dietary resource for large carnivores (Farlow and Holtz, 2003) – including mammalian ones (Hu *et al.*, 2005). Intra-guild predation – that is, the predation on other carnivores, or even juveniles of the same species – can be regarded as an additional factor increasing the biomass available for dinosaur predators (Van Valkenburgh and Molnar, 2002). In mammalian carnivores, intra-guild predation is common and may be important for the evolution of carnivore diversity (Palomares and Caro, 1999; Caro and Stoner, 2003; Donadio and Buskirk, 2006).

SCAVENGING

Whether large dinosaur carnivores were predators or scavengers has been at the heart of a historical debate (Farlow and Holtz, 2003; Ruxton and Houston, 2003) that will not be reviewed here. Scavenging is important with respect to our argument because evidently, once adult megaherbivores – whether dinosaurs or mammals – die (by the necessity of our definition due to other causes than predation), they represent trophic energy available for scavengers. Following Farlow and Holtz (2003), we consider it likely that terrestrial, non-flying carnivores are facultative but not obligatory scavengers, a view that is also supported by theoretical considerations (Ruxton and Houston, 2004). The concept of scavenging raises two questions that have, to our knowledge, not been answered conclusively. First, it is debatable to what extent scavengers rely on carcasses that were produced by the predatory action of other carnivores, or that are the result of non-predatory death. Second, if non-predatory death does occur, is it a reliable event, and at which rate does it occur? Note that the study of Houston (1979), which is mostly used in calculations concerning scavenging, suggests a very large number of non-predatory deaths in the Serengeti, whereas the studies of Sinclair *et al.* (2003) and Owen-Smith and Mills (2008) indicate that in all but megaherbivores, predation is by far the most predominant cause of death [note also the low numbers of wildlife carcasses reported by Butler and du Toit (2002)]. With respect to habitat productivity and carnivore diversity, it should be noted that compared with predation opportunities on juveniles, scavenging opportunities on adult megaherbivores invariably represent the more rare events. Metaphorically speaking, considering scavenging to be equal to predation with respect to biomass turnover is like thinking that one can get the same amount of timber out of a forest by waiting for the trees to fall down as one can get by logging. Therefore, if there was no competition from avian scavengers (Ruxton and Houston, 2004), scavenging on megaherbivore carcasses could moderately reduce the trophic sink effect in mammalian ecosystems, but not eliminate it completely.

SYNTHESIS

Juvenile sauropods should have faced far greater predation pressure than adults. Case (1978) postulates an especially high growth rate for animals with a very high infant to adult mortality ratio. In fact, an increase in ontogenetic growth rate, not a prolongation of growth, has been suggested as the major facilitation of dinosaur gigantism (Erickson *et al.*, 2004; Sander *et al.*, 2004), and was most likely associated with a non-reptile metabolism (Case, 1978). Therefore, the biomass turnover of a dinosaur ecosystem should have been much higher than that of a mammalian ecosystem. Populations with higher turnover rates should be able to support a greater biomass of predators (Farlow, 1980). However, population turnovers of a completely different magnitude most likely limit the potential use of extrapolations: correlations between adult body mass and home range or population density most likely cannot be transferred between mammalian and dinosaur ecosystems. Unfortunately, it is not possible to estimate at what life stage dinosaur herbivores were most affected by predation; this would allow conclusions about the size of carnivores that potentially fed on them (Farlow, 1993). Comparative data for other oviparous, terrestrial herbivores such as ostriches are lacking. By producing a high number of vulnerable offspring, dinosaurs made trophic energy of both megaherbivore and megacarnivore populations available at high rates for secondary or even tertiary consumers. In contrast, mammalian megaherbivores, by producing a more limited number of better-protected offspring, limit secondary consumers and act as trophic energy sinks.

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