Giants on the landscape: modelling the abundance of megaherbivorous dinosaurs of the Morrison Formation (Late Jurassic, western USA)

James O. Farlow[a]; I. Dan Coroian[b]; John R. Foster[c]

[a] Department of Geosciences, Indiana-Purdue University, Fort Wayne, IN, USA [b] Department of Mathematical Sciences, Indiana-Purdue University, Fort Wayne, IN, USA [c] Museum of Western Colorado, Grand Junction, CO, USA

First published on: 21 July 2010

PLEASE SCROLL DOWN FOR ARTICLE

Giants on the landscape: modelling the abundance of megaherbivorous dinosaurs of the Morrison Formation (Late Jurassic, western USA)

James O. Farlow[a]*, I. Dan Coroian[b] and John R. Foster[c]

[a]Department of Geosciences, Indiana-Purdue University, 2101 East Coliseum Boulevard, Fort Wayne, IN 46805, USA; [b]Department of Mathematical Sciences, Indiana-Purdue University, 2101 East Coliseum Boulevard, Fort Wayne, IN 46805, USA; [c]Museum of Western Colorado, P.O. Box 20000, Grand Junction, CO 81502, USA

The ecosystem impact of megaherbivorous dinosaurs of the Morrison Formation would have depended on their abundance (number of animals per unit of habitat area) on the landscape. We constrain Morrison megaherbivore abundance by modelling dinosaur abundance in terms of carrying capacity (K), average body mass (ABM) and animal's energy needs. Two kinds of model are presented: 'demand-side' models that estimate K in terms of the aggregate energy demand of the dinosaur community, and 'supply-side' models that estimate K in terms of retrodicted primary productivity. Baseline values of K, ABM and energy needs for the models are further derived from comparisons with modern large herbivores, and from the composition of the megaherbivore fauna from a particular stratigraphic interval of the Morrison, but in all models a broad range of fractions and multiples of these baseline parameters are considered. 'Best-guess' estimates of Morrison megaherbivore abundance suggest an upper limit of a few hundred animals across all taxa and size classes per square kilometre, and up to a few tens of individuals of large subadults and adults.

Keywords: Morrison Formation; terrestrial paleoecology; herbivorous dinosaurs

Introduction: really big herbivores

Cenograms have become a standard tool in mammalian paleoecology (Legendre 1986, 1989; Gingerich 1989; Ducrocq et al. 1994; Gunnell and Bartels 1994; Maas and Kraus 1994; Montuire 1995, 1998, 1999; Morgan et al. 1995; Gibernau and Montuire 1996; Gunnell 1997; Montuire and Desclaux 1997; Dashzeveg et al. 1998; Wilf et al. 1998; Croft 2001; Montuire and Marcolini 2002; Storer 2003; Palombo et al. 2005; Tsubamoto et al. 2005; Geraads 2006; Gómez Cano et al. 2006; Palombo and Giovinazzo 2006; Costeur and Legendre 2008), albeit with some reservations expressed (Rodríguez 1999). Graphs that plot the natural logarithm of body mass (in grams) of each species of non-volant, non-predatory mammal in a fauna against the decreasing rank order of each species' body mass in the fauna (Figure 1) are thought to reflect the structure of the vegetation and climate, but what interests us here is what cenograms show about the structure of large-herbivore faunas. Figure 1 plots cenograms of the biggest [body mass = 8000 g (natural log *ca.* 9) or larger] herbivores in a selection of Cenozoic large-mammal (and bird) faunas and two dinosaur faunas. Marsupials and dromornithid birds comprise the large herbivores in the two Australian faunas (Murray and Vickers-Rich 2004). The Argentinian fauna not only includes edentates, litopterns and notoungulates, but also large rodents, a horse, a peccary, camelids, deer and a gomphothere. The remaining large-mammal faunas mostly are Plio-Pleistocene assemblages characterised by proboscideans, rhinos, horses, hippos, cervids and bovids. The two dinosaur faunas come from particular stratigraphic levels in the Late Cretaceous Dinosaur Park Formation (Currie and Russell 2005) and the Late Jurassic Morrison Formation (Foster 2003, 2007), selected to make them as comparable to the paleomammal faunas as possible by minimising time averaging.

Several interesting observations can be made. The biggest members of the Australian faunas were small compared with other big herbivores, perhaps reflecting the small land area and/or harsh conditions of Australia (Farlow et al. 1995; Burness et al. 2001; Murray and Vickers-Rich 2004). There is a broad overlap in the sizes of the larger members of most of the remaining mammalian faunas and the Dinosaur Park assemblage (although comparison is complicated by the different ways in which body masses were estimated, with dental measurements usually used for Eurasian mammals, and postcranial dimensions or scale models used for other groups). Some of the Pleistocene mammalian herbivores seem to have been substantially bigger animals than the hadrosaurs, ceratopsians and ankylosaurs of the Dinosaur Park Formation (*cf.* Christiansen 2004).

But one assemblage stands out as being especially characterised by giants. The trend defined by the nine largest plant-eating dinosaur species (in this conservative tabulation of valid species and their estimated body masses) from Zone
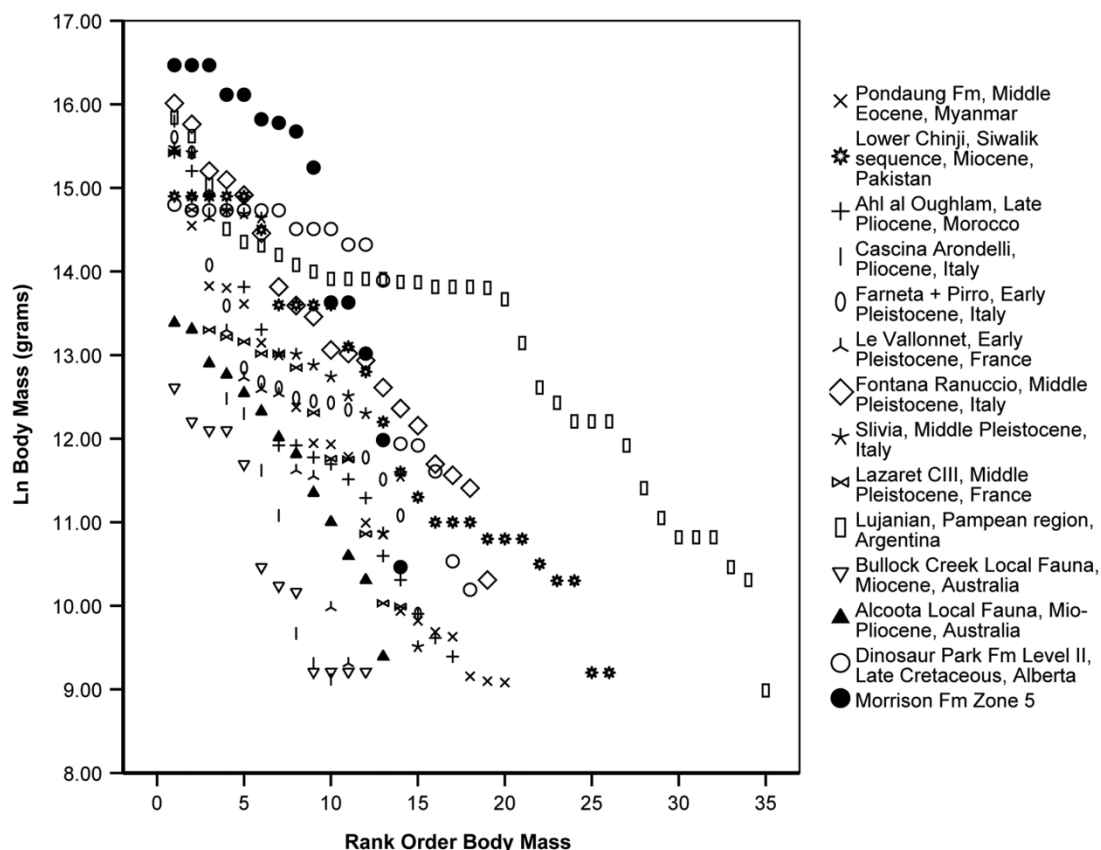
Figure 1.   Comparative cenograms of paleofaunas of 'large' (estimated body mass = 8000 g or more) herbivorous mammals, birds and dinosaurs. As the mammal body sizes are conventional allometric estimates based on skeletal or dental parameters, the body masses of the larger taxa may be somewhat off (?too large). The Morrison dinosaur body-size estimates are based on the version of an allometric equation relating body mass to propodial circumferences presented by Packard et al. (2009); estimating dinosaur masses this way probably minimises differences in mass estimates between the Morrison dinosaurs and the megamammals. Data from Croft (2001 and personal communication); Montuire and Desclaux (1997), Montuire and Marcolini (2002), and Montuire personal communication; Morgan et al. (1995); P. Murray personal communication; Currie and Russell (2005); Palombo et al. (2005), Palombo and Giovinazzo (2006), and Palombo personal communication; Tsubamoto et al. (2005); Geraads (2006) and personal communication.

5 of the Morrison Formation (updated from Foster 2007) shows no overlap with the other faunas. Most of these dinosaurs were sauropods, and their sizes are comparable to those seen in other sauropod faunas (*cf.* Paul 1998; Henderson 1999; Seebacher 2001; Aberhan et al. 2002; Mazzetta et al. 2004; Carpenter 2006; Foster 2007; Lovelace et al. 2007; Gunga et al. 2008; Sander and Clauss 2008; Royo-Torres et al. 2009; Taylor 2009; Klein et al. in press).

Body mass is related to numerous aspects of organism physiology and ecology (Peters 1983), including the abundance of animals in ecological communities (Damuth 1987, 1993, 2007; White et al. 2007), and animal abundances will in turn affect their contribution to ecosystem processes. The giantism of sauropods and other Morrison herbivores, by affecting their abundance on the landscape, would thus presumably have influenced the extent to which they affected the physical structure of the ecosystem (Dodson et al. 1980), their cropping impact on the vegetation and the amount of meat and other organic matter they provided to carnivorous dinosaurs, scavengers

and (ultimately) decomposer organisms. So, if we could constrain how common the herbivorous giants were, we could better reconstruct the nature of interactions between the dinosaurs and their environment. This paper, by modelling the interaction of physiological and ecological parameters we consider most likely to have affected the maximum abundance of Morrison plant-eating dinosaurs, attempts to set reasonable limits on how common these giants could have been.

Some proportion of the secondary productivity of Morrison megaherbivores was undoubtedly consumed by carnivores (*cf.* Farlow 2007; Hummel and Clauss 2008; Russell 2009; Sampson 2009), as live kills, carrion or more likely both. Young and (rarely) even adult individuals of modern megaherbivores sometimes fall victim to predation (Joubert 2006; Plotz and Linklater 2009; Power and Compion 2009). Given the small size of sauropod hatchlings (Chiappe and Dingus 2001), young sauropods may have been much more vulnerable to predation than elephant or rhinoceros calves (*cf.* Wilson et al. 2010).

Given the large size of several Morrison theropod species, growing Morrison sauropods may have been in danger of attack until they were elephant sized or larger, although it seems likely that the biggest individuals would have been nearly invulnerable. Consequently, we do not rule out the possibility that predation may have played a greater role in limiting the size of Morrison megaherbivore populations than those of mammalian megaherbivores. However, in our models, we are interested in constraining estimates of the upper limits of Morrison herbivorous dinosaur population sizes, which would have been set by the abundance and productivity of the vegetation that supported them (*cf.* Pettorelli et al. 2009). We will therefore model Morrison megaherbivore abundance on the assumption that it was limited by trophic resources, and not by other ecological factors such as predation.

At present, there are no data on the population density or biomass of Morrison large herbivorous dinosaurs, but we will predict values from models based on judicious (we hope) comparisons with the ecology and physiology of extant vertebrate plant eaters. We will then use the results of our models to consider the role of sauropods in Morrison ecosystem processes. Finally, we will discuss the kinds of data that might potentially allow further constraints on estimates of large-dinosaur population sizes.

The Morrison paleoenvironment

A number of authors have attempted to characterise the physical and floristic environment in which Morrison dinosaurs lived (e.g., Dodson et al. 1980; Russell 1989, 2009; Bakker 1996; Ayer 1999; Dunagan 2000; Engelmann et al. 2004; Turner and Peterson 2004; Foster and Lucas 2006; Foster 2007; Hotton and Baghai-Riding 2010). Evidence from ancient soils (Retallack 1997), plant fossils (Parrish et al. 2004) and invertebrate trace fossils (Hasiotis 2004) indicates that, for the most part, the climate of the Western Interior of the USA during deposition of the Morrison Formation was rather dry, at least seasonally. Temperatures were quite warm, and annual rainfall was low enough for conditions to be described as semi-arid, at least in places (Moore and Ross 1996). The dryness was likely ameliorated to some extent by groundwater reaching the Morrison plains from mountainous areas to the west (Turner and Peterson 2004), and fossils of aquatic animals were abundant enough that there was probably some surface water year round, at least in the larger watercourses, and particularly in more northerly Morrison regions (e.g. parts of Wyoming) – although it is worth noting that many of the aquatic animals of the Morrison were forms that were probably tolerant of drought conditions.

Although several taxa of Morrison plant megafossils and palynomorphs have been described, uncertainty remains about the relative abundance of different kinds of plants in the vegetation. One interpretation is that trees and tall shrubs mainly grew along rivers, and that for the most part the vegetation away from watercourses was of low stature, and herbaceous rather than woody (Parrish et al. 2004; Rees et al. 2004; Turner and Peterson 2004; Carpenter 2006; Foster 2007). The landscape would have looked something like a modern savanna, albeit with ferns likely replacing grasses as the dominant ground cover (Figure 2). If this reconstruction of the vegetation is correct, on a regional scale, the bulk of plant biomass and net primary productivity (NPP) would likely be contributed by ferns and cycadophytes. However, palynological evidence (Hotton and Baghai-Riding 2010) suggests that conifers may have been dominant components of the vegetation even away from the wetter places, in which case the regional vegetation may have been more parkland like than savanna like, and conifers may have been significant contributors to community primary productivity.

In their evaluation of modern counterparts of potential sauropod food plants, Hummel et al. (2008) found horsetails to be particularly good sources of metabolisable energy per unit dry mass, ferns to be of variable quality across species, ginkgo and some conifers to be comparable in quality to modern temperate browse plants and podocarp conifers and cycads to be of poor quality (also see Gee in press; Sander et al. 2010). The food quality
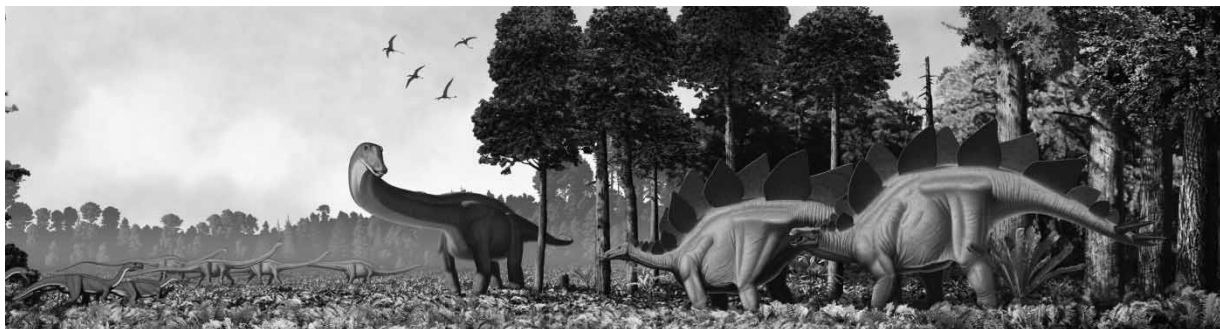

Figure 2. Reconstruction of a Morrison landscape. A single *Apatosaurus* encounters a pair of *Stegosaurus* in a woody habitat, perhaps near a watercourse. A herd of *Diplodocus* is seen in the distance, and a group of small, carnivorous *Ornitholestes* move across the foreground. Morrison Mural, c. 2007 Carnegie Museum of Natural History. Digital illustrations by Walters and Kissinger.

of cycadophytes is unknown, and that of Morrison ferns is hard to predict, given the wide range of metabolisable energy yields of modern ferns, but to the extent that these plants dominated vegetation biomass on the landscape they may perforce have comprised the bulk of food consumed by the Morrison large herbivore community.

Although warmer Late Jurassic climates than those of today (possibly related to higher Jurassic atmospheric CO_2 concentrations) may have stimulated plant productivity (Beerling and Woodward 2001), the dry Morrison climate may have limited the amount of available fodder during the dry season. This may have forced large herbivores to live at low population densities (particularly if they were endotherms; see below), and to move widely across the landscape to find forage (Engelmann et al. 2004).

Herbivorous dinosaurs of the Morrison Formation

Uncertainty remains about how many valid species of each genus of Morrison dinosaur there are, and about which of these dinosaurs coexisted over the several million years of Morrison time, and the Morrison dinosaurs that lived at any one time may not all have lived in the same places. Even so, it is clear that a half dozen or more species of really big plant eaters coexisted at any given place and time (Dodson et al. 1980).

The sample from Dinosaur National Monument and vicinity (Fiorillo 1994; Foster 2007) nicely illustrates this point. These are animals that lived in the same area at the same time. There is at least one species each of *Camarasaurus*, *Apatosaurus*, *Barosaurus*, *Diplodocus* and possibly *Haplocanthosaurus*, all at well over 5000 kg adult size, and *Stegosaurus*, at about 5000 kg, plus smaller but still sizeable plant eaters like the black rhino (*Diceros bicornis*)-sized *Camptosaurus* and the wapiti (*Cervus elaphus*)-sized *Dryosaurus* (Foster 2007). Furthermore, this basic kind of herbivore community maintained itself over most or all of the time that the Morrison Formation was being deposited, a duration of at least 4–6 million years (Foster 2003, 2007).

Herbivorous dinosaur metabolic requirements

The food requirements of dinosaurs would have depended largely on their body masses and rates of metabolism. Dinosaurian metabolic physiology has been a controversial topic (Russell 1965; Ostrom 1970; Bakker 1971, 1972; Spotila et al. 1973; Thomas and Olson 1980; Weaver 1983; Farlow 1990; Paladino et al. 1990; Paul 1991, 1994, 1998, 2001; Barrick and Showers 1994, 1995, 1999; Farlow et al. 1995; Ruben 1995; Barrick et al. 1996; Ruben et al. 1996; Reid 1997; Horner et al. 1999, 2000; O'Connor and Dodson 1999; Seebacher et al. 1999; Fricke and Rogers 2000; Seymour and Lillywhite 2000; Burness et al. 2001; Jones and Ruben 2001; Schweitzer and Marshall

2001; McNab 2002, 2009b; Showers et al. 2002; Seebacher 2003; Chinsamy and Hillenius 2004; Hillenius and Ruben 2004a; Padian and Horner 2004; Seymour et al. 2004; Chinsamy-Turan 2005; Amiot et al. 2006; Gillooly et al. 2006; Grellet-Tinner 2006; Sander and Andrassy 2006; Lehman 2007; Erickson et al. 2009a, 2009b; Perry et al. 2009; Pontzer et al. 2009; Klein et al. in press). The degree to which dinosaurs elevated metabolic rates above expectations for extant non-avian reptiles is related to the broader question of how and why endotherms evolve from ectotherms (McNab 1983; Hillenius 1992, 1994; Block et al. 1993; Farmer 2000, 2001, 2002; Dickson and Graham 2004; Frappell and Butler 2004; Grigg et al. 2004; Hillenius and Ruben 2004b; Kemp 2004; Pörtner 2004; Seymour 2004; Blob 2006; Geiser 2008; Clarke and Pörtner 2010). A definitive assessment of herbivorous dinosaur metabolic rates is beyond the scope of this paper, but we can bracket metabolic expectations for these animals by expectations for extant non-avian reptiles, on the one hand, and birds and mammals on the otherhand.

But here, too, there is controversy that must be acknowledged. An important school of ecological thought argues that a single comprehensive theory based on first principles of physics and chemistry can explain a wide range of physiological and ecological scaling relationships (West et al. 1997; Ernest et al. 2003; Brown et al. 2004; Savage et al. 2004; Economo et al. 2005). Among the results of this programme of research is an explanation for the widely accepted idea that the metabolism of all organisms should scale to the 3/4 power of body mass, in terms of the fractal geometry of organismal internal branching networks (e.g. circulatory and respiratory systems). However, although empirical analyses of metabolic scaling in vertebrates tend to show metabolic scaling exponents near 3/4, they generally do not support the conclusion that there is a common exponent relating metabolism to body mass (White and Seymour 2003, 2004, 2005; McKechnie and Wolf 2004; Glazier 2005, 2010; Clarke 2006; White et al. 2006, 2007; Downs et al. 2008; Makarieva et al. 2008; McNab 2008, 2009a; Sieg et al. 2009). In birds and mammals basal metabolic rate (BMR) or standard metabolic rate (SMR) as conventionally analysed scales to body mass to somewhere between 0.64 and 0.75 power, while the metabolic exponent for reptiles is greater, about 0.76–0.80 or even higher; the difference is observed whether non-phylogenetic or phylogenetically corrected analyses are employed. Other complications arise from the animal size range used in determining the value of the metabolic exponent; the exponent may be larger for bigger than smaller endotherms (Glazier 2005, 2010). This may in part be due to the fact that the largest terrestrial endotherms are herbivorous mammals, the metabolism of whose endo-symbiontic micro-organisms is added that of their mammalian hosts in most measurements of the latters'

BMRs (White and Seymour 2003; Clauss et al. 2007a, 2007b, 2008). Further complicating interpretations of the mass-scaling of BMR in birds, at least, is the fact that BMR shows short-term, reversible adjustments related to seasonal conditions, and that in some species scaling of BMR to body mass has a lower slope for captive-reared than wild birds (McKechnie et al. 2006; McKechnie 2008). Flighted birds typically have a higher BMR than do flightless birds of the same body mass, and the largest birds are flightless (McNab 2009a). Such complications aside, differences between endotherms and non-avian reptiles are also seen in the scaling of field metabolic rate (FMR: Nagy 2005) or food consumption rates (Farlow 1976, 1990; Peters 1983; Nagy 2001) against body mass.

In birds and mammals, metabolic rate is affected mainly by body mass, but body temperature, activity levels, diet, reproductive output, phylogeny, climate and habitat have second-order influences on metabolism that interact in a complex manner (see above references and Williams et al. 1993; Lovegrove 2000, 2004; Tieleman and Williams 2000; McNab 2002, 2003, 2006, 2007, 2008; Anderson and Jetz 2005; Muñoz-Garcia and Williams 2005; Withers et al. 2006; White et al. 2007; Wiersma et al. 2007; Clarke and Rothery 2008). Mammalian consumers of low-quality food (e.g. arthropods, due to their indigestible chitinous exoskeletons) have lower BMRs than consumers of high-quality food (vertebrates, nuts and grass), and eaters of fruit and leaves have intermediate metabolic levels (McNab 2007, 2008). Diet also affects BMR in birds, with relatively high BMRs in eaters of nectar, pollen, nuts and aquatic vegetation, intermediate level BMRs in eaters of grass, insects and vertebrates and the relatively lowest BMRs in species that feed mainly on fruit (McNab 2009a). Sedentary animals living in warm climates, and/or dry situations with variable precipitation, have lower metabolic rates than species living in cooler, and/or more mesic and predictable situations (Lovegrove 2000; Anderson and Jetz 2005; White et al. 2007; Wiersma et al. 2007; McNab 2008, 2009a), although migratory birds and large, mobile mammals may escape such depressing impacts on metabolism by their ability to cut out for more suitable areas on the landscape (Lovegrove 2000; McNab 2008).

Evaluating how these variables likely impacted dinosaur SMRs is difficult, but it seems plausible that dinosaurian herbivores would have had lower rates of metabolism (controlling for body mass) than large theropods. The heat (and perhaps dryness) of the Morrison environment may have had a depressing impact on dinosaurian metabolism (and may also have affected their diel patterns of activity and habitat utilisation [as with modern desert elephants: Kinahan et al. 2007; Leggett 2009]).

Living and fossil herbivorous xenarthrans (glyptodonts, tree sloths and ground sloths) of a particular body size generally have a smaller aggregate dental occlusion surface area than do other herbivorous mammals of comparable body size (Vizcaíno et al. 2006). Extant xenarthrans likewise have lower BMRs than most other mammals (McNab 1985). Mylodontid ground sloths have especially low tooth surface occlusion surface areas for their body size. These observations suggest that most extinct xenarthrans, and mylodontids in particular, employed less thorough oral grinding of fodder, requiring longer fermentation time in the gut, or lower food requirements than expected for other mammals of the same body mass, or both (Vizcaíno et al. 2006).

Paleontologists (e.g. Christiansen 1999) have generally thought that sauropods were capable of eschewing chewing because they hypothesised that sauropods had a bird-like gizzard in which plant materials would be ground (*cf.* Reilly et al. 2001; Battley and Piersma 2005). This hypothesis was based on the occasional discovery of large stones (gastroliths) in the gut region of sauropod skeletons. However, the aggregate mass of stomach stones in sauropods, compared to the body mass of the sauropods, appears to have been far less in sauropods than in birds, which suggests that sauropods were not employing stomach stones in a gizzard (Wings and Sander 2007) – unlike some smaller herbivorous dinosaurs (Cerda 2008 and references therein). Perhaps sauropod gizzards could comminute fodder without the need for gastroliths, which may act mainly to enhance the gizzard's action (Reilly et al. 2001; Schwenk and Rubega 2005). But if sauropods did not grind food in either their mouths or guts, or did so only moderately well, fodder would have arrived in the stomach in large bits. Wings and Sander (2007), Sander and Clauss (2008), and Franz et al. (2009) suggested that sauropods may have compensated for their inability to grind food to small pieces by subjecting it to very long retention times in the gut.

If so, this raises the possibility that a significantly slower rate of fodder fermentation due to large fodder particle size may have been a bottleneck that reduced the rate at which sauropods were able to extract ME from their food – it might have taken considerably longer than the 72 h of the experiments of Hummel et al. (2008) for sauropods to get the same amount of metabolisable energy from a given amount of plant material (*cf.* Bjorndal et al. 1990; Bjorndal 1997; Moore 1999; Ellis et al. 2005; Hatt et al. 2005; Clauss et al. 2009; Fritz et al. 2009). If so, this may have had a depressing effect on sauropod metabolic levels (Clauss et al. 2009) – perhaps even more than inferred for most ground sloths (Vizcaíno et al. 2006).

As if the complications involved in assessing dinosaurian metabolism already discussed were not daunting enough, there are further analytical considerations that are equally problematic. To begin with, equations relating metabolic rate to body mass in extant animals (e.g. Nagy 2001, 2005) are based on animals considerably smaller than Morrison large herbivores, and so the problem of extrapolating well beyond the data range used to create the equations (*cf.* Franz et al. 2009)

is unavoidable. Furthermore, recent analyses indicate that conventional allometric analyses of the kind used to estimate body masses of dinosaurs from osteological measurements (Packard et al. 2009), and to scale metabolic rate to body mass (Packard and Birchard 2008; Packard and Boardman 2009) result in inaccurate estimates for large animals.

All of these complications mean that presently available allometric equations for predicting dinosaurian metabolic rates from estimated body masses are to varying degrees suspect. We will attempt to get around these theoretical problems by a modelling approach in which body masses and metabolic rates are allowed to vary over wide enough ranges to accommodate all the uncertainties involved in particular values of either kind of parameter.

We will attempt to bracket the metabolic requirements of large herbivorous dinosaurs by extrapolating expectations for dinosaur-sized, non-dinosaurian reptiles at the lower end, and dinosaur-sized mammals at the upper end. Metabolic requirements will be expressed in terms of the daily metabolisable energy requirement and the daily FMR.

Modelling the abundance of dinosaurs on the landscape

We will present three kinds of model. First, we will constrain a likely range of population densities of a hypothetical large sauropod species, based on ranges of metabolic requirement, average body mass (ABM) and potential carrying capacity of the Morrison environment, the last extrapolated from values known to be possible for extant megaherbivores. We will then extend this kind of model to the entire megaherbivore fauna for a particular interval of Morrison time. Finally, we will model dinosaur abundance on the basis of published 'retrodicted' values of terrestrial NPP for the Late Jurassic of the Morrison region. As our goal is to estimate the maximum likely population densities of Morrison megaherbivores, baseline values of parameters used in our models will generally reflect values of parameters (e.g. body mass and habitat carrying capacity) that allow for the most generous estimates of population sizes. We will present models that reflect the entire range of plausible values of the relevant parameters, and also 'best-guess' models that reflect a narrower range of parameter values.

In the course of our calculations, we will have to consider animal metabolic requirements and ecosystem productivity, in terms of energy required or provided per day or year. A slight complication here is that the number of days in a year was greater, and the number of hours per day fewer, during the Late Jurassic than at present (Rosenberg 1997). The difference is minor, however (*ca.* 370–380 days per year, and *ca.* 23 h/day for the Jurassic; Rosenberg 1997), and this will be ignored in our models.

Key to parameter acronyms

As we will use several acronyms for parameters throughout this paper, brief summary definitions are presented here for easy reference. Definitions, and explanations of parameter units, are given in the appropriate places in the text.

Abbreviations: ABM, average body mass; BMR, basal metabolic rate; D, population density (number of animals per unit area of the landscape); DME, daily metabolisable energy requirement of a single animal; FMR, field metabolic rate; = FEE (field energy expenditure); K, environmental carrying capacity; ME, daily population metabolisable energy requirement; msMER, daily mass-specific metabolisable energy requirement; NPP, net primary productivity; SMR, standard metabolic rate

'Demand-side' model of the abundance of a single sauropod species

We start by comparing the potential abundance of a single sauropod species with that of the largest extant mammalian herbivore, the African elephant (Table 1). The basic equation in our model is

$$D = K/\text{DME},$$

Table 1. Aggregate metabolisable energy (ME) requirement [kJ/(km^2 × day)] of a hypothetical African elephant population.

Age class	% of population	Estimated body mass (kg)[a]
Juveniles (0–5 years)	31	793
Immatures (5–10 years)	20	1784
Subadults (10–15 years)	11	2616
Young adults (15–20 years)	8	3029
Adults (20 + years)	29.5	3544

ABM across the entire population = 2178 kg
Average per animal DME requirement across the entire population = 175,350 kJ/(animal × day)
Population density[b] = 3.85 animals/km^2; population density of young adults + adults = (37.5/99.5) × 3.85 animals/km^2 = 1.45 animals/km^2
Aggregate population ME requirement = (175,350 kJ/[animal × day]) × (3.85 animals/km^2) = 675,000 kJ/(km^2 × day)

Notes: Population structure based on Leuthold (1976) for Tsavo East, after Owen-Smith (1988), for a population thought to have been stable during the specified time interval (1962–1966). The msMER of all individuals, regardless of age, is assumed to be 550 kJ/(kg body mass$^{0.75}$ day) (Hummel et al. 2008), which probably underestimates the msMER requirements for younger animals.
[a] Following Leuthold (1976), we used age-class: body length relationships for a breeding herd from Croze (1972: table 1) to estimate the body length for the midpoint of each age-class as a proportion of the body length of a female of maximum size: juvenile body length = 0.583 that of a female of maximum size; immature body length = 0.764; subadult = 0.868, young adult = 0.9115, adult = 0.9605 and female of maximum size = 1.000. The body mass of each size class was assumed to be proportional to the cube of its body length. Maximum adult female body mass was assumed to be 4000 kg (Owen-Smith 1988 table I.1).
[b] We used population density for a particularly large elephant population (Murchison Falls Park South, long grass habitat (Laws et al. 1975: table 4.3; *cf.* Chamaillé-Jammes et al. 2009). Biomass was 8601 kg/km^2, with a unit animal body mass of 2234 kg (close to that of our hypothetical population).

D = population density (number of animals/km^2) on the landscape. This is what we want to obtain from the model.

K = the environmental carrying capacity, in terms of how much total ME (in kJ) each unit area of landscape can provide per day. The calculations are presented in Table 1, which estimates how much ME would be needed by an unusually large African elephant population. The reason for using this number is that we know that, under favourable conditions, a landscape (or at least certain habitats on a landscape) can support a population at least that large, and so K can be at least as much as needed to support an elephant population of that size. With a total population density of 3.85 animals/km^2, and the large individuals (young adults + adults) comprising 1.45 animals/km^2, the population ME requirement of our very large elephant population, and thus our basic estimate of K, is 675,000 kJ/(km^2 day). In our model of a sauropod population, we will allow K to vary between 1/10 and twice this value.

DME is the daily metabolisable energy requirement of a single animal. DME is calculated as

$$\{\text{kJ metabolisable energy requirement}/[(\text{unit body mass} \\ (\text{kg})^{0.75}) \times \text{day}]\} \times [\text{average body mass} (\text{kg})^{0.75}/\text{animal}].$$

Two parameters vary in this calculation: (1) the mass-specific daily kJ metabolisable energy requirement (msMER), which we will allow to vary between 55 and 550 kJ/(unit body mass$^{0.75}$ × day) (Hummel et al. 2008) and (2) the average animal body mass (ABM) in kg, which is raised to the 0.75 power for the calculation, and which will vary as described below.

What population density of sauropods would a specified value of K support? We must take into account the fact that sauropods were oviparous rather than viviparous animals, and so young individuals may have comprised a much larger proportion of the population than in elephants (Janis and Carrano 1992; Paul 1994; Sander et al. 2008; Erickson et al. 2009a). Foster (2005) tabulated the relative abundance of juveniles (specimens with linear dimensions of bones <50% of average asymptotic adult size) of Morrison sauropod genera. Juveniles constitute about 17% of Morrison sauropod specimens for the formation as a whole, and can comprise 39% of sauropod specimens at those quarries where juvenile specimens occur. However, these proportions likely undercount the proportion of very young sauropods, whose bones would have been less likely to survive taphonomic filters than those of older individuals (Engelmann and Fiorillo 2000). On the other hand, we must not overestimate the abundance of young sauropods. If immature sauropods segregated from their elders on the basis of size/age (Myers and Fiorillo 2009; *cf*. Varricchio et al. 2008), size/frequency distributions derived from sauropod

bonebeds or tracksites that sampled younger animals might overestimate the proportion of young individuals in the population at any given time.

We will model our sauropod population size-class structure after that of the ostrich (*Struthio camelus*), so selected because it is the largest extant oviparous endotherm (Table 2). Interestingly, however, the relative abundance of 'older' individuals (adults + young adults; 36%) in the ostrich model of the population differs little from that of the hypothetical elephant population. The 'younger' segment of the population (chicks + juveniles + immatures) comprises 64% of the population (in a cassowary population, the proportion of young birds [chicks + subadults] is somewhat less than that assumed here; Moore 2007). We will allow the proportions of 'younger' vs. 'older' individuals in the population to vary, but will keep the abundance of chicks, juveniles and immatures constant with respect to each other within the 'younger' segment, and the abundance of young adults and adults will remain constant with respect to each other in the 'older' segment of the population. The 'younger' segment of the population will vary between 25 and 90% of the entire population, and the 'older' segment in consequence will vary between 10 and 75% of the population (Table 3). Thus, the proportion of the total population composed of chicks will range ([0.25 − 0.90] × 0.7662) = 0.19155 – 0.68958, and so on for the rest of the population.

Erickson et al. (2009a) reconstructed the population life table for a mass assemblage of the ornithischian dinosaur *Psittacosaurus lujiatunensis* from the Early Cretaceous Yixian Formation of China. On the basis of osteohistology and skeletochronology, these dinosaurs were thought to have reached sexual maturity sometime during the ninth year of life. Animals that were 8 years old and older comprised 15% of individual dinosaurs in the sample, which value is bracketed by the range of values for the 'older' segment of our hypothetical sauropod population. Erickson et al. (2009a) concluded that the life history survivorship pattern of *Psittacosaurus* was probably typical for dinosaurs.

The ABM of dinosaurs in each size/age class in our model is calculated assuming geometric similarity throughout ontogeny (Table 2). The asymptotic average adult body mass is assumed to be 30,000 kg, which would make this a fairly large sauropod (*cf*. Seebacher 2001; Gunga et al. 2008; Packard et al. 2009; Taylor 2009). ABM for the entire population is calculated by multiplying the ABM of each size class by the proportional abundance of that size class according to the schedule in Table 3, and then adding the prorated body masses, so calculated, of all the size classes (Table 4). ABM thus varies between 2512 and 16,140 kg. We bracket these values by allowing ABM to vary between 2500 and 20,000 kg. The value of ABM is then used to calculate DME.

Table 2.   Population density (D, number of animals per km^2) of a hypothetical sauropod population.

Age class[a]	% of population	Estimated total length (m)[b]	Estimated body mass (kg)[b]
Chicks	48.7 (95/195)	2.5	59
Juveniles	9.7 (19/195)	5	470
Immatures	5.1 (10/195)	10	3700
Young adults	18.5 (36/195)	15	13,000
Adults	17.9 (35/195)	20	30,000

ABM across the entire population = 8049 kg

Assume that population ME requirement is same as for hypothetical elephant population (Table 1): 675,000 kJ/(km^2 × day)

Scenario 1: Animal msMER = 550kJ/(kg body mass$^{0.75}$ × day)

Average per animal DME requirement across the entire population = 467,375 kJ/(animal × day)

D = (675,000 kJ/[km^2 × day]) × (1 animal × day/467,375 kJ) = 1.44 animals/km^2; D of young adults + adults = (71/195) × (1.44 animals/km^2) = 0.526 animals/km^2

Scenario 2: Animal msMER = 55 kJ/(kg body mass$^{0.75}$ × day)

Average per animal DME requirement across the entire population = 46,738 kJ/(animal × day)

D = (675,000 kJ/[km^2 × day]) × (1 animal × day/46,738 kJ) = 14.4 animals/km^2; D of young adults + adults = (71/195) × (14.4 animals/km^2) = 5.24 animals/km^2

Notes: Population structure loosely based on Bertram (1992) for ostriches. The metabolic-mass-scaled metabolic energy requirement (msMER) of individuals of all sizes in the population is assumed to be the same in each of two metabolic scenarios, which probably underestimates the metabolisable energy requirements for smaller/younger animals.
[a] Bertram (1992) divided his ostrich population into adults (71% of birds), immatures (two-year-olds; 10%) and juveniles (one-year-olds; 19%). He made no count of birds younger than that, but thought that the survival rate of chicks to the age of one year was likely to be 10–15%, based on other ostrich populations (p. 89). We assumed that, relative to a one-year-old juvenile count of 19 out of 100 birds in the one-year and older segment of the population, there would be an initial hatchling count of 190 birds, and that the average number of such chicks over the time interval between hatching and an age of one year would be half that, or 95 birds. In translating from ostriches to a hypothetical sauropod population, then, we based relative proportions of the age classes on a count of 195 animals. We further split Bertram's count of adults into roughly equal numbers of young adults and adults. Obviously the ages associated with these age classes would span a much greater time interval than for ostriches. We presume that sexual maturity would be reached sometime in the young adult size class.
[b] We assumed that total length of large adults was 20 m, with a body mass of 30,000 kg. Hatchling total length was assumed to be 0.3 m (Chiappe and Dingus 2001). We assumed that midpoint of total length of sauropods during the chick interval (however long that was) was 2.5 m. Juveniles were assigned a length of 5 m, immatures 10 m and young adults 15 m. Body proportions were assumed to be geometrically symmetrical across all size classes. Thus, the body mass of chicks was calculated as (2.5/20)^3 × 30,000 kg = 59 kg.

Abundance of the Morrison megaherbivore fauna: FMR 'demand-side' model

Table 5 summarises the taxonomic composition and specimen count of herbivorous dinosaurs from a relatively narrow stratigraphic interval (Zone 5) relatively high in the Morrison Formation (Foster 2007). Estimates of the average adult biomass of each taxon are presented. Two assumptions are made here: (1) that the specimens on which mass estimates were based are typical for that taxon and (2) that the average adult biomass approximates the asymptotic adult body mass for each taxon, neither of which is likely to be completely true. We first calculate the average asymptotic body mass across all taxa of the megaherbivore fauna by multiplying the number of individuals in each taxon (Table 5) by the average

asymptotic body mass of that taxon, and dividing the sum of these multiples by the total number (148) of dinosaur specimens. Two such calculations are done, one using body masses based on conventional allometric projections from osteological measurements (Anderson et al. 1985), and the second using the equation of Packard et al. (2009): these yield average asymptotic body masses across the megaherbivore fauna of 13,700 and 9110 kg, respectively.

Table 6 estimates the proportion each taxon of herbivore contributes to overall community biomass on the assumption that the ratio of ABM to asymptotic adult body mass is the same as in our hypothetical sauropod population (0.268: Table 2). Multiplying ABM by the count of specimens of each taxon estimates the proportion of community biomass that each taxon comprised.

Table 3.   Range of values of the proportional abundance of different size/age classes of a hypothetical sauropod population in our model of sauropod population density.

Segment of population	Size class	Segment proportion		Size-class proportion within segment of population	Minimum proportional abundance of size class within entire population	Maximum proportional abundance of size class within entire population
'Younger'	Chicks	0.25	0.90	0.7662	0.19155	0.68958
	Juveniles			0.1532	0.03830	0.13788
	Immatures			0.0807	0.02017	0.07263
'Older'	Young Adults	0.75	0.10	0.5070	0.38025	0.05070
	Adults			0.4930	0.36975	0.04930

Table 4. Proportional contribution of each size class to ABM in a hypothetical sauropod population, reflecting the extremes of the proportional abundance of each size class (Table 3).

Size class	ABM (kg)	Proportional abundance	Proportional contribution to ABM (kg)	
Chicks	59	0.19155	11.3015	–
	59	0.68958	–	40.68522
Juveniles	470	0.03830	18.001	–
	470	0.13788	–	64.8036
Immatures	3700	0.02017	74.629	–
	3700	0.07263	–	268.731
Young adults	13,000	0.38025	4943.25	–
	13,000	0.05070	–	659.1
Adults	30,000	0.36975	11,092.5	–
	30,000	0.04930	–	1479.0
ABM (kg)			16,140	2512

Table 5. Composition of the herbivorous dinosaur fauna from Zone 5 of the Morrison Formation across all localities (updated from Foster 2007), with emphasis on the megaherbivore (estimated adult body mass $>/ = 1000$ kg) taxa.

Taxon	Number of specimens	Estimated adult body mass (kg)[c]	Biomass [(Number of specimens × average adult mass) × 10^3] (kg)
Sauropods[a]			
Apatosaurus (possibly three species)	31	26,200	812
		14,200	440
Camarasaurus (possibly three species)	47	12,600	592
		9970	469
Diplodocus longus/carnegii	36	10,800	389
		7430	267
Barosaurus lentus	8	10,800	86.4
		7120	57.0
?Haplocanthosaurus	3	9000	27.0
		6420	19.3
Stegosaurs			
Stegosaurus armatus[b]	23	5280	121
		4170	95.9
Megaherbivore total count of specimens and average asymptotic body mass	148	Mean Adult 13,700 Body Mass 9110	
Ankylosaurs			
Mymoorapelta maysi and indeterminate ankylosaurs	2	450	
Ornithopods			
Camptosaurus (two species)	15	830	
Dryosaurus altus	8	160	
Othnielosaurus consors	6	35	
Total number of dinosaur specimens	179		

Notes: Mass estimates modified from Foster (2007), based on propodial midshaft circumferences. For animals weighing 1000 kg or more, two mass estimates were made: one using the conventional allometric equations (Anderson et al. 1985), and the second using the revised equation of Packard et al. (2009). From these two mass estimates for each taxon, an average adult body mass across all the megaherbivore taxa is calculated. Specimen counts and one estimate of body mass are also reported for each category of smaller herbivorous dinosaurs. No correction was made for possible size-related taphonomic biases in dinosaur specimen preservation [see Foster (2007) for an approach that attempts such corrections].
[a] The large sauropod *Brachiosaurus* occurs in the Morrison Formation in Zones 2–4 (Foster 2007). It has been provisionally reported from the Stovall Quarry 1 in Oklahoma, a quarry that is in Zone 5, based on a single metacarpal (Bonnan and Wedel 2004), but will not be considered further in the present paper.
[b] We follow Maidment et al. (2007) in provisionally assigning *Stegosaurus stenops* to *S. armatus*
[c] For sauropods, both of the mass estimates made from humeral and femoral midshaft circumferences were reduced by 10%. Wedel (2005) suggested that such a reduction should be applied to mass estimates based on volumes of scale models of sauropods because of skeletal pneumaticity, but stated that such a correction was not needed for mass estimates made from allometric equations scaling body mass to skeletal dimensions. Since we want to err on the side of overestimating rather than underestimating dinosaur population density estimates, we reduced our allometric mass estimates even though we recognise that this is probably overkill.

Table 6. Proportional composition of community biomass of the herbivorous dinosaur fauna from Zone 5 of the Morrison Formation across all localities.

Taxon	Number of specimens	Estimated adult body mass (kg)	ABM (adult body mass × 0.268)	Biomass (number of specimens × ABM) × 10³ (kg)	% of total
Sauropods					
Apatosaurus (possibly three species)	31	26,200	7020	218	39.8
		14,200	3810	118	32.3
Camarasaurus (possibly three species)	47	12,600	3380	159	29.0
		9970	2670	126	34.4
Diplodocus longus/carnegii	36	10,800	2890	104	19.0
		7430	1990	71.7	19.6
Barosaurus lentus	8	10,800	2890	23.2	4.23
		7120	1910	15.3	4.18
?Haplocanthosaurus	3	9000	2410	7.24	1.32
		6420	1720	5.17	1.41
Stegosaurs					
Stegosaurus armatus	23	5280	1420	32.5	5.94
		4170	1120	25.7	7.04
Ankylosaurs					
Mymoorapelta maysi and indeterminate ankylosaurs	2	450	121	0.241	0.0441
					0.0660
Ornithopods					
Camptosaurus (two species)	15	830	222	3.34	0.609
					0.913
Dryosaurus altus	8	160	42.9	0.343	0.0627
					0.0939
Othnielosaurus consors	6	35	9.38	0.0563	0.0103
					0.0154
Totals	179			548	
				365	

The sauropods plus *Stegosaurus* constitute nearly all of the community biomass. This tabulation makes no attempt to correct for the possibility that Morrison megaherbivores are over represented relative to smaller herbivorous dinosaurs due to taphonomic biases associated with very large size (*cf.* Coe et al. 1987; Russell 1989; Foster 2007). Such a correction would only slightly reduce the relative contribution of the megaherbivores to overall herbivorous dinosaur community biomass, and would not affect the rank-order contribution to biomass of the megaherbivores (Foster 2001). In our further calculations, we will only consider the sauropods plus *Stegosaurus*.

To account for departures from our assumptions, and as in our model for a single sauropod species, we will let ABM vary on either side around the value used for calculations in Table 6 to reflect uncertainty about the proportion of young and older individuals in the dinosaur populations. To simplify calculations, however, we will assume that the age-class structure is the same for all dinosaur species (*cf.* Erickson et al. 2009a). In our model of a hypothetical sauropod population, the ratio of ABM/asymptotic adult body mass ranged 2500/30,000–

20,000/30,000 or 0.0833–0.667. We will use the same limits to bracket the ABM/adult body mass ratio of the entire megaherbivore community.

We can compare the community metabolism of the Morrison megaherbivore community with that of a modern African ungulate community (Table 7). Again, we deliberately select a modern community characterised by a particularly high biomass (associated with a very large population density of hippos). This time we characterise community metabolism (and therefore K) in terms of the FMR. With a community population density of 44.64 animals/km^2 and a community biomass of 28,038 kg/km^2, the overall community FMR is about 3,580,000 kJ/(km^2 × day). This is probably an overestimate, because hippos have a relatively low metabolic rate (Schwarm et al. 2006). In our full range of models, we will allow K to vary from 1/10 to twice this value.

What community abundance of Morrison megaherbivores would be supported by a comparable community FMR? Three scenarios will be considered (Table 8): (1) dinosaur daily metabolic needs correspond to extrapolated daily FMRs of mammals; (2) dinosaur daily

Table 7. Estimated community metabolism of an African large-mammal community characterised by a particularly large biomass [riverine habitat, Murchison Falls Park, South; data from Laws et al. (1975: table 4.3)].

				Metabolism	
Species	ABM (kg)	Population density (km^{-2})	Biomass (kg/km^2)	Individual animal (kJ/day) $\times 10^3$	Population (kJ/[km$^2 \times$ day]) $\times 10^3$
Loxodonta africana	2234	2.00	4468	179	357
				220	441
Hippopotamus amphibius	1000	19.00	19,000	97.8	1858
				122	2320
Syncerus caffer	395	7.80	3081	48.7	380
				61.8	482
Kobus kob	65	7.80	507	12.6	98.2
				16.4	128
Kobus lechwe	160	3.40	544	24.7	84.1
				31.8	108
Alcelaphus buselaphus	136	2.40	326	21.9	52.6
				28.3	67.8
Potamochoerus aethiopicus	50	2.24	112	10.3	23.2
				13.6	30.4
Totals		44.64	28,038		2853
					3580

Notes: Two estimates of metabolism are presented for each species: (1) First line: metabolisable energy requirement, calculated as in Table 1; (2) Second line: FMR (kJ/day) estimated as $4.82 \times$ body mass (g)$^{0.734}$ (Nagy 2005).

metabolic needs equal the daily msMERs of endotherms (as in our single sauropod species model); (3) dinosaur daily metabolic needs correspond to extrapolated daily FMRs for varanid lizards. Each of these estimates will take the place of DME used in our model of a sauropod population.

Abundance of the Morrison megaherbivore fauna: 'supply-side' retrodicted NPP model

Beerling and Woodward (2001) published model predictions of terrestrial NPP for several intervals of the geologic past. For the Late Jurassic of the Morrison region, their model retrodicted NPP values of 2–10 tonnes organic

Table 8. Estimated Morrison large herbivorous dinosaur metabolism.

			FMR^a = 4.82 $\times$ mass (g)$^{0.734}$ (mammals)		msMER 550 kJ/(mass [kg]$^{0.75}$ $\times$ day); (endotherms)		FMR = 3.950 $\times$ mass (g)$^{0.603}$ − 70 (varanid lizards)	
Taxon	Number of specimens	ABM (kg)	Individual ($\times 10^3$)	Population ($\times 10^3$)	Individual ($\times 10^3$)	Population ($\times 10^3$)	Individual ($\times 10^3$)	Population ($\times 10^3$)
Apatosaurus	31	7020	511	15,800	422	13,100	53.0	1640
		3810	326	10,100	267	8270	36.6	1140
Camarasaurus	47	3380	299	14,000	244	11,500	34.1	1600
		2670	251	11,800	204	9600	29.6	1390
Diplodocus	36	2890	266	9590	217	7800	31.0	1120
		1990	202	7290	164	5900	24.8	891
Barosaurus	8	2890	266	2130	217	1730	31.0	248
		1910	196	1570	159	1270	24.1	193
?Haplocanthosaurus	3	2410	233	699	189	568	27.8	83.4
		1720	182	546	147	441	22.7	68.0
Stegosaurus	23	1420	158	3640	127	2930	20.2	464
		1120	133	3050	106	2450	17.5	402
Totals				45,900		37,600		5160
				34,400		27,900		4080

Notes: FMR = field metabolic rate; equations from Nagy (2005) for mammals, and Packard and Boardman (2009; modified from Nagy et al. 1999) for varanid lizards; msMER = metabolisable energy requirement ([550 kJ/unit body mass$^{0.75}$] $\times$ body mass [kg]$^{0.75}$); equation from Hummel et al. (2008). Totals may not correspond exactly to sums of columns due to rounding.
^{a} The equation for mammals is used, rather than that for birds, because larger animals were used in creating the mammalian equation.
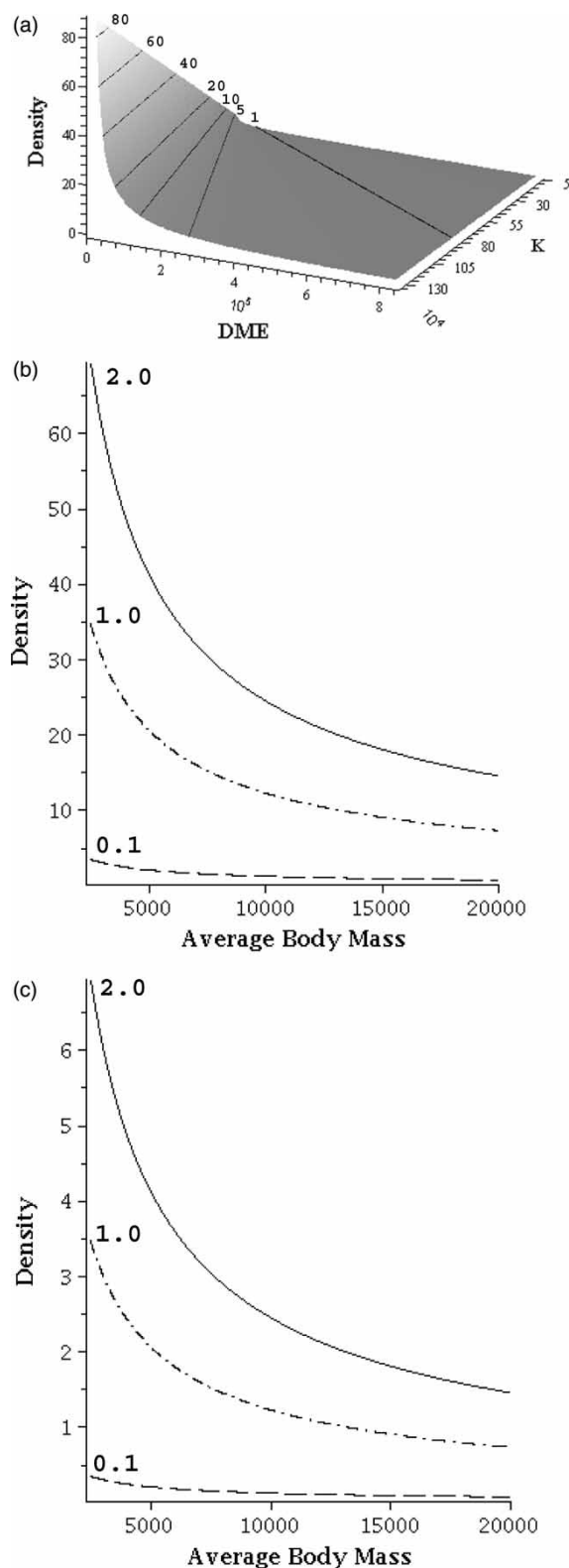
Figure 3. 'Demand-side' model of population density (number of animals/km^2) of a hypothetical sauropod species as a function of environmental carrying capacity K (in terms of kilojoules of metabolisable energy provided by the environment per square kilometre per day) and DME (daily per animal ME requirement).

carbon fixed per hectare per year. Assuming that NPP in terms of organic carbon fixed is about half of NPP in terms of plant dry matter (Huston and Wolverton 2009: Fig. 10), this becomes an NPP of 400,000–2,000,000 kg of plant dry matter/(km^2 × year).

The experiments of Hummel et al. (2008) indicated that modern plants similar to those generally available to sauropods should yield 6000–10,000 kJ metabolisable energy/kg dry mass (but recall our earlier uncertainty about how quickly this energy would be made available in the absence of mastication or gut grinding). Therefore, the potential K of the Morrison environment can be estimated by combining these sets of numbers, such that K in terms of ME potentially provided to big herbivores by NPP would range 6,580,000–54,800,000 kJ/(km^2 × day).

It is unrealistic to assume that the large herbivorous dinosaurs of the Morrison paleocommunity were able to consume all of the potential NPP. Some unknown but likely large fraction would likely have been consumed by other herbivores (presumably insects in particular; *cf.* Hasiotis 2004; Poinar and Poinar 2008; Sampson 2009), and some fraction would likely have been either unavailable or unpalatable to herbivores. Consequently, we will present scenarios in which the range of K values actually consumed by Morrison large herbivorous dinosaurs is 0.1, 0.5 and 0.9 times the potential values.

McNab (2009b) modelled dinosaur energetics using an equation relating field energy expenditure (FEE = FMR) to body mass in six species of large varanid: FEE (kJ/day) = 1.07 mass (g)$^{0.735}$ [extrapolating from his equation to a 7000-kg animal yields an estimate about twice that based on the equation of Packard et al. (2009)]. McNab suggested that dinosaur FEEs approximated those

DME is the multiple of the ABM of animals in the population, and the msMER of individual animals. K is expressed as multiples (0.1–2.0) of the ME requirement of a large modern population of African elephants (Table 1): 675,000 kJ/(km^2 day). ABM ranges 2500–20,000 kg, depending on the size-class structure of the population (Tables 3 and 4); msMER ranges 55–550 kJ/(kg body mass$^{0.75}$ × day). (a) The complete model; labelled contours indicate lines of equal values of animal density across the curved interaction surface created by DME and K. (b) Bivariate plot of density as a function of ABM with msMER set at 55 kJ/(kg body mass$^{0.75}$ × day), and three values of K: 0.1, 1.0 and 2.0 × 675,000 kJ/(km^2 day). (c) Bivariate plot of density as a function of ABM with msMER set at 550 kJ/(kg body mass$^{0.75}$ × day), and three values of K: 0.1, 1.0 and 2.0 × 675,000 kJ/(km^2 day). Population density is directly proportional to K, and inversely proportional to msMER and ABM. The highest population densities (up to about 80 animals/km^2) are associated with (unrealistically?) high values of K (levels sufficient to sustain twice the daily population ME requirement of a very large modern elephant population), very low msMER (equivalent to that of extant reptiles), and a population dominated by very young individuals.

of varanids, and would have been ~22% those of mammals of comparable size.

In our present set of models, we will, as before, set upper values of msMER of herbivorous dinosaurs at 550 kJ/(unit body mass$^{0.75}$ × day), and lower values of msMER at 22% of that value, or 121 kJ/(unit body mass$^{0.75}$ × day). ABM will again range 759–9140 kg. As DME = msMER × ABM, the total range of DME in this set of models will be 17,500–514,000 kJ/(animal × day). *D* will then be calculated as *K*/DME.

Results

'Demand-side' model of the abundance of a single sauropod species

Figure 3 shows calculated values of *D* across the full range of our estimates of *K*, ABM and DME. Table 2 calculates *D* of sauropods in a narrower part of that range, on the assumption that the age-class structure corresponds to that of ostriches, and that *K* is 675,000 kJ/(km^2 day), under two scenarios: one in which each animal's msMER is comparable to that of an endotherm and the second in which each animal's msMER is 1/10 that of an endotherm.

Under the first scenario, with endothermic sauropods with high rates of metabolism, we obtain a *D* of 1.44 animals/km^2; of these, 0.526 animals/km^2 would be large individuals (young adults + adults). The overall sauropod population density would be less than half that of the elephants. In the second scenario, with sauropods having metabolic rates comparable to those of ectotherms, population densities would be 10 times those of endothermic sauropods, and 3.5–4 times those of the hypothetical elephant population. Substantially lower estimates for *D* (much less than one animal/km^2) are obtained if we assume *K* values 1/10 those calculated for the very large modern elephant population, coupled with msMER expectations for an endotherm, even if we assume that the population is largely composed of very young individuals. Substantially higher values of *D* (as much as 80 animals/km^2) are associated with *K* values greater than those associated with the very large modern elephant population, msMER expectations for an ectotherm, and a population dominated by very young animals (Figure 3). Note, however, that a population dominated by small juveniles also means that the number of mature animals per unit area of landscape would be correspondingly low.

Abundance of the Morrison megaherbivore fauna: FMR 'demand-side' model

Tables 8 and 9 present calculations of total megaherbivore community metabolism for the three scenarios using our baseline ratio of ABM/asymptotic adult body mass, with two sets of values of the adult body mass of each taxon

Table 9. Proportion of Morrison large-herbivore community metabolism contributed by each taxon (taxon population metabolism/total large-herbivore community metabolism).

Taxon	Mammal FMR model	Endotherm msMER model	Varanid FMR model
Apatosaurus	0.344	0.348	0.318
	0.294	0.296	0.279
Camarasaurus	0.305	0.306	0.310
	0.343	0.344	0.341
Diplodocus	0.209	0.207	0.217
	0.212	0.211	0.218
Barosaurus	0.0464	0.0460	0.0481
	0.0456	0.0455	0.0473
?Haplocanthosaurus	0.0152	0.0151	0.0162
	0.0159	0.0158	0.0167
Stegosaurus	0.0793	0.0779	0.0899
	0.0887	0.0878	0.0985

(Table 5). In all three scenarios, *Apatosaurus*, *Diplodocus* and *Camarasaurus* together dominate community metabolism. The mammal FMR model predicts slightly larger individual animal metabolic rates than does the endotherm msMER model; because we want to bracket ranges of values in our predictions of dinosaur population densities, from here only the estimates based on FMRs of mammals and varanids will be reported.

Figure 4 shows the full range of estimated Morrison megaherbivore population densities predicted in our model. To reiterate, the baseline value of *K* (Table 7) is 3,580,000 kJ/(km^2 × day) and *K* varies between 358,000 and 7,160,000 kJ/(km^2 × day). There are two baseline values of ABM, (0.268 × 9110 kg), or 2441 kg, and (0.268 × 13,700 kg), or 3670 kg (Tables 5 and 6), and ABM varies from (0.0833 × 9110 kg), or 759 kg, to (0.667 × 13,700 kg), or 9140 kg. For any given ABM, the FMR (kJ/day) for an animal of that average mass will range between [3.950 × body mass (g)$^{0.603}$ − 70] and [4.82 × body mass (g)$^{0.734}$].

Tables 10 and 11 present calculations of abundance for individual taxa for two sets of scenarios with specified values of *K* and ABM, and of a particular FMR vs. body mass equation. In a scenario in which *K* takes the baseline value of 3,580,000, ABM is a specified proportion (0.268, as in our model of a single sauropod species – Table 2) of asymptotic body mass, and the dinosaurs have the FMRs of mammals (Table 10), the total abundance of dinosaurian megaherbivores is 11–15 animals/km^2, about 1/3–1/4 that of the African large herbivore community; 4–6 animals/km^2 are large individuals (Table 10). The dinosaurian megaherbivore biomass is up to half again that of the African large herbivores. In the varanid FMR scenario (Table 11), there are an incredible 100+ animals/km^2, of which about 40 animals/km^2 are large individuals. The biomass is an astonishing
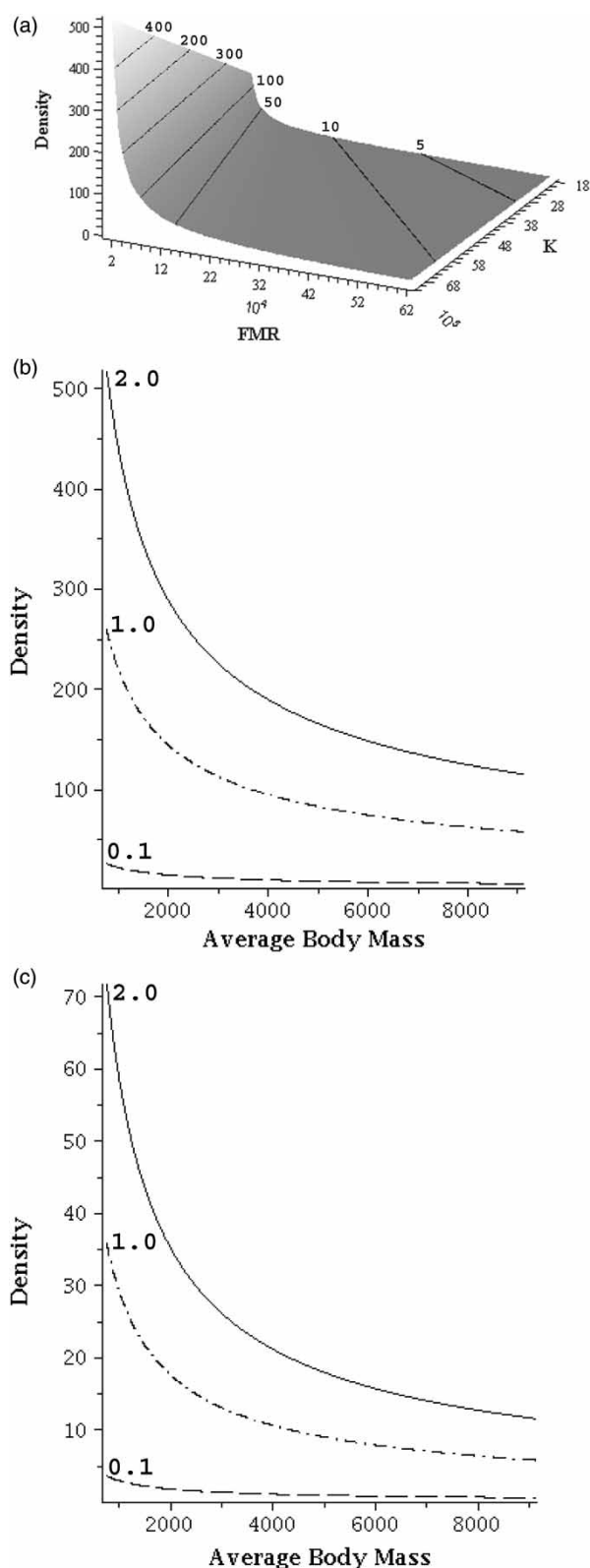
(a)

(b)

(c)

Figure 4. 'Demand-side' model of total population density (number of animals/km^2) across species of Morrison megaherbivorous dinosaurs as a function of environmental carrying capacity K (in terms of kilojoules of energy provided per

300,000 + kg/km^2 [*cf.* Coe et al. (1979) for a comparison of the biomass of Aldabra tortoises with that of African ungulates]. Even higher (unrealistically so?) animal densities are predicted if K values are greater than the baseline 3,580,000 value, in combination with dinosaur FMRs like those of varanids, and very high proportions of juveniles in the populations (Figure 4).

Abundance of the Morrison megaherbivore fauna: 'supply-side' retrodicted NPP model

The number of megaherbivorous dinosaurs calculated to occupy each square kilometre of landscape in this 'supply-side' model (Figures 5 and 6) shows overlap with estimates from our earlier 'demand-side' model (Figure 4) at lower values of potential K, and of the proportion of that potential K actually available to the dinosaurs. The higher values of K, and of the proportion of K actually available to dinosaurs, imply the most fantastic dinosaur community abundances yet, with hundreds or (with low msMERs and a high proportion of juveniles in the fauna) even thousands of animals/km^2 of landscape. Such numbers are hard to credit.

Discussion

Sources of uncertainty in our models

Estimates of Morrison megaherbivore abundance in our models span a huge range, reflecting lack of firm knowledge about most of the relevant features of

square kilometre per day) and daily per animal metabolic need. K is expressed as multiples (0.1–2.0) of the total FMR of a very large modern African large herbivore community (Table 7). This baseline value of K (Table 7) is 3,580,000 kJ/(km^2 day) and K varies between 358,000 and 7,160,000 kJ/(km^2 day). There are two baseline values of ABM, 2441 kg, and 3670 kg (Tables 5 and 6), and ABM varies from 759 to 9140 kg, reflecting different estimates of the proportion of very young vs. older animals in the dinosaur community. For any given ABM, the FMR (kJ/day) for an animal of that average mass will range between [varanid equation: $3.950 \times$ body mass (g)$^{0.603} - 70$], and [mammal equation: $4.82 \times$ body mass (g)$^{0.734}$]. (a) The complete model; labelled contours indicate lines of equal values of density across the curved interaction surface created by ABM, FMR and K. (b) Bivariate plot of density as a function of ABM, with FMR following the varanid equation of Packard and Boardman (2009): FMR (kJ/day) = $3.950 \times$ Mass (g)$^{0.603} - 70$, and three values of K: 0.1, 1.0 and $2.0 \times 3,580,000$ kJ/(km^2 day). (c) Bivariate plot of D as a function of ABM, with FMR following the mammal equation of Packard and Boardman (2009): (kJ/day) = $4.82 \times$ Mass (g)$^{0.734}$, and three values of K: 0.1, 1.0 and $2.0 \times 3,580,000$ kJ/(km^2 day). As in the model for a single sauropod species (Figure 3), astonishingly (unrealistically?) high community population densities are associated with very high values of K, FMRs extrapolated from modern varanid lizards and a very high proportion of juveniles in the dinosaur populations.

Table 10. Estimated population density of Morrison large herbivores based on a total large-herbivore community metabolism equal to the total FMR of the African large-herbivore community (Table 7).

Taxon	Average animal body mass (kg)	Individual animal metabolism (FMR: kJ/day) $\times 10^5$	Taxon metabolism/ community metabolism	Estimated population density (animals/km^2)		Biomass (kg/km^2)
				All sizes	Large	
Apatosaurus	7020	5.11	0.344	2.41	0.88	16,918
	3810	3.26	0.294	3.23	1.18	12,301
Camarasaurus	3380	2.99	0.305	3.65	1.33	12,343
	2670	2.51	0.343	4.89	1.78	13,062
Diplodocus	2890	2.66	0.209	2.81	1.02	8129
	1990	2.02	0.212	3.76	1.37	7477
Barosaurus	2890	2.66	0.0464	0.62	0.23	1805
	1910	1.96	0.0456	0.83	0.30	1591
?Haplocanthosaurus	2410	2.33	0.0152	0.23	0.085	563
	1720	1.82	0.0159	0.31	0.11	538
Stegosaurus	1420	1.58	0.0793	1.80	0.65	2551
	1120	1.33	0.0887	2.39	0.87	2674
Totals				11.52	4.19	42,309
				15.41	5.61	37,643

Notes: Population density is calculated as (taxon metabolism/total large-herbivore community metabolism) $\times$ (3.58×10^6 kJ/[km$^2 \times$ day]) $\times$ ([1 animal $\times$ day]/individual animal metabolism (kJ). Individual animal metabolism is assumed to be that extrapolated for the FMR of a mammal (Table 8). All sizes = entire population; Large = large individuals only. 'Large' animal population density = total population density $\times$ 0.364, the proportion of 'large' (young adult + adult) individuals in the hypothetical sauropod population (Table 2). Biomass = population density (all sizes) $\times$ ABM. Totals may not correspond to exact sums of columns due to rounding.

dinosaurian natural history. However, some of the relevant parameters are better constrained than others. Estimates of adult (asymptotic?) body mass in each taxon are probably less speculative than any other parameter (but keep in mind that we chose deliberately slightly to underestimate the body masses of sauropods; Table 5, comment C).

Estimates of the proportion of immature animals in dinosaur populations are more speculative, but recent studies (summarised in Erickson et al. 2009a) suggest that immatures may consistently have comprised 70% or more of the population, which means that the average-sized dinosaur in a population may have been considerably

Table 11. Estimated population density of Morrison large herbivores based on a total large-herbivore community metabolism equal to the total FMR of the African large-herbivore community (Table 7).

Taxon	Average animal body mass (kg)	Individual animal metabolism (FMR: kJ/day) $\times 10^3$	Taxon metabolism/ community metabolism	Estimated population density (animals/km^2)		Biomass (kg/km^2)
				All sizes	Large	
Apatosaurus	7020	53.0	0.318	21.48	7.82	150,790
	3810	36.6	0.279	27.29	9.93	103,976
Camarasaurus	3380	34.1	0.310	32.55	11.85	110,004
	2670	29.6	0.341	41.24	15.01	110,118
Diplodocus	2890	31.0	0.217	25.06	9.12	72,423
	1990	24.8	0.218	31.47	11.45	62,624
Barosaurus	2890	31.0	0.0481	5.55	2.02	16,053
	1910	24.1	0.0473	7.03	2.56	13,420
?Haplocanthosaurus	2410	27.8	0.0162	2.09	0.76	5028
	1720	22.7	0.0167	2.63	0.96	4530
Stegosaurus	1420	20.2	0.0899	15.93	5.80	22,625
	1120	17.5	0.0985	20.15	7.33	22,568
Totals				102.66	37.37	376,923
				129.81	47.24	317,236

Notes: Population density is calculated as (taxon metabolism/total large-herbivore community metabolism) $\times$ (3.58×10^6 kJ/[km$^2 \times$ day]) $\times$ ([1 animal $\times$ day]/individual animal metabolism (kJ). Individual animal metabolism is assumed to be that extrapolated for the FMR of a varanid lizard (Table 8). All sizes = entire population; Large = large individuals only. 'Large' animal population density = total population density $\times$ 0.364, the proportion of 'large' (young adult + adult) individuals in the hypothetical sauropod population (Table 2). Biomass = population density (all sizes) $\times$ ABM. Totals may not correspond to exact sums of columns due to rounding.
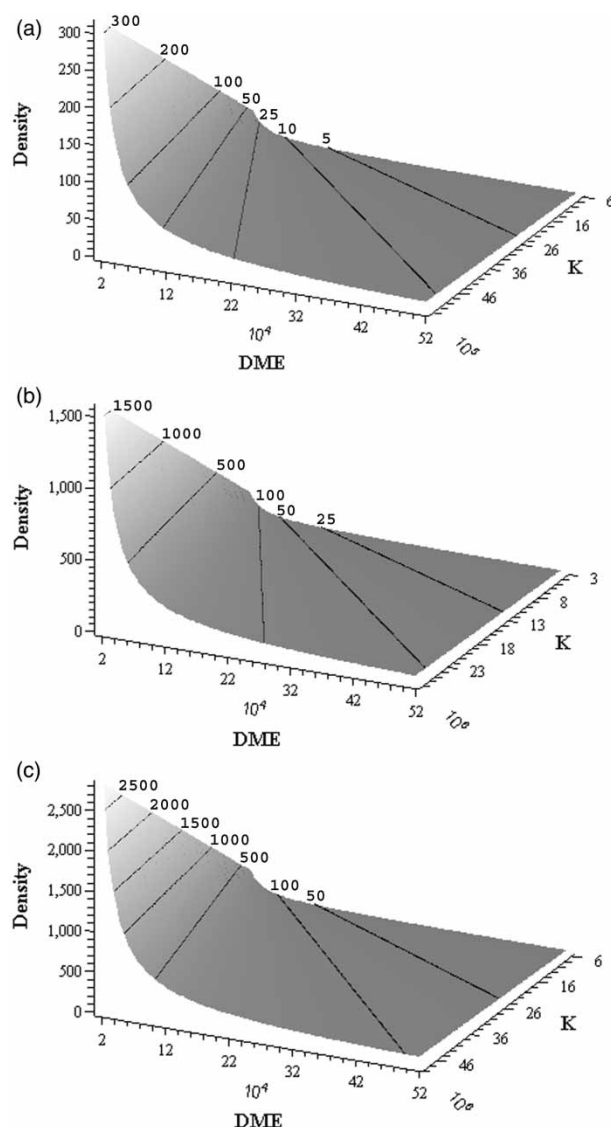
Figure 5. 'Supply-side' model of total population density (number of animals/km^2) across species of Morrison megaherbivorous dinosaurs as a function of environmental carrying capacity K (kilojoules of energy provided per square kilometre per day) and daily per animal DME. K is expressed in terms of retrodicted NPP of the Morrison region during the Late Jurassic (Beerling and Woodward 2001) potentially available to herbivores, and ranges 6,580,000–54,800,000 kJ/(km^2 day). DME is the multiple of the ABM of animals in the megaherbivore community, and the msMER of individual animals. ABM ranges 759–9140 kg, reflecting different estimates of the proportion of very young and older individuals in the dinosaur community; msMER ranges 121–550 kJ/(kg body mass$^{0.75}$ × day). As DME = msMER × ABM, the total range of DME will be 17,500–514,000 kJ/(animal × day). (a) The proportion of K actually available to large herbivores = 0.1 × the potential values. (b) Proportion of K actually available to large herbivores = 0.5 × potential values. (c) Proportion of K actually available to large herbivores = 0.9 × potential values. Labelled contours indicate lines of equal values of density across the curved interaction surface created by DME and K.

smaller than the average-sized fossil specimen. Most of the immatures presumably 'disappeared down the gullets' (Farlow and Holtz 2002: 255) of various-sized carnivorous dinosaurs and other predators, particularly if post-hatching parental care was limited (Isles 2009), and so were lost to the fossil record.

Even the much-debated topic of dinosaurian metabolic physiology is arguably approaching consensus; dinosaurian metabolic rates are almost certainly constrained at the low end by extrapolations from varanid lizards (McNab 2009b), and at the high end by the lower range of values for modern endotherms, such as marsupials (Erickson et al. 2009a, 2009b). As described above, examination of the factors that impact metabolic rates in extant mammals and birds suggest that the sauropods and stegosaurs of the Morrison Formation may have had particularly low metabolic rates for large dinosaurs.

Probably the least certain parameter in our models is K, the carrying capacity for megaherbivores of the Morrison environment. We presented two kinds of estimates of K. Our 'demand-side' estimates used as their starting points abundances of single species of megaherbivores (African elephants) or entire large-mammal communities known to occur in the modern world. As levels of productivity sufficient to meet the metabolic requirements of these animals obviously can occur, we used those values as the bases for estimating K of the Morrison environment.

Keep in mind, that in our demand-side models, predictions were made on the basis of unusually high (local?) biomasses of modern large mammals, whether of an elephant population or an entire large-herbivore community. Furthermore, in the case of the African large-mammal community, the estimated community FMR is probably too large, given that community biomass is dominated by a species that has a relatively low metabolic rate.

Higher carbon dioxide levels in the Jurassic atmosphere than at present might have stimulated primary productivity (*cf.* Beerling and Woodward 2001), resulting in larger dinosaur populations than one would otherwise expect. This may have been counteracted, however, by the dryness of the Morrison environment (at least in comparison with the modern African habitats used as the bases for our demand-side models), and the possible low biomass of vegetation on the dry uplands distal to watercourses (*cf.* Owen-Smith 1988; Olff et al. 2002; Kerkhoff and Enquist 2006). Consequently, we think that our demand-side scenarios have predicted the likely high ends of Morrison dinosaur abundances on the landscape for any given metabolic regime of the dinosaurs.

Our supply-side models estimated K from the paleoclimatic and paleovegetation models of Beerling and Woodward (2001), which retrodicted Late Jurassic NPP values for the area of Morrison deposition, from which we estimated potential K to range
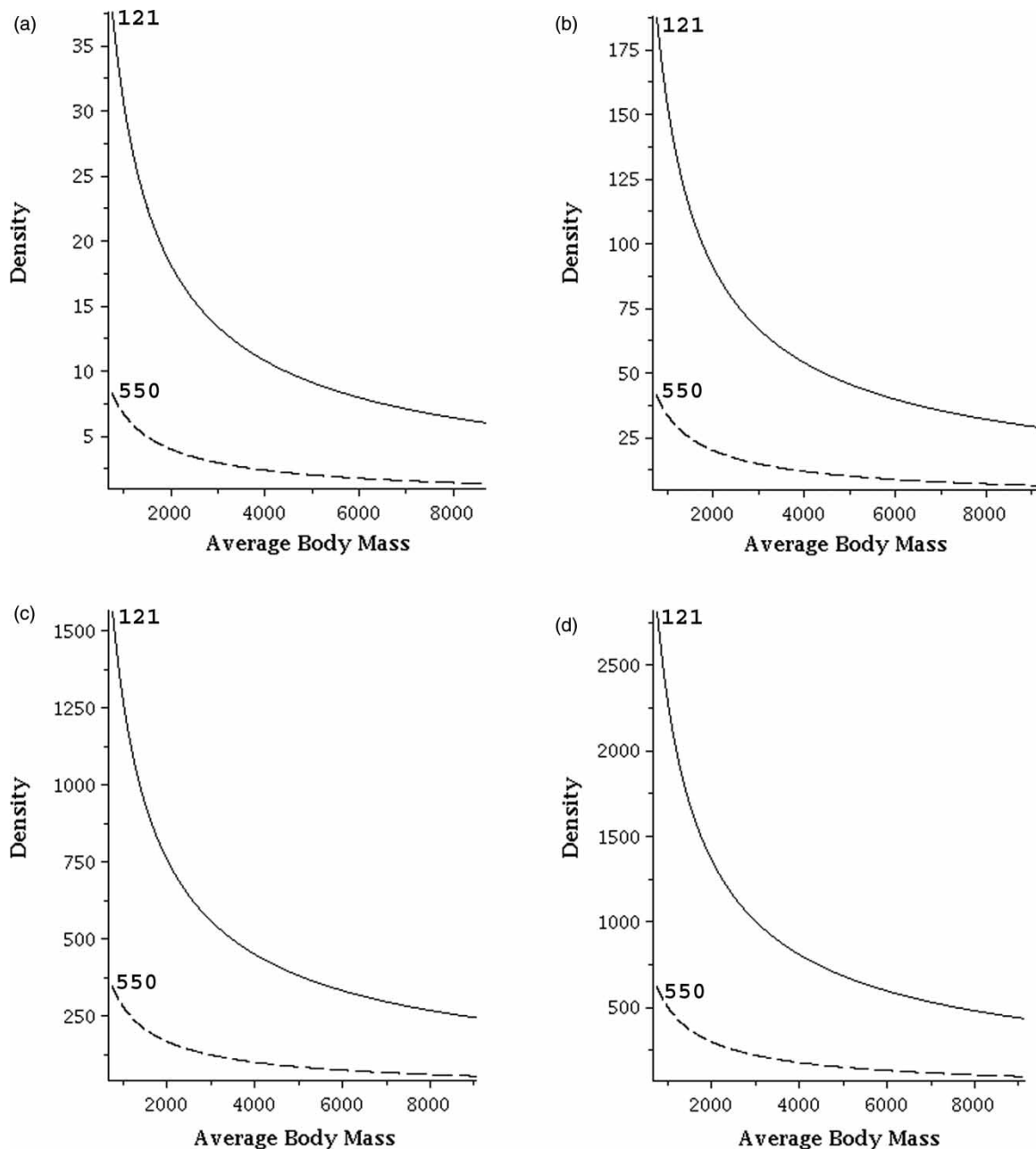
Figure 6. Alternate bivariate versions of the 'supply-side' model of megaherbivore community population density as a function of ABM, given specified values of carrying capacity *K*, and the msMER of individual animals, extracted from the more inclusive models shown in Figure 5. In each panel, the value of *K* and msMER is set at specified values. The value of msMER is set at either 121 or 550 kJ/(kg body mass$^{0.75}$ × day). The value of *K* in each panel is a multiple of either the lowest or highest value of potential *K* in Figure 5 (6,580,000 or 54,800,000 kJ/[km^2 × day]), and 0.1, 0.5 or 0.9 times that value, the latter reflecting different assumptions about the proportion of potential *K* actually available to and consumed by large herbivores. ABM ranges 759–9140 kg. (a) $K = 0.1 \times 6,580,000$. (b) $K = 0.5 \times 6,580,000$. (c) $K = 0.5 \times 54,800,000$. (d) $K = 0.9 \times 54,800,000$. As in previous models, extremely high values of density are associated with high values of *K*, low values of msMER and high proportions of very young individuals in the dinosaur community, but the largest values in this set of models seem even more unrealistic than the largest values in our demand-based models.

6,580,000–54,800,000 kJ/(km^2 × day). Assuming that these values are accurate, an overall average for the Morrison would have been some intermediate value. Even more uncertain than these NPP values of potential *K* are what proportion of that productivity was actually consumed by Morrison megaherbivores. In modern terrestrial ecosystems, large herbivores crop anywhere from 10 to 80% of available above-ground NPP (Milchunas and Lauenroth 1993), which provides considerable latitude for modelling.

Abundance of the Morrison megaherbivore fauna: 'best-guess models'

Since our demand-side and supply-side models present such a wide range of megaherbivore densities, it seems appropriate to present a narrower range of possibilities that reflect what seem the most likely ranges of values of the relevant parameters.

If we generalise the size/age class structure reported by Erickson et al. (2009a) for *Psittacosaurus* to dinosaurs more generally, and assume as a first approximation geometric similarity among the members of different size classes within a species, the ratio of the body mass of an average-sized individual to that of large adults will be about 0.124. We will assume that this ratio applies for all of the Morrison megaherbivores (Table 5). Then, the ABM for an individual megaherbivore across all taxa will be the sum of (number of specimens of each taxon) × [adult body mass (using the lower body mass value in Table 5)] × 0.124, divided by the total number of specimens (148) across all taxa. This gives a megaherbivore community ABM of 1130 kg. We will assume this value in both of our best-guess models.

In both models, we will assume that msMER ranged from 50 to 80% (*cf.* McNab 2002, 2009b; Erickson et al. 2009a, 2009b) of the values for an endotherm used by Hummel et al. (2008): (0.5 to 0.8) × 550 kJ/(kg body mass$^{0.75}$ × day), or 275–440 kJ/(kg body mass$^{0.75}$ × day). Because K is the least constrained parameter in our models, in the demand-side model we will let it span the entire range of values previously used in our 'unconstrained' (Figure 4) model: 358,000–7,160,000 kJ/km^2 × day).

With ABM fixed at 1130 kg, D is now calculated as K/(1130$^{0.75}$ kg × msMER). Using the specified values of msMER and K, D ranges from 4 to 134 animals/km^2 (Figure 7(a)), with K having a greater impact on the value of D than msMER. With 15% of the animals being sexually mature adults (*cf.* Erickson et al. 2009a), the D of such adults will range 0.6–20 individuals/km^2. The range of densities calculated by this demand-side model includes the values for both endothermic and ectothermic dinosaurs in our baseline demand-side model (Tables 10 and 11).

In our supply-side NPP model, the highest values of potential K, and of the proportion of K consumed by dinosaurs, resulted in values of D so high as to be unbelievable (Figures 5 and 6). We suspect that intermediate values are more plausible. For example, if average potential K had been in the middle of the two extreme values, or 30,700,000 kJ/(km^2 day), if half of that had actually been available to dinosaurs, and the ABM of a Morrison megaherbivorous dinosaur across all size classes and species had been 2440 kg (Tables 10 and 11: divide total community biomass by total community population density using the lower set of values of body mass), the
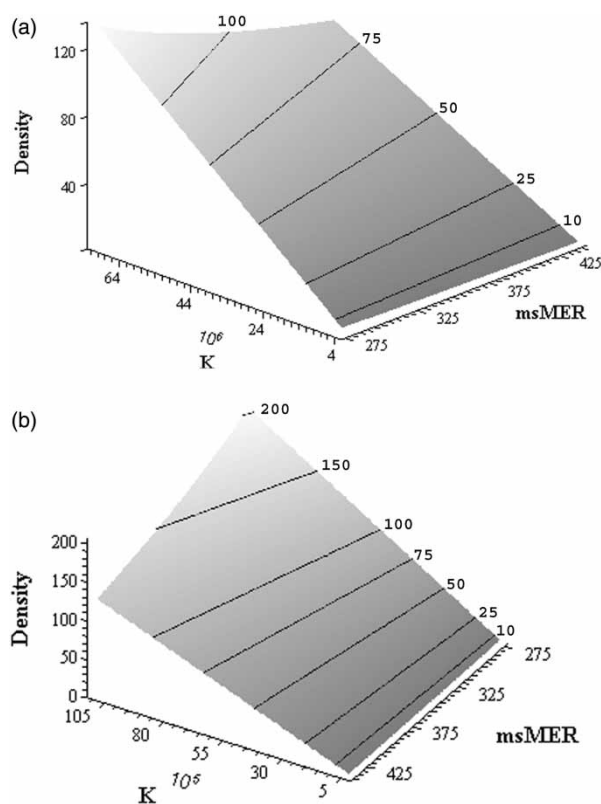

Figure 7. 'Best-guess' models of total population density (number of animals/km^2) across species of Morrison megaherbivorous dinosaurs as a function of environmental carrying capacity K (in terms of kilojoules of energy provided per square kilometre per day) and daily per animal metabolic need (ABM × msMER). ABM is set at 1130 kg, and msMER ranges (0.5–0.8) × 550 kJ/(kg body mass$^{0.75}$ × day). Labelled contours indicate lines of equal values of density across the curved interaction surface created by msMER and K. (a) Demand-side model: K ranges 358,000–7,160,000 kJ/(km^2 × day). (b) Supply-side model: K ranges 329,000–11,000,000 kJ/(km^2 × day).

total community population densities of dinosaurs of all ages would have been somewhere between 80 and 365 animals/km^2, depending on whether their msMERs were mammal-like or varanid-like. The larger individuals more likely to be preserved as fossils would have been fewer than that; if the ratio of large individuals were the same (0.364) as used in the calculations for Tables 10 and 11, these would have an abundance of 29 to 133 animals/km^2. Although these numbers are a few times higher than the comparable estimates based on the demand-side models (Tables 10 and 11), they are close to being in the same ballpark.

For our best-guess supply-side model, however, we will constrain NPP in yet another way. The same paleoproductivity models used to retrodict Late Jurassic NPP estimate modern NPP in eastern Africa at 6–16 tonnes of organic carbon per hectare-year (Beerling and

Woodward (2001: figures 4.22, 4.23). Using the same conversions as in our Morrison supply-side model, this translates into a potential K of 32,900,000–87,700,000 kJ/(km^2 × day). The aggregate ME requirement of the high-biomass African large-herbivore community (Table 7) is 2,850,000 kJ/(km^2 day), which is 2–9% of the estimated regional NPP.

On this basis, we will allow the proportion of NPP consumed by Morrison megaherbivores to range 5–20% (thus ranging from a bit more to twice the percentages in the African large-herbivore community) of the potential NPP, which ranged 6,580,000–54,800,000 kJ/(km^2 × day) in the less constrained supply-side NPP model presented earlier (Figure 5). Thus, in our best-guess supply-side model K will range from (smallest NPP estimate × smallest percentage consumed) to (largest NPP estimate × largest percentage consumed), or about 329,000–11,000,000 kJ/(km^2 × day). As in our best-case demand-side Morrison community model, we will set ABM at 1130 kg, and allow msMER to range 275–440 kJ/(kg body mass$^{0.75}$ × day). D in this best-case supply-side model ranges about 4–200 dinosaurs/km^2 (Figure 7(b)). If we further assume that the K actually consumed by dinosaurs, averaged across the entire Morrison ecosystem, was the midpoint of the range of values in our best-case model, about 5,640,000 kJ/(km^2 × day), then D would range 65–105 dinosaurs of all size/age classes/km^2, and about 10–16 adult animals.

Our best-guess models (Figure 7), and our baseline calculations (Tables 2, 10 and 11) put Morrison dinosaur population densities at up to a few hundred animals per square kilometre, and large adults at up to several tens of individuals. The largest estimated population sizes reflect the lowest estimates of animal metabolic rates, and the most generous estimates of energy availability to the herbivorous dinosaur community. Recall again that the baseline values of modern large-mammal (whether elephants alone or entire large-herbivore communities) population energy needs (Tables 1 and 7) upon which our models are based were deliberately chosen to be high-end values, reflecting particularly large populations of the modern animals. Our body mass estimates of sauropods were also chosen to be slight underestimates. Consequently, to the extent that our estimates of Morrison dinosaur abundance are off, we suspect that they are more likely to be too high than too low. With that in mind, we suspect that the abundance of Morrison adult and subadult dinosaurs – those individuals on taphonomic grounds most likely to have left preservable skeletons – to have lived on the landscape at an average abundance of a few individuals (Table 10: mammal FMR model), or a few tens of individuals (Table 11: varanid FMR model), per square kilometre. By analogy with modern elephants (Roux and Bernard 2007; Chamaillé-Jammes et al. 2009; Ngene et al. 2009), Morrison megaherbivore population densities may

have been largest, whether permanently or seasonally, near sources of drinking water and higher vegetation concentrations, than on drier parts of the landscape.

Morrison sauropods as keystone species and ecosystem engineers

Sauropods are the biggest continental herbivores that ever lived, and their huge size undoubtedly made them have a significant impact on their habitat (as with modern mammalian megaherbivores: *cf.* Skarpe et al. 2004; Owen-Smith 2006; Guldemond and van Aarde 2008; Cowling et al. 2009; Goheen et al. 2009; Luske et al. 2009; Mapaure and Moe 2009). The simple act of walking would have compacted or disrupted soil and disturbed the herb and shrub strata of the vegetation (Butler 1995), as well as any cryptobiotic soil textures that might have developed on Morrison dryland soils, and the large footprints of sauropods probably created microhabitats for small organisms different from those in undisrupted soils (*cf.* Jones et al. 1997).

Cropping activities would likewise have severely affected or even destroyed individual plants – possibly even entire patches of food plants. Sauropod faeces would have been concentrations of plant debris, particularly if sauropod digestion of fibrous plant tissues was relatively inefficient (*cf.* Olivier et al. 2009). Consequently, sauropod scats were likely an attractive food source for arthropods, and presumably rapidly colonised by fungi and other decomposers. Similarly, sauropod carcasses would have been trophic bonanzas for scavengers and decomposers (particularly in catastrophic die-offs during droughts), mass concentrations of energy and nutrients (Farlow 2007) that comprised 'cadaver decomposition islands' (Russell 2009:185), much as whale carcasses provide similar concentrations for the modern deep-sea benthos (*cf.* Sampson 2009 and references therein). Consequently, accumulations of sauropod scats, and sauropod carcasses, presumably comprised local micro-habitats on the landscape that hosted small-scale decomposer-based communities of high biomass, and possibly species richness.

Given their likely dominance of Morrison herbivore community biomass, sauropods must have been on the menu of carnivorous dinosaurs, whether killed or scavenged (Foster 2003, 2007; Farlow 2007). The amount of sauropod secondary productivity that fed theropods would have depended on sauropod abundance, the productivity/biomass ratio of sauropod populations [which was likely higher than expectations for mega-mammals due to sauropod oviparity (Paul 1994; Hummel and Clauss 2008)], and the age/size class in which sauropod productivity was concentrated. If the greatest proportion of sauropod productivity was in eggs and the smallest size classes, it would have been available to a host

of large and small theropods, as well as crocodylomorphs (Foster 2003). To the extent that sauropod productivity was concentrated in large individuals, much of it may have been available to consumers only as carrion.

Our models suggest that if dinosaurian metabolic physiology was close to that of extant endotherms, then for any given level of K the number of individual dinosaurs per unit area on the landscape is likely to have been less than in modern large-mammal (megaherbivore plus typical ungulate) communities (compare Tables 7 and 10). Dinosaur biomass, on the other hand, would likely have been greater than that of large herbivorous mammals. If dinosaur populations were numerically dominated by younger individuals (Janis and Carrano 1992; Paul 1994; Erickson et al. 2009a), large adult dinosaurs would have been relatively uncommon, and unless the amount of K available to herbivorous dinosaurs was substantially greater than in modern terrestrial ecosystems, large adult dinosaurs would have been scarce in absolute terms (number of animals per unit area of landscape) as well.

If sauropods lived in herds segregated on the basis of size or age (Myers and Fiorillo 2009), the numbers of large individuals of any particular species at any moment may have been dramatically clumped: huge concentrations of biomass in small areas, with much of the landscape either devoid of that species, or only occupied by smaller, younger individuals. Disruptive sauropod effects on ecosystem processes – physical alteration of the habitat, cropping of plants – would likely have been disproportionately exerted by large individuals, and have constituted roving hot spots of intense impact, separated by (long?) intervals of time with little or no presence of that species at any given location, especially if sauropods were herding animals, and particularly if sauropods had high metabolic rates.

In contrast, if sauropods were solitary animals, the biggest animals would generally have been separated by large distances, and so their impact would have been less clumped at any given time, but possibly still less diffuse than that exerted by modern large herbivorous mammals. This more diffuse impact could have been accentuated to the extent that the metabolic needs of adult sauropods were less than expected for typical large mammalian herbivores. As seen in our models, lower msMERs translate into a larger number of animals for a given level of K. This in turn would indicate a greater absolute number of large adults whose carcasses would have a reasonable chance of being preserved as fossils.

Proxies for Morrison megaherbivore abundance?

Is it possible, even in principle, to test predictions of our models about the abundance of herbivorous dinosaurs on the Morrison landscape? We can no longer census live dinosaurs, but we could potentially compare the abundance of fossils of Morrison sauropods and stegosaurs with those of large mammalian herbivores in Cenozoic paleofaunas. In modern large herbivorous mammals, population density is negatively correlated with body size (Damuth 1993), a trend that likely also applied to extinct mammals. It might therefore be possible to take advantage of this relationship to compare the relative abundance of fossil specimens of Morrison sauropods and stegosaurs with those of mammalian megaherbivores in Cenozoic faunas.

Due allowance would have to be made for differences between the Morrison Formation and Cenozoic formations in outcrop area and thickness and collecting effort (see White et al. (1998) for quantification of the number of dinosaur specimens per area of outcrop searched for the Hell Creek Formation). Ideally the Morrison Formation would be compared with a stratigraphic unit(s) that was similar in tectonic setting, inferred sedimentation rate and reconstructed paleoclimatic regime, and that like the Morrison Formation preserved a diverse megaherbivore fauna; faunas from the Siwalik Group of Pakistan might be candidates (Morgan et al. 1995).

If, after taking into account the confounding variables, the prorated number of large (adult and subadult) individuals of Morrison megaherbivores (and sauropods in particular), summed across taxa (because some megaherbivore taxa seem to have been much less common than others), was considerably less (in terms of number of articulated specimens, minimum number of individuals, number of identifiable specimens or other parameters; *cf.* Badgley 1986) than that of the typically smaller megaherbivores in the Cenozoic unit(s), as would be expected from the population density: body mass relationships described by Damuth (1993), this would be consistent with the idea that large sauropods and stegosaurs were indeed rather rare on the Morrison landscape (skeletal outcome 1). On the other hand, if specimens of large dinosaurian plant eaters turned out to be about as common, or even more common, than specimens of mammalian megaherbivores, this would be difficult to explain except in terms of higher population densities of megaherbivorous dinosaurs than expected for (hypothetical) equally gigantic herbivorous mammals (skeletal outcome 2).

Another possible proxy for the abundance of dinosaurian vis-à-vis mammalian megaherbivores could be the occurrence of trackways and tracksites, and this might be even more informative about the role of Morrison megaherbivores in ecosystem processes than the alternative skeletal outcomes. If the total number of individuals of large (adult and subadult) sauropods and stegosaurs per unit area on the Morrison landscape had been very low, we would expect that at any given time there would have been few such giants to leave footprints. If we compared the

Morrison Formation with a Cenozoic formation(s) that was comparable in tectonic, sedimentary and paleoenvironmental setting, we might then expect: (1) that the number of individual large dinosaur trackways, at tracksites of a particular size, would be much less than the number of trackways per tracksite size of the generally smaller mammalian megaherbivores in the matched Cenozoic formation(s); (2) the number of tracksites containing trackways of large sauropods and stegosaurs, as a function of outcrop area and/or thickness, to be relatively fewer than the similarly prorated number of Cenozoic tracksites containing trackways of mammalian megaherbivores or (3) both. In contrast, if large individuals of sauropods and stegosaurs had been much more common than expectations based on megamammals, we would expect the prorated number of trackways at tracksites, tracksites in stratigraphic units, or both, to be about as abundant as, or even more abundant, than those of very large mammalian herbivores.

If trackways of Morrison large herbivorous dinosaurs turned out to be relatively less common at tracksites of specified size than trackways of Cenozoic mammalian megaherbivores, and the number of tracksites containing large individuals of Morrison megaherbivore species relative to outcrop extent likewise turned out to be less than for the matched Cenozoic formation(s), this would suggest that large individuals of Morrison megaherbivores had been very rare on the landscape. Unless their populations had been regulated by predation (reflecting the presumed higher proportion of smaller individuals in dinosaur than megamammal populations?) or some other ecological factor substantially below the productive carrying capacity of the Morrison environment, this would suggest that Morrison megaherbivores had relatively high metabolic rates. The ecosystem impact of megaherbivores across Morrison habitats could have been heavy, but would have been somewhat diffuse. This scenario would be consistent with skeletal outcome 1, described above.

In contrast, if the relative abundance of trackways of Morrison large dinosaurs at tracksites of given sizes turned out to be greater than for mammalian megaherbivores, but the prorated number of tracksites containing trackways of Morrison large herbivores relatively less than for Cenozoic megaherbivores, this would suggest that herbivorous dinosaur distributions on the landscape were strongly clumped. Although this scenario might be consistent with the hypothesis that Morrison megaherbivores had low metabolic rates, but also showed strong preferences for the habitats in which trackways were likely to be preserved, it seems very unlikely that all species of Morrison megaherbivores would have preferred the same habitats (*cf.* Dodson et al. 1980; Bakker 1996). This scenario would instead, like that described in the preceding paragraph, seem more consistent with skeletal outcome 1, and with

the hypothesis that Morrison megaherbivores had high metabolic rates, but with the proviso that Morrison megaherbivores lived in herds (*cf.* Isles 2009). If so, their ecosystem impact across the Morrison landscape could have been as great as in the preceding scenario, but would correspond to the roving hot-spot situation described above.

Still another interesting potential scenario would be for the prorated number of trackways of Morrison large herbivores at tracksites, and the prorated number of tracksites containing trackways in the Morrison Formation, to turn out to be relatively larger than for Cenozoic mammalian megaherbivores. This scenario, like skeletal outcome 2, would suggest that large individuals of Morrison megaherbivores had been relatively common on the landscape, and that their metabolic rates were rather low. The total ecosystem impact of megaherbivores across Morrison habitats could have been just as heavy as in the two preceding scenarios, but would have been much more diffuse than in the preceding two scenarios.

Conclusions

Retrodicting the number of megaherbivorous dinosaurs that one could have encountered per unit area on the Morrison landscape at any given time is an example of attempting to solve an equation with too many unknowns. We have nonetheless tried to constrain estimates using what seem like plausible ranges of values of the relevant parameters. When in doubt, we have chosen parameter values that would cause us to err on the side of overestimating dinosaur abundances. Perhaps most importantly in this context, our models assume that herbivorous dinosaur population densities were limited by trophic resources, rather than predation or other ecological factors that could have prevented herbivorous dinosaur populations from attaining the sizes otherwise permitted by food availability. We therefore offer our model predictions as estimates of maximum plausible dinosaur abundances.

With that in mind, we suggest that the maximum average standing population density of Morrison megaherbivorous dinosaurs, summed across species, would have been on the order of a few tens of individuals of all sizes/ages, and a few adult and subadult individuals of large size (the animals whose skeletons would have the best chance of passing through taphonomic filters to be preserved as fossils), per square kilometre, if the DMEs of dinosaurs approached or equalled those expected for mammals of comparable size. If dinosaurian metabolisable energy requirements had been closer to expectations for gigantic varanid lizards, the upper limit of dinosaur population sizes could have been higher: a few hundred individuals of all sizes, and a few tens of individuals of large size, per square kilometre.

The ecosystem impact of Morrison megaherbivores would have depended on where within (or below?) these ranges of values the true values of community population density actually lay, and the extent to which dinosaur populations were evenly dispersed or clumped on the landscape. Although there may never be a way of determining what the absolute values of dinosaur population density actually were, we have proposed taphonomic and ichnological tests by which the relative abundance of Morrison megaherbivorous dinosaurs and Cenozoic mammalian megaherbivores might possibly be compared.

Acknowledgements

References

Aberhan M, Bussert R, Heinrich W-D, Schrank E, Schultka S, Sames B, Kriwet J, Kapilima S. 2002. Palaeoecology and depositional environments of the Tendaguru beds (Late Jurassic to Early Cretaceous, Tanzania). Mitteilungen Museum für Naturkunde Berlin, Geowissenschaften Reihe. 5:19–44.

Amiot R, Lécuyer C, Buffetaut E, Escarguel G, Fluteau F, Martineau F. 2006. Oxygen isotopes from biogenic apatites suggest widespread endothermy in Cretaceous dinosaurs. Earth Planet Sci Lett. 246:41–54.

Anderson JF, Hall-Martin A, Russell DA. 1985. Long-bone circumference and weight in mammals, birds and dinosaurs. J Zool Lond (A). 207:53–61.

Anderson KJ, Jetz J. 2005. The broad-scale ecology of energy expenditure of endotherms. Ecol Lett. 8:310–318.

Ayer J. 1999. The Howe Ranch dinosaurs. Zürich (Switzerland): Aathal Sauriermuseum.

Badgley C. 1986. Counting individuals in mammalian fossil assemblages from fluvial environments. Palaios. 1:328–338.

Bakker RT. 1971. Dinosaur physiology and the origin of mammals. Evolution. 25:636–658.

Bakker RT. 1972. Anatomical and ecological evidence of endothermy in dinosaurs. Nature. 238:81–85.

Bakker RT. 1996. The real Jurassic Park: dinosaurs and habitats at Como Bluff, Wyoming. In: Morales M, editor. The Continental Jurassic. Vol. 60. Flagstaff (AZ): Museum of Northern Arizona Bulletin. p. 35–49.

Barrick RE, Showers WJ. 1994. Thermophysiology of *Tyrannosaurus rex*: evidence from oxygen isotopes. Science. 265:222–224.

Barrick RE, Showers WJ. 1995. Oxygen isotope variability in juvenile dinosaurs (*Hypacrosaurus*): evidence for thermoregulation. Paleobiology. 21:552–560.

Barrick RE, Showers WJ. 1999. Thermophysiology and biology of *Giganotosaurus*: comparison with *Tyrannosaurus*. Palaeontologia Electronica. 2(2). Available from: http://palaeo-electronica.org/1999_2/gigan/issue2_99.htm

Barrick RE, Showers WJ, Fischer AG. 1996. Comparison of thermoregulation of four ornithischian dinosaurs and a varanid lizard from the Cretaceous Two Medicine Formation: evidence from oxygen isotopes. Palaios. 11:295–305.

Battley P, Piersma T. 2005. Adaptive interplay between feeding ecology and features of the digestive tract in birds. In: Starck JM, Wang T, editors. Physiological and ecological adaptations to feeding in vertebrates. Enfield (NH): Science Publishers, Inc. p. 201–228.

Beerling DJ, Woodward FI. 2001. Vegetation and the terrestrial carbon cycle: modelling the first 400 million years. Cambridge (UK): Cambridge University Press.

Bertram BCR. 1992. The ostrich communal nesting system. Princeton (NJ): Princeton University Press.

Bjorndal KA. 1997. Fermentation in reptiles and amphibians. In: Mackie RI, White BA, editors. Gastrointestinal microbiology. Gastrointestinal ecosystems and fermentations. Vol. 1. New York: Chapman and Hall. p. 199–230.

Bjorndal KA, Bolten AB, Moore JE. 1990. Digestive fermentation in herbivores: effect of food particle size. Physiol Zool. 63:710–721.

Blob RW. 2006. Scaling of the hind limb skeleton in cynognathian cynodonts: implications for ontogeny and the evolution of mammalian endothermy. In: Carrano MT, Gaudin TJ, Blob RW, Wible JR, editors. Amniote paleobiology: perspectives on the evolution of mammals, birds, and reptiles. Chicago: University of Chicago Press. p. 410–431.

Block BA, Finnerty JR, Stewart AFR, Kidd J. 1993. Evolution of endothermy in fish: mapping physiological traits on a molecular phylogeny. Science. 260:210–214.

Bonnan MF, Wedel MJ. 2004. First occurrence of *Brachiosaurus* (Dinosauria, Sauropoda) from the Upper Jurassic Morrison Formation of Oklahoma. PaleoBios. 24:13–21.

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004. Toward a metabolic theory of ecology. Ecology. 85:1771–1789.

Burness GP, Diamond J, Flannery T. 2001. Dinosaurs, dragons, and dwarfs: the evolution of maximal body size. Proc Natl Acad Sci USA. 98:14518–14523.

Butler DR. 1995. Zoogeomorphology: animals as geomorphic agents. Cambridge (UK): Cambridge University Press.

Carpenter K. 2006. Biggest of the big: a critical re-evaluation of the mega-sauropod *Amphicoelias fragillimus* Cope, 1878. In: Foster JR, Lucas SG, editors. Paleontology and geology of the Upper Jurassic Morrison Formation. Vol. 36. Albuquerque (NM): New Mexico Museum of Natural History and Science Bulletin. p. 131–137.

Cerda IA. 2008. Gastroliths in an ornithopod dinosaur. Acta Palaeontologica Polonica. 53:351–355.

Chamaillé-Jammes S, Valeix M, Bourgarel M, Murindagomo F, Fritz H. 2009. Seasonal density estimates of common large herbivores in Hwange National Park, Zimbabwe. Afr J Ecol. 47:804–808.

Chiappe LM, Dingus L. 2001. Walking on eggs: the astonishing discovery of thousands of dinosaur eggs in the badlands of Patagonia. New York: Scribner.

Chinsamy-Turan A. 2005. The microstructure of dinosaur bone: deciphering biology with fine-scale techniques. Baltimore (MD): Johns Hopkins University Press.

Chinsamy A, Hillenius WJ. 2004. Physiology of nonavian dinosaurs. In: Weishampel DB, Dodson P, Osmólska H, editors. The Dinosauria. Berkeley (CA): University of California Press. p. 643–659.

Christiansen P. 1999. On the head size of sauropodomorph dinosaurs: implications for ecology and physiology. Hist Biol. 13:269–297.

Christiansen P. 2004. Body size in proboscideans, with notes on elephant metabolism. Zool J Linn Soc. 140:523–549.

Clarke A. 2006. Temperature and the metabolic theory of ecology. Funct Ecol. 20:405–412.

Clarke A, Pörtner H-O. 2010. Temperature, metabolic power and the evolution of endotherm. Biol Rev (in press).

Clarke A, Rothery P. 2008. Scaling of body temperature in mammals and birds. Funct Ecol. 22:58–67.

Clauss M, Hummel J, Streich WJ, Südekum K-H. 2008. Mammalian metabolic rate scaling to 2/3 or 3/4 depends on the presence of gut contents. Evol Ecol Res. 10:153–154.

Clauss M, Nunn C, Fritz J, Hummel J. 2009. Evidence for a tradeoff between retention time and chewing efficiency in large mammalian herbivores. Comp Biochem Physiol A. 154:376–382.

Clauss M, Schwarm A, Ortmann S, Streich WJ, Hummel J. 2007a. A case of non-scaling in mammalian physiology? Body size, digestive capacity, food intake, and ingesta passage in mammalian herbivores. Comp Biochem Physiol A. 148:249–265.

Clauss M, Streich WJ, Schwarm A, Ortmann S, Hummel J. 2007b. The relationship of food intake and ingesta passage predicts feeding ecology in two different megaherbivore groups. Oikos. 116:209–216.

Coe MJ, Bourn D, Swingland IR. 1979. The biomass, production and carrying capacity of giant tortoises on Aldabra. Philos Trans R Soc Lond B. 286:163–176.

Coe MJ, Dilcher DL, Farlow JO, Jarzen DM, Russell DA. 1987. Dinosaurs and land plants. In: Friis EM, Chaloner WG, Crane PR, editors. The origins of angiosperms and their biological consequences. Cambridge (UK): Cambridge University Press. p. 225–258.

Costeur L, Legendre S. 2008. Mammalian communities document a latitudinal environmental gradient during the Miocene climatic optimum in western Europe. Palaios. 23:280–288.

Cowling RM, Kamineth A, Difford M, Campbell EE. 2009. Contemporary and historical impacts of megaherbivores on the population structure of tree euphorbias in South African subtropical thicket. Afr J Ecol. 48:135–145.

Croft DA. 2001. Cenozoic environmental change in South America as indicated by mammalian body size distributions (cenograms). Divers Distrib. 7:271–287.

Croze H. 1972. A modified photogrammetric technique for assessing age-structures of elephant populations and its use in Kidepo National Park. East Afr Wildl J. 10:91–115.

Currie PJ, Russell DA. 2005. The geographic and stratigraphic distribution of articulated and associated dinosaur remains. In: Currie PJ, Koppelhus EB, editors. Dinosaur Provincial Park: a spectacular ancient ecosystem revealed. Bloomington (IN): Indiana University Press. p. 537–569.

Damuth J. 1987. Interspecific allometry of population density in mammals and other animals: the independence of body mass and population energy use. Biol J Linn Soc. 31:193–246.

Damuth J. 1993. Cope's rule, the island rule and the scaling of mammalian population density. Nature. 365:748–750.

Damuth J. 2007. A macroevolutionary explanation for energy equivalence in the scaling of body size and population density. Am Nat. 169:621–631.

Dashzeveg D, Hartenberger J-L, Martin T, Legendre S. 1998. A peculiar minute Glires (Mammalia) from the early Eocene of Mongolia. Bull Carnegie Mus Nat Hist. 34:194–209.

Dickson KA, Graham JB. 2004. Evolution and consequences of endothermy in fishes. Physiol Biochem Zool. 77:998–1018.

Dodson P, Behrensmeyer AK, Bakker RT, McIntosh JS. 1980. Taphonomy and paleoecology of the dinosaur beds of the Jurassic Morrison Formation. Paleobiology. 6:208–232.

Downs CJ, Hayes JP, Tracy CR. 2008. Scaling metabolic rate with body mass and inverse body temperature: a test of the Arrhenius fractal supply model. Funct Ecol. 22:239–244.

Ducrocq S, Chaimanee Y, Suteethorn V, Jaeger J-L. 1994. Ages and paleoenviroment of Miocene mammalian faunas from Thailand. Palaeogeogr Palaeoclimatol Palaeoecol. 108:149–163.

Dunagan SP. 2000. Constraining Late Jurassic paleoclimate within the Morrison Formation paleoecosystem: insights from the continental carbonate record of the Morrison Formation (Colorado, USA). GeoResearch Forum. 6:523–532.

Economo EP, Kerkhoff AJ, Enquist BJ. 2005. Allometric growth, life-history invariants and population energetics. Ecol Lett. 8:353–360.

Ellis WC, Mahlooji M, Lascano CE, Matis JH. 2005. Effects of size of ingestively masticated fragments of plant tissues on kinetics of digestion of NDF. J Anim Sci. 83:1602–1615.

Engelmann GF, Chure DJ, Fiorillo AR. 2004. The implications of a dry climate for the paleoecology of the fauna of the Upper Jurassic Morrison Formation. Sediment Geol. 167:297–308.

Engelmann GF, Fiorillo AR. 2000. The taphonomy and paleoecology of the Upper Jurassic Morrison Formation determined from a field study of fossil localities. GeoResearch Forum. 6:533–540.

Erickson GM, Makovicky PJ, Inouye BD, Zhou C-F, Gao K-Q. 2009a. A life table for *Psittacosaurus lujiatunensis*: initial insights into ornithischian dinosaur population biology. Anat Rec. 292:1514–1521.

Erickson GM, Rauhut OWM, Zhou Z, Turner AH, Inouye DC, Hu D, Norell MA. 2009b. Was dinosaurian physiology inherited by birds? Reconciling slow growth in *Archaeopteryx*. Public Libr Sci One. 4, doi:10.1371/journal.pone.0003790.

Ernest SKM, Enquist BJ, Brown JH, Charnov EL, Gillooly JF, Savage VM, White EP, Smith FA, Hadly EA, Haskell JP, et al. 2003. Thermodynamic and metabolic effects on the scaling of production and population energy use. Ecol Lett. 6:990–995.

Farlow JO. 1976. A consideration of the trophic dynamics of a Late Cretaceous large-dinosaur community (Oldman Formation). Ecology. 57:841–857.

Farlow JO. 1990. Dinosaur energetics and thermal biology. In: Weishampel DB, Dodson P, Osmólska H, editors. The Dinosauria. 1st ed. Berkeley (CA): University of California Press. p. 43–55.

Farlow JO. 2007. A speculative look at the paleoecology of large dinosaurs of the Morrison Formation, or, life with *Camarasaurus* and *Allosaurus*. In: Kvale EP, Brett-Surman MK, Farlow J, editors. Dinosaur paleoecology and geology: the life and times of Wyoming's Jurassic dinosaurs and marine reptiles. Shell (WY): GeoScience Adventures. p. 98–151.

Farlow JO, Dodson P, Chinsamy A. 1995. Dinosaur biology. Annu Rev Ecol Syst. 26:445–471.

Farlow JO, Holtz TR Jr. 2002. The fossil record of predation in dinosaurs. In: Kowalewski M, Kelley PH, editors. The fossil record of predation. Vol. 8. New Haven (CT): Paleontological Society Paper. p. 251–265.

Farmer CG. 2000. Parental care: the key to understanding endothermy and other convergent features in birds and mammals. Am Nat. 155:326–334.

Farmer CG. 2001. A new perspective on the origin of endothermy. In: Gauthier J, Gall LF, editors. New perspectives on the origin and early evolution of birds. New Haven (CT): Peabody Museum of Natural History, Yale University. p. 389–409.

Farmer CG. 2002. Reproduction: the adaptive significance of endothermy. Am Nat. 162:826–840.

Fiorillo AR. 1994. Time resolution at Carnegie Quarry (Morrison Formation): Dinosaur National Monument, Utah). Univ Wyo Contrib Geol. 30:149–156.

Foster JR. 2001. Relative abundances of the Sauropoda (Dinosauria, Saurischia) of the Morrison Formation and implications for Late Jurassic paleoecology of North America. In: McCord RD, Boaz D, editors. Proceedings of the Western Association of Vertebrate Paleontologists and Southwest Paleontological Symposium. Vol. 8. Mesa (AZ): Southwest Museum Bulletin. p. 47–60.

Foster JR. 2003. Paleoecological analysis of the vertebrate fauna of the Morrison Formation (Upper Jurassic), Rocky Mountain region, U.S.A. Bulletin 23, New Mexico Museum of Natural History and Science, Albuquerque.

Foster JR. 2005. New juvenile sauropod material from western Colorado, and the record of juvenile sauropods from the Upper Jurassic Morrison Formation. In: Tidwell V, Carpenter K, editors. Thunder-lizards: the sauropodomorph dinosaurs. Bloomington (IN): Indiana University Press. p. 141–153.

Foster JR. 2007. Jurassic west: the dinosaurs of the Morrison Formation and their world. Bloomington (IN): Indiana University Press.

Foster JR, Lucas SG, editors. 2006. Paleontology and geology of the Upper Jurassic Morrison Formation. Vol. 36. Albuquerque (NM): New Mexico Museum of Natural History and Science Bulletin.

Franz J, Hummel J, Kienzle E, Kölle P, Gunga H-C, Clauss M. 2009. Allometry of visceral organs in living amniotes and its implications for sauropod dinosaurs. Proc R Soc B. 276:1731–1736.

Frappell PB, Butler PJ. 2004. Minimal metabolic rate, what it is, its usefulness, and its relationship to the evolution of endothermy: a brief synopsis. Physiol Biochem Zool. 77:865–868.

Fricke HC, Rogers RR. 2000. Multiple taxon-multiple locality approach to providing oxygen isotope evidence for warm-blooded theropod dinosaurs. Geology. 28:799–802.

Fritz J, Hummel J, Kienzle E, Arnold C, Nunn C, Clauss M. 2009. Comparative chewing efficiency in mammalian herbivores. Oikos. 118:1623–1632.

Gee CT. In press. Dietary options for the sauropod dinosaurs from an integrated botanical and paleobotanical perspective. In: Klein N, Remes K, Sander PM, editors. Biology of the sauropod dinosaurs. Bloomington (IN): Indiana University Press.

Geiser F. 2008. Ontogeny and phylogeny of endothermy and torpor in mammals and birds. Comp Biochem Physiol 150A :176–180.

Geraads D. 2006. The late Pliocene locality of Ahl al Oughlam, Morocco: vertebrate fauna and interpretation. Trans R Soc South Afr. 61:97–101.

Gibernau M, Montuire S. 1996. Mammalian diversity and environmental change during the Plio-Pleistocene in east Africa. Hum Evol. 11:193–204.

Gillooly JF, Allen AP, Charnov EL. 2006. Dinosaur fossils predict body temperatures. Public Libr Sci Biol. 4:1467–1469.

Gingerich PD. 1989. New Earliest Wasatchian mammalian fauna from the Eocene of northwestern Wyoming: composition and diversity in a rarely sampled high-floodplain assemblage. Univ Mich Pap Paleontol. 28. 97 pp.

Glazier DS. 2005. Beyond the '3/4-power law': variation in the intra- and interspecific scaling of metabolic rate in animals. Biol Rev. 80:611–662.

Glazier DS. 2010. A unifying explanation for diverse metabolic scaling in animals and plants. Biol Rev. 85:111–138.

Goheen JR, Palmer TM, Keesing F, Riginos C, Young TP. 2009. Large herbivores facilitate savanna tree establishment via diverse and indirect pathways. J Anim Ecol. 79:372–382.

Gómez Cano A, García Yelo BA, Hernández Fernández M. 2006. Cenogramas, análisis bioclimático y muestreo en faunas de mamíferos: implicaciones para la aplicación de métodos de análisis paleoecológico. Estudios Geológicos. 62:135–144.

Grellet-Tinner G. 2006. Oology and the evolution of thermophysiology in saurischian dinosaurs: homeotherm and endotherm deinonychosaurians? Papés Avulsos de Zoologia. 46(1):1–10.

Grigg GC, Beard LA, Augee ML. 2004. The evolution of endothermy and its diversity in mammals and birds. Physiol Biochem Zool. 77:982–997.

Guldemond R, van Aarde R. 2008. A meta-analysis of the impact of African elephants on savanna vegetation. J Wildl Manag. 72:892–899.

Gunga H-C, Suthau T, Bellmann A, Stoinski S, Friedrich A, Trippel T, Kirsch K, Hellwich O. 2008. A new body mass estimation of *Brachiosaurus brancai* Janensch, 1914 mounted and exhibited at the Museum of Natural History (Berlin, Germany). Fossil Record. 11:33–38.

Gunnell GF. 1997. Wasatchian-Bridgerian (Eocene) paleoecology of the western interior of North America: changing paleoenvironments and taxonomic composition of omomyid (Tarsiiformes) primates. J Hum Evol. 32:105–132.

Gunnell GF, Bartels WS. 1994. Early Bridgerian (middle Eocene) vertebrate paleontology and paleoecology of the southern Green River Basin, Wyoming. Contrib Geol Univ Wyo. 30:57–70.

Hasiotis ST. 2004. Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses. Sediment Geol. 167:177–268.

Hatt J-M, Clauss M, Gisler R, Liesegang A, Wanner M. 2005. Fiber digestibility in juvenile Galapagos tortoises (*Geochelone nigra*) and implications for the development of captive animals. Zoo Biol. 24:185–191.

Henderson DM. 1999. Estimating the masses and centers of mass of extinct animals by 3-D mathematical slicing. Paleobiology. 25:88–106.

Hillenius WJ. 1992. The evolution of nasal turbinates and mammalian endothermy. Paleobiology. 18:17–29.

Hillenius WJ. 1994. Turbinates in therapsids: evidence for Late Permian origins of mammalian endothermy. Evolution. 48:207–229.

Hillenius WJ, Ruben JA. 2004a. The evolution of endothermy in terrestrial vertebrates: Who? When? Why? Physiol Biochem Zool. 77:1019–1042.

Hillenius WJ, Ruben JA. 2004b. Getting warmer, getting colder: reconstructing crocodylomorph physiology. Physiol Biochem Zool. 77:1068–1072.

Horner JR, de Ricqlés AJ, Padian K. 1999. Variation in dinosaur skeletochronology indicators: implications for age assessment and physiology. Paleobiology. 25:295–304.

Horner JR, de Ricqlés AJ, Padian K. 2000. Long bone histology of the hadrosaurid dinosaur *Maiasaura peeblesorum*: growth dynamics and physiology based on an ontogenetic series of skeletal elements. J Vertebr Paleontol. 20:115–129.

Hotton CL, Baghai-Riding NL. 2010. Palynological evidence for conifer dominance within a heterogeneous landscape in the Late Jurassic Morrison Formation, U.S.A. In: Gee CT, editor. Plants in Mesozoic time: morphological innovations, phylogeny, ecosystems. Bloomington (IN): Indiana University Press. p. 294–328.

Hummel J, Clauss M. 2008. Megaherbivores as pacemakers of carnivore diversity and biomass: distributing or sinking trophic energy? Evol Ecol Res. 10:925–930.

Hummel J, Gee CT, Südekum K-H, Sander PM, Nogge G, Clauss M. 2008. *In vitro* digestibility of fern and gymnosperm foliage: implications for sauropod feeding ecology and diet selection. Proc R Soc B. 275:1015–1021.

Huston MA, Wolverton S. 2009. The global distribution of net primary production: resolving the paradox. Ecol Monogr. 79:343–377.

Isles TE. 2009. The socio-sexual behaviour of extant archosaurs: implications for understanding dinosaur behaviour. Hist Biol. 21:139–214.

Janis CM, Carrano M. 1992. Scaling of reproductive turnover in archosaurs and mammals: why are large terrestrial mammals so rare? Ann Zool Fenn. 28:201–216.

Jones CG, Lawton JH, Shachak M. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology. 78:1946–1957.

Jones TD, Ruben JA. 2001. Respiratory structure and function in theropod dinosaurs and some related taxa. In: Gauthier J, Gall LF, editors. New perspectives on the origin and early evolution of birds. New Haven (CT): Peabody Museum of Natural History, Yale University. p. 443–461.

Joubert D. 2006. Hunting behavior of lions (*Panthera leo*) on elephants (*Loxodonta africana*) in the Chobe National Park, Botswana. Afr J Ecol. 44:279–281.

Kemp TS. 2004. The origin and evolution of mammals. Oxford (UK): Oxford University Press.

Kerkhoff AJ, Enquist BJ. 2006. Ecosystem allometry: the scaling of nutrient stocks and primary productivity across plant communities. Ecol Lett. 9:419–427.

Kinahan AA, Pimm SL, van Aarde RJ. 2007. Ambient temperature as a determinant of landscape use in the savanna elephant, *Loxodonta africana*. J Therm Biol. 32:47–58.

Klein N, Remes K, Sander PM, editors. In press. Biology of the sauropod dinosaurs. Bloomington (IN): Indiana University Press.

Laws RM, Parker ISC, Johnstone RCB. 1975. Elephants and their habitats: the ecology of elephants in North Bunyoro, Uganda. Oxford (UK): Clarendon Press.

Leggett K. 2009. Daily and hourly movement of male desert-dwelling elephants. Afr J Ecol. 48:197–205.

Legendre S. 1986. Analysis of mammalian communities from the late Eocene and Oligocene of southern France. Palaeovertebrata. 16:191–212.

Legendre S. 1989. Les communautès de mammifères du Paléogène (Eocène supérieur et Oligocène) d'Europe occidentale: structures, milieux et évolution. Münchner Geowissenschaftliche Abhandlungen (A). 16:1–110.

Lehman TM. 2007. Growth and population age structure in the horned dinosaur *Chasmosaurus*. In: Carpenter K, editor. Horns and beaks: ceratopsian and ornithopod dinosaurs. Bloomington (IN): Indiana University Press. p. 259–317.

Leuthold W. 1976. Age structure of elephants in Tsavo National Park, Kenya. J Appl Ecol. 13:435–444.

Lovegrove BG. 2000. The zoogeography of mammalian basal metabolic rate. Am Nat. 156:201–219.

Lovegrove BG. 2004. Locomotor mode, maximum running speed, and basal metabolic rate in placental mammals. Physiol Biochem Zool. 77:916–928.

Lovelace DM, Hartman SA, Wahl WR. 2007. Morphology of a specimen of *Supersaurus* (Dinosauria, Sauropoda) from the Morrison Formation of Wyoming, and a re-evaluation of diplodocid phylogeny. Arquivos do Museu Nacional, Rio de Janeiro. 65:527–544.

Luske BL, Mertens T, Lent PC, de Boer WF, Prins HHT. 2009. Impact of the black rhinoceros (*Diceros bicornis minor*) on a local population of *Euphorbia bothae* in the Great Fish River Reserve, South Africa. Afr J Ecol. 47:509–517.

Maas MC, Kraus DW. 1994. Mammalian turnover and community structure in the Paleocene of North America. Hist Biol. 8:91–128.

Maidment SCR, Norman DB, Barrett PM, Upchurch P. 2007. Systematics and phylogeny of Stegosauria (Dinosauria: Ornithischia). J Syst Paleontol. 6:367–407.

Makarieva AM, Gorshkov VG, Li B-L, Chown SL, Reich PB, Gavrilov VM. 2008. Mean mass-specific metabolic rates are strikingly similar across life's major domains: evidence for life's metabolic optimum. Proc Natl Acad Sci USA. 105:16994–16999.

Mapaure I, Moe SR. 2009. Changes in the structure and composition of miombo woodlands mediated by elephants (*Loxodonta africana*) and fire over a 26-year period in north-western Zimbabwe. Afr J Ecol. 47:175–183.

Mazzetta GV, Christiansen P, Fariña RA. 2004. Giants and bizarres: body size of some southern South American Cretaceous dinosaurs. Hist Biol. 16:71–83.

McKechnie AE. 2008. Phenotypic flexibility in basal metabolic rate and the changing view of avian physiological diversity: a review. J Comp Physiol B. 178:235–247.

McKechnie AE, Freckleton RP, Jetz W. 2006. Phenotypic plasticity in the scaling of avian basal metabolic rate. Proc R Soc B. 273:931–937.

McKechnie AE, Wolf BO. 2004. The allometry of avian basal metabolic rate: good predictions need good data. Physiol Biochem Zool. 77:502–521.

McNab BK. 1983. Energetics, body size, and the limits to endothermy. J Zool Lond. 199:1–29.

McNab BK. 1985. Energetics, population biology, and distribution of xenarthrans, living and extinct. In: Montgomery GG, editor. Evolution and ecology of armadillos, sloths, and vermilinguas. Washington (DC): Smithsonian Institution Press. p. 219–232.

McNab BK. 2002. The physiological ecology of vertebrates: a view from energetics. Ithaca (NY): Cornell University Press.

McNab BK. 2003. Ecology shapes bird bioenergetics. Nature. 426:620–621.

McNab BK. 2006. The energetics of reproduction in endotherms and its implication for their conservation. Integr Comp Biol. 46:1159–1168.

McNab BK. 2007. The evolution of energetics in birds and mammals. In: Kelt DA, Lessa EP, Salazar-Bravo J, Patton JL, editors. The quintessential naturalist: honoring the life and legacy of Oliver P. Pearson. Vol. 134. University of California Publications in Zoology. p. 67–110.

McNab BK. 2008. An analysis of the factors that influence the level and scaling of mammalian BMR. Comp Biochem Phys A. 151:5–28.

McNab BK. 2009a. Ecological factors affect the level and scaling of avian BMR. Comp Biochem Physiol A. 152:22–45.

McNab BK. 2009b. Resources and energetics determined dinosaur maximal size. Proc Natl Acad Sci USA. 106:12184–12188.

Milchunas DG, Lauenroth WK. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecol Monogr. 63:327–366.

Montuire S. 1995. Evolution climatique et diversité chéz les mamifères en Europe central depuis le Pliocène. Geobios NS. 18:313–327.

Montuire S. 1998. Analyse paléoécologique d'une première séquence de faunes de mammifères et évolution des environnements en Allemagne au Plèistocene. Comptes Rendus Academie Sciences Paris, Sciences de la terre et des planètes. 326:221–226.

Montuire S. 1999. Mammalian faunas as indicators of environmental and climatic changes in Spain during the Pliocene-Quaternary transition. Quat Res. 52:129–137.

Montuire S, Desclaux E. 1997. Palaeoecological analysis of mammalian faunas and environmental evolution in the south of France during the Pleistocene. Boreas. 26:355–365.

Montuire S, Marcolini F. 2002. Palaeoenvironmental significance of the mammalian faunas of Italy since the Pliocene. J Quat Sci. 17:87–96.

Moore GT, Ross CA. 1996. Late Jurassic (Kimmeridgian-Tithonian) dinosaur paleoecology interpreted from a paleoclimate simulation. In: Morales M, editor. The continental Jurassic. Vol. 60. Flagstaff (AZ): Bulletin. p. 581–588.

Moore LA. 2007. Population ecology of the southern cassowary *Casuarius casuarius johnsonii*, Mission Beach north Queensland. J Ornithol. 148:357–366.

Moore SJ. 1999. Food breakdown in an avian herbivore: who needs teeth? Aust J Zool. 47:625–632.

Morgan ME, Badgley C, Gunnell GF, Gingerich PD, Kappelman JW, Maas MC. 1995. Comparative paleoecology of Paleogene and Neogene mammalian faunas: body-size structure. Palaeogeogr Palaeoclimatol Palaeoecol. 115:287–317.

Murray PF, Vickers-Rich P. 2004. Magnificent mihirungs: the colossal flightless birds of the Australian Dreamtime. Bloomington (IN): Indiana University Press.

Muñoz-Garcia A, Williams JB. 2005. Basal metabolic rate in carnivores is associated with diet after controlling for phylogeny. Physiol Biochem Zool. 78:1039–1056.

Myers TS, Fiorillo AR. 2009. Evidence for gregarious behavior and age segregation in sauropod dinosaurs. Palaeogeogr Palaeoclimatol Palaeoecol. 274:96–104.

Nagy KA. 2001. Food requirements of wild animals: predictive equations for free-living mammals, reptiles, and birds. Nutr Abstr Rev Ser B: Livest Feeds Feed. 71(10):1R–12R.

Nagy KA. 2005. Field metabolic rate and body size. J Exp Biol. 208:1621–1625.

Nagy KA, Girard IA, Brown TK. 1999. Energetics of free-ranging mammals, reptiles, and birds. Annu Rev Nutr. 19:247–277.

Ngene SM, Skidmore AK, Van Gils H, Douglas-Hamilton I, Omondi P. 2009. Elephant distribution around a volcanic shield dominated by a mosaic of forest and savanna (Marsabit, Kenya). Afr J Ecol. 47:234–245.

O'Connor MP, Dodson P. 1999. Biophysical constraints on the thermal ecology of dinosaurs. Paleobiology. 25:341–368.

Olff H, Ritchie ME, Prins HNT. 2002. Global environmental controls of diversity in large herbivores. Nature. 415:901–904.

Olivier PI, Ferreira SM, van Aarde RJ. 2009. Dung survey bias and elephant population estimates in southern Mozambique. Afr J Ecol. 47:202–213.

Ostrom JH. 1970. Terrestrial vertebrates as indicators of Mesozoic climates. Proc North Amer Paleontol Convention D :347–376.

Owen-Smith RN. 1988. Megaherbivores: the influence of very large body size on ecology. Cambridge (UK): Cambridge University Press.

Owen-Smith N. 2006. Elephants, woodlands and ecosystems: some perspectives. Pachyderm. 41:90–94.

Packard GC, Birchard GF. 2008. Traditional allometric analysis fails to provide a valid predictive model for mammalian metabolic rates. J Exp Biol. 211:3581–3587.

Packard GC, Boardman TJ. 2009. A comparison of methods for fitting allometric equations to field metabolic rates of animals. J Comp Physiol B. 179:175–182.

Packard GC, Boardman TJ, Birchard GF. 2009. Allometric equations for predicting the body mass of dinosaurs. J Zool Lond. 279:102–110.

Padian K, Horner JR. 2004. Dinosaur physiology. In: Weishampel DB, Dodson P, Osmólska H, editors. The Dinosauria. Berkeley (CA): University of California Press. p. 660–671.

Paladino FV, O'Connor MP, Spotila JR. 1990. Metabolism of leatherback turtles, gigantothermy, and thermoregulation of dinosaurs. Nature. 344:858–860.

Palombo MR, Giovinazzo C. 2006. What do cenograms tell us about mammalian palaeoecology? The example of Plio-Pleistocene Italian faunas. Courier Forschungs-Institut Senckenburg. 256:215–235.

Palombo MR, Raia P, Giovinazzo C. 2005. Early-middle Pleistocene structural changes in mammalian communities from the Italian

peninsula. In: Head MJ, Gibbard PL, editors. Early-middle Pleistocene transitions: the land-ocean evidence. Vol. 247. London (UK): Society of London Special Publication. p. 251–262.

Parrish JT, Peterson F, Turner CE. 2004. Jurassic "savannah"–plant taphonomy and climate of the Morrison Formation (Upper Jurassic, western USA). Sediment Geol. 167:137–162.

Paul GS. 1991. The many myths, some old, some new, of dinosaurology. Mod Geol. 16:69–99.

Paul GS. 1994. Dinosaur reproduction in the fast lane: implications for size, success, and extinction. In: Carpenter K, Hirsch KF, Horner JR, editors. Dinosaur eggs and babies. Cambridge (UK): Cambridge University Press. p. 244–255.

Paul GS. 1998. Terramegathermy and Cope's rule in the land of titans. Mod Geol. 23:179–217.

Paul GS. 2001. Were the respiratory complexes of predatory dinosaurs like crocodilians or birds? In: Gauthier J, Gall LF, editors. New perspectives on the origin and early evolution of birds. New Haven (CT): Peabody Museum of Natural History, Yale University. p. 463–482.

Perry SF, Christian A, Breuer Pajor N, Codd JR. 2009. Implications of an avian-style respiratory system for gigantism in sauropod dinosaurs. J Exp Zool. 311A:600–610.

Peters RH. 1983. The ecological implications of body size. Cambridge (UK): Cambridge University Press.

Pettorelli N, Bro-Jørgensen J, Durant SM, Blackburn T, Carbone C. 2009. Energy availability and density estimates in African ungulates. Am Nat. 173:698–704.

Plotz RD, Linklater WL. 2009. Black rhinoceros (*Diceros bicornis*) calf succumbs after lion predation attempt: implications for conservation management. Afr Zool. 44:283–287.

Poinar G Jr., Poinar R. 2008. What bugged the dinosaurs? Insects, disease, and death in the Cretaceous. Princeton (NJ): Princeton University Press.

Pontzer H, Allen V, Hutchinson JR. 2009. Biomechanics of running indicates endothermy in bipedal dinosaurs. Public Libr Sci One. 4(11):e7783, doi:10.1371/journal.pone.0007783.

Pörtner HO. 2004. Climate variability and the energetic pathways of evolution: the origin of endothermy in mammals and birds. Physiol Biochem Zool. 77:959–981.

Power RJ, Compion RXS. 2009. Lion predation on elephants in the Savuti, Chobe National Park, Botswana. Afri Zool. 44:36–44.

Rees PM, Noto CR, Parrish JM, Parrish JT. 2004. Late Jurassic climates, vegetation, and dinosaur distributions. J Geol. 112:643–653.

Reid REH. 1997. Dinosaurian physiology: the case for "intermediate" dinosaurs. In: Farlow JO, Brett-Surman MK, editors. The complete dinosaur. Bloomington (IN): Indiana University Press. p. 449–473.

Reilly SM, McBrayer LD, White TD. 2001. Prey processing in amniotes: biomechanical and behavioral patterns of food reduction. Comp Biochem Physiol A. 128:397–415.

Retallack GJ. 1997. Dinosaurs and dirt. In: Wolberg DL, Stump E, Rosenberg GD, editors. Dinofest International. Philadelphia (PA): Academy of Natural Sciences. p. 345–359.

Rodríguez J. 1999. Use of cenograms in mammalian palaeoecology: a critical review. Lethaia. 32:331–347.

Rosenberg GD. 1997. How long was the day of the dinosaur? And why does it matter? In: Wolberg DL, Stump E, Rosenberg GD, editors. Dinofest International. Philadelphia (PA): Academy of Natural Sciences. p. 493–512.

Roux C, Bernard RTF. 2007. Home range size, spatial distribution and habitat use of elephants in two enclosed game reserves in the Easter Cape Province, South Africa. Afr J Ecol. 47:146–153.

Royo-Torres R, Cobos A, Luque L, Aberasturi A, Espílez E, Fierro I, González A, Mampel L, Alcalá L. 2009. High European sauropod dinosaur diversity during Jurassic-Cretaceous transition in Riodeva (Teruel, Spain). Palaeontology. 52:1009–1027.

Ruben J. 1995. The evolution of endothermy in mammals and birds: from physiology to fossils. Annu Rev Physiol. 57:69–95.

Ruben JA, Hillenius WJ, Geist NR, Leitch A, Jones TD, Currie PJ, Horner JR, Espe G. 1996. The metabolic status of some Late Cretaceous dinosaurs. Science. 272:1204–1207.

Russell DA. 1989. An odyssey in time: the dinosaurs of North America. Toronto: University of Toronto Press and National Museum of Natural Sciences, Canada.

Russell DA. 2009. Islands in the cosmos: the evolution of life on land. Bloomington (IN): Indiana University Press.

Russell LS. 1965. Body temperature of dinosaurs and its relation to their extinction. J Paleontol. 39:497–501.

Sampson SD. 2009. Dinosaur odyssey: fossil threads in the web of life. Berkeley (CA): University of California Press.

Sander PM, Andrassy P. 2006. Lines of arrested growth and long bone histology in Pleistocene large mammals from Germany: what do they tell us about dinosaur physiology? Palaeontographica A. 277:143–159.

Sander PM, Clauss M. 2008. Sauropod gigantism. Science. 322:200–201.

Sander PM, Gee CT, Hummel J, Clauss M. 2010. Mesozoic plants and dinosaur herbivory. In: Gee CT, editor. Plants in deep Mesozoic time: morphological innovations, phylogeny, ecosystems. Bloomington (IN): Indiana University Press. p. 330–359.

Sander PM, Peitz C, Jackson FD, Chiappe LM. 2008. Upper Cretaceous titanosaur nesting sites and their implications for sauropod dinosaur reproductive biology. Palaeontographica A. 284:69–107.

Savage VM, Gillooly JF, Brown JH, West GB, Charnov EL. 2004. Effects of body size and temperature on population growth. Am Nat. 163:429–653.

Schwarm A, Ortmann S, Hofer H, Streich WJ, Flach EJ, Kühne R, Hummel J, Castell JC, Clauss M. 2006. Digestion studies in captive Hippopotamidae: a group of large ungulates with an unusually low metabolic rate. J Anim Physiol Anim Nutr. 90:300–308.

Schweitzer MH, Marshall CL. 2001. A molecular model for the evolution of endothermy in the dinosaur-bird lineage. J Exp Zool (Molecular Development and Evolution). 291:317–338.

Schwenk K, Rubega M. 2005. Diversity of vertebrate feeding systems. In: Starck JM, Wang T, editors. Physiological and ecological adaptations to feeding in vertebrates. Enfield (NH): Science Publishers. p. 1–41.

Seebacher F. 2001. A new method to calculate allometric length-mass relationships of dinosaurs. J Vertebr Paleontol. 21:51–60.

Seebacher F. 2003. Dinosaur body temperatures: the occurrence of endothermy and ectothermy. Paleobiology. 29:105–122.

Seebacher F, Grigg GC, Beard LA. 1999. Crocodiles as dinosaurs: behavioural thermoregulation in very large ectotherms leads to high and stable body temperatures. J Exp Biol. 102:77–86.

Seymour RS. 2004. Reply to Hillenius and Ruben. Physiol Biochem Zool. 77:1073–1075.

Seymour RS, Bennett-Stamper CL, Johnston SD, Carrier DR, Grigg GC. 2004. Evidence for endothermic ancestors of crocodiles at the stem of archosaur evolution. Physiol Biochem Zool. 77:1051–1067.

Seymour RS, Lillywhite HB. 2000. Hearts, neck posture and metabolic intensity of sauropod dinosaurs. Proc R Soc Lond B. 267:1883–1887.

Showers WJ, Barrick R, Genna B. 2002. A new pyrolysis technique provides direct evidence that some dinosaurs were warm-blooded. Anal Chem. 74:143A–150A.

Sieg AE, O'Connor MP, McNair JN, Grant BW, Agosta SJ, Dunham AE. 2009. Mammalian metabolic allometry: do intraspecific variation, phylogeny, and regression models matter? Am Nat. 174:720–733.

Skarpe C, Aarrestad PA, Andreassen HP, Dhillion SS, Dimakatso T, du Toit JT, Duncan JH, Hytteborn H, Makhabu S, Mari M, et al. 2004. The return of the giants: ecological effects of an increasing elephant population. Ambio. 33:276–282.

Spotila JR, Lommen PW, Bakken GS, Gates DM. 1973. A mathematical model for body temperatures of large reptiles: implications for dinosaur ecology. Am Nat. 107:391–404.

Storer JE. 2003. Environments of Pleistocene Beringia: analysis of faunal composition using cenograms. Deinsea. 9:405–414.

Taylor MP. 2009. A re-evaluation of *Brachiosaurus altithorax* Riggs 1903 (Dinosauria, Sauropoda) and its generic separation from *Giraffatitan brancai* (Janensch 1914). J Vertebr Paleontol. 29:787–806.

Thomas RDK, Olson EC, editors. 1980. A cold look at the warm-blooded dinosaurs. Boulder (CO): Westview Press.

Tieleman BI, Williams JB. 2000. The adjustment of avian metabolic rates and water fluxes to desert environments. Physiol Comp Zool. 73:461–479.

Tsubamoto T, Egi N, Takai M, Sein C, Maung M. 2005. Middle Eocene ungulate mammals from Myanmar: a review with description of new specimens. Acta Palaeontologica Polonica. 50:117–138.

Turner CE, Peterson F. 2004. Reconstruction of the Upper Jurassic Morrison Formation extinct ecosystem–a synthesis. Sediment Geol. 167:309–355.

Varricchio DJ, Sereno PC, Xijin Z, Tan L, Wilson JA, Lyon GH. 2008. Mud-trapped herd captures evidence of distinctive dinosaur sociality. Acta Palaeontologica Polonica. 53:567–578.

Vizcaíno SG, Bargo MS, Cassini GH. 2006. Dental occlusal surface area in relation to body mass, food habits and other biological features in fossil xenarthrans. Ameghiniana. 43:11–26.

Weaver JC. 1983. The improbable endotherm: the energetics of the sauropod dinosaur *Brachiosaurus*. Paleobiology. 9:173–182.

Wedel MJ. 2005. Postcranial skeletal pneumaticity in sauropods and its implications for mass estimates. In: Curry Rogers KA, Wilson JA, editors. The sauropods: evolution and paleobiology. Berkeley (CA): University of California Press. p. 201–228.

West GB, Brown JH, Enquist BJ. 1997. A general model for the origin of allometric scaling laws in biology. Science. 276:122–126.

White CR, Blackburn TM, Martin GR, Butler PJ. 2007. Basal metabolic rate of birds is associated with habitat temperature and precipitation, not primary productivity. Proc R Soc B. 274:287–293.

White CR, Cassey P, Blackburn TM. 2007. Allometric exponents do not support a universal metabolic allometry. Ecology. 88:315–323.

White CR, Phillips NF, Seymour RS. 2006. The scaling and temperature dependence of vertebrate metabolism. Biol Lett. 2:125–127.

White CR, Seymour RS. 2003. Mammalian basal metabolic rate is proportional to body mass$^{3/4}$. Proc Natl Acad Sci USA. 100:4046–4049.

White CR, Seymour RS. 2004. Does basal metabolic rate contain a useful signal? Mammalian BMR allometry and correlations with a selection of physiological, ecological, and life-history variables. Physiol Biochem Zool. 77:929–941.

White CR, Seymour RS. 2005. Allometric scaling of mammalian metabolism. J Exp Biol. 208:1611–1619.

White EP, Morgan Ernest SK, Kerkoff AJ, Enquist BJ. 2007. Relationship between body size and abundance in ecology. Trends Ecol Evol. 22:323–330.

White PD, Fastovsky DE, Sheehan PM. 1998. Taphonomy and suggested structure of the dinosaurian assemblage of the Hell Creek Formation (Maastrichtian), eastern Montana and western North Dakota. Palaios. 13:41–51.

Wiersma P, Muñoz-Garcia A, Walker A, Williams JB. 2007. Tropical birds have a slow pace of life. Proc Natl Acad Sci USA. 104:9340–9345.

Wilf P, Beard KC, Davies-Vollum KS, Norejko JW. 1998. Portrait of a late Paleocene (Early Clarkforkian) terrestrial ecosystem: Big Multi Quarry and associated strata, Washakie Basin, southwestern Wyoming. Palaios. 13:514–532.

Williams JB, Siegfried WR, Milton SJ, Adams NJ, Dean WRJ, Du Plessis MA, Jackson S. 1993. Field metabolism, water requirements, and foraging behavior of wild ostriches in the Namib. Ecology. 74:390–404.

Wilson JA, Mohabey DM, Peters SE, Head JJ. 2010. Predation upon hatchling dinosaurs by a new snake from the Late Cretaceous of India. PloS Biol. 8(3):e1000322, doi:10.1371/journal.pbio.100032.

Wings O, Sander PM. 2007. No gastric mill in sauropod dinosaurs: new evidence from analysis of gastrolith mass and function in ostriches. Proc R Soc B. 274:635–640.

Withers PC, Cooper CE, Larcombe AN. 2006. Environmental correlates of physiological variables in marsupials. Physiol Biochem Zool. 79:437–453.