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Differences in global biomass and energy use between dinosaurs and mammals

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ABSTRACT:

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Estimates derived from the literature suggest that dinosaurs, even if they had a mammalian-type metabolism, produced globally much more biomass than mammals for the same amount of energy consumed. The average body mass of an individual dinosaur was several thousand times greater than in the case of mammals. Dinosaurs were one to several hundred times less numerous than mammals and, in comparison to mammals, the average number of individuals per dinosaur species was several to a dozen or so times lower than in mammals.

Key words: Dinosaurs; Mammals; Global biomass; Global energy use; Diversity; Body size.

INTRODUCTION

The mean body mass of dinosaur genera amounted to between 3,331 and 8,975 kg and their median mass was between 1,000 and 4,000 kg as calculated using the data of Peczkis (1994). Similar results are given by calculations based on the estimates of Seebacher (2001; mean = 5,141 kg , median = 1,689 kg) and of Paul (2010; mean = 4,390 kg, median = 1,600 kg). On the other hand, the median body mass of the genera of extant mammals is about 0.3 kg (Maurer *et al.* 1992). Thus, in the age of dinosaurs, the biomass – representing almost all of the terrestrial vertebrate fauna – occurred in large bodies or was concentrated in comparison to mammals, in which biomass was or is dispersed in many relatively small bodies.

Because mass-specific metabolic rate (= rate per unit of mass) declines with body size, the energetic cost of maintaining concentrated biomass in a few large bodies is strikingly lower than that required to maintain the same biomass in many small bodies. Food consumption of a mammal that weighs 5,000 kg amounts to 4,257 joules/second, while 5,000 kg of mammals weighing 1 kg each requires the consumption of 54,800 J/sec – nearly thirteen times more as computed using the fitted regression equation of Farlow (1976, 1990; see also Peters 1983). By analogy, to cover the same distance, 400 motorbikes, each weighing 100 kg, need 22 times more fuel than a single truck carrying all 400 cycles. Nevertheless, the total population of an extant large-sized animal species may have a higher energy use than the population of a smaller ones, if the geographic range and thus the biomass of the larger species is significantly larger (Maurer and Brown 1988; Brown and Maurer 1989).

As it is not currently known whether Mesozoic dinosaurs or Cenozoic mammals had a greater biomass and a higher energy use as a whole group, the purpose of this contribution is an attempt to estimate the global dinosaurian biomass and energy use, and to contrast these figures with those for mammals.

METHODS

To calculate the global biomass of a given terrestrial animal group in an instant of time, one needs to know the number of species that exist or existed at that time, the average body masses of individual species (M), their population densities (D), i.e. the number of individuals per km², and the areas of their geographic ranges (R). The global biomass will be the sum of the products M times D times R computed for all species.

The sum of products D times R will be the number of individual animals of a given group. The metabolic rates and energy demands are correlated with the individual body mass. Thus, knowing M, one may obtain the energy use of an individual (E) and hence the global energy use of a given group will be the sum of the products E times D times R computed for the particular species of which the group is composed.

After the estimation of Russell (1995), I assume that there were about 3,500 dinosaur genera in all. Given that the mean number of species per genus is 1.2 (Wang and Dodson 2006), I multiplied 3,500 by 1.2 and obtained 4,200 species of Dinosauria. I have taken the proportions of taxa existing in six Mesozoic epochs after Wang and Dodson (2006) and computed the dinosaur species diversity for each epoch (Text-fig. 1). To determine the number of species that occurred together in the 'average' instant of time of the particular epochs, I divided the number of species for each epoch (Text-fig. 1) by the number of its stages divided by 1.25, assuming that the average longevity of a dinosaur species approximates 1.25 of a stage in analogy to the longevities of other reptilian and mammalian species (Raup and Boyajian 1988). For example, for the Late Cretaceous that comprises six stages (Ogg *et al.* 2008), I divided 1,671 (compare Text-fig. 1) by 6 divided by 1.25, that is by 4.8. The obtained species diversities for instants of time in Mesozoic epochs vary from 55 to 348 and are presented in Text-fig. 2.

EPOCH	Number of species
LATE CRETACEOUS	1671
EARLY CRETACEOUS	1239
LATE JURASSIC	479
MIDDLE JURASSIC	496
EARLY JURASSIC	177
LATE TRIASSIC	138

Text-fig. 1. Estimated dinosaur species diversity for six Mesozoic epochs

EPOCH	Number of species
LATE CRETACEOUS	348
EARLY CRETACEOUS	258
LATE JURASSIC	200
MIDDLE JURASSIC	155
EARLY JURASSIC	55
LATE TRIASSIC	57

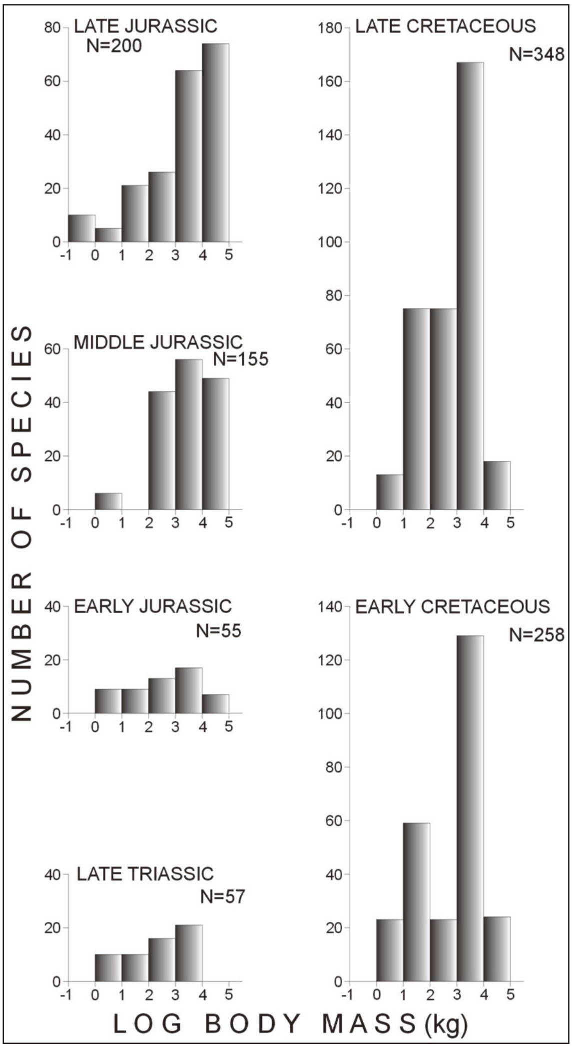
Text-fig. 2. Estimated dinosaur species diversity for the average instants of time of six Mesozoic epochs

As the number of species of extant mammals is nearly 5,000 (Smith *et al.* 2003), Text-fig. 2 suggests that dinosaurs had only 1–7% of the specific diversity of mammals, albeit this comparison does not account for preservational bias inherent in the dinosaur data. However, independent calculations of the numbers of fossil dinosaur and mammal species per million years give similar results. Tiffney (1997) estimated that 9 dinosaurian species existed per million years over the duration of the group, while 185 mammalian species existed per 1 million years in the Tertiary. Thus, the dinosaurian diversity seems to represent just 5% of that of mammals.

I have estimated the body-mass frequency distribution of the dinosaurian species in particular epochs (Text-fig. 3) using the data of Peczkis (1994). More recent mass estimates do not differ significantly (Seebacher 2001) from estimates in the literature compiled by Peczkis (1994). I have assumed that the proportions between the particular body-masses within the estimated numbers of species (Text-fig. 2) were the same as those found in the fossil record (Peczkis 1994). As the dinosaurian body mass estimates vary, Peczkis (1994) does not necessarily present accurate values of dinosaurian masses but rather of body mass categories, e.g. 100–400 kg. For the calculations I averaged such values. Furthermore, the body mass data of Peczkis (1994) are cumulated over intervals of time and do not represent instants of time. I am aware that this may somewhat bias the number of species in different mass categories (Text-fig. 3) if there was a significant difference in the turnover rate of species with a different body size.

There are three main opinions concerning the metabolism of dinosaurs: (1) they had a mammalian-type metabolism (e.g. Russell 1965; Bakker 1972); (2) they were 'cold-blooded' reptiles (e.g. Spotilla *et al.* 1973; Paladino *et al.* 1997), and (3) they were characterized by rates of metabolism intermediate between those of extant reptiles and mammals (e.g. de Ricqlès 1974; Reid 1984, 1990; McNab 2009).

There is a correlation between body mass and population density. Provided that dinosaurs had a mammalian-type metabolism, they could also have had mammalian densities. Therefore, to estimate the densities of the dinosaurian species, I used the empirical equations for mammals from Silva *et al.* (1997): log density (individuals/km²) = – 0.899 log (g body mass) + 3.985 [for masses between 0.1 – 100 kg], and log density (individuals/km²) = 0.049 log (g body mass) –



Text-fig. 3. Estimated body-mass distribution of dinosaur species for the average instants of time of six Mesozoic epochs

0.451 [for masses ≥ 100 kg]. Because the regressions of Silva *et al.* (1997) do not relate to values of mass exceeding 5,000 kg, I have used this mass figure for all animals >5,000 kg. This is probably reasonable as the population density of animals heavier than 100 kg does not change much with mass. Other densities that are more applicable to reptilian or intermediate metabolism are also discussed (see ‘Results’ below).

In calculating dinosaurian densities I used mammalian and not avian equations (Silva *et al.* 1997) because mammals attain larger body sizes than birds and are mostly non-volant animals like dinosaurs. Furthermore, flying vertebrates have much lower population densities and a narrower range of body sizes than non-volant ones (Silva *et al.* 1997).

Species of big extant animals tend to have a geographic range size of about 7% of the area of the continent where they live (Letcher and Harvey 1994; Murray and Dickman 2000; Barnosky 2008). For my calculations of global biomass and energy use, I assumed that the ranges of species with a mass over 1 kg were the sum of the areas of all continents multiplied by 0.07 divided by the number of continents. The obtained values vary for the particular epochs as the continental areas and numbers of continents were not constant throughout the Mesozoic and Cenozoic (Smith *et al.* 1994). I obtained the following ranges for animals heavier than 1 kg: 3,000,000 km² for the Late Triassic and Early Jurassic; 2,200,000 km² for the Middle and Late Jurassic; 1,500,000 km² for the Early and Late Cretaceous, and 1,890,000 km² for the present time. For animals having a mass of 1 kg and less, I assumed a range of 300,000 km² (compare Brown and Maurer 1989).

In calculating the energy requirements of the individuals, I used the following equations: 1) energy use (joules/second) = 10.96 (kg body mass)$^{0.70}$ – for endotherms (Farlow 1976, 1990; see also White and Seymour 2005), and 2) energy use (joules/second) = 0.84 (kg body mass)$^{0.84}$ for ectotherms (Farlow 1990; see also Farlow *et al.* 2010).

For the calculation of global biomass and energy use of mammals, I have taken into consideration both all extant terrestrial species as well as 180 species of megafauna that are extinct or were killed by humans in the Quaternary (see e.g. Martin 1967; Alroy 2001; Barnosky 2008) to obtain results approximating the situation from times before significant human impacts on the biosphere.

The body mass distribution for mammals was taken from Maurer *et al.* (1992), Smith *et al.* (2003) and Barnosky (2008). In order to estimate the density of mammals lighter than 0.1 kg I used the regression of Silva *et al.* (1997):

log density (individuals/km²) = 0.434 log (g body mass) + 1.701.

For the density of mammals having other masses I used the regressions of Silva *et al.* (1997) cited above.

RESULTS

According to the calculations (Text-fig. 4), the total global biomass of Quaternary mammals was 0.3 times 10^{12} kg and their global energy use accounted to 1.5 times 10^{12} J/sec (for comparison: the total energy use by humans and domestic livestock is 3.9 times 10^{12} J/sec after the estimation of Wright 1990; see also Brown 1995). On the other hand, dinosaurs had

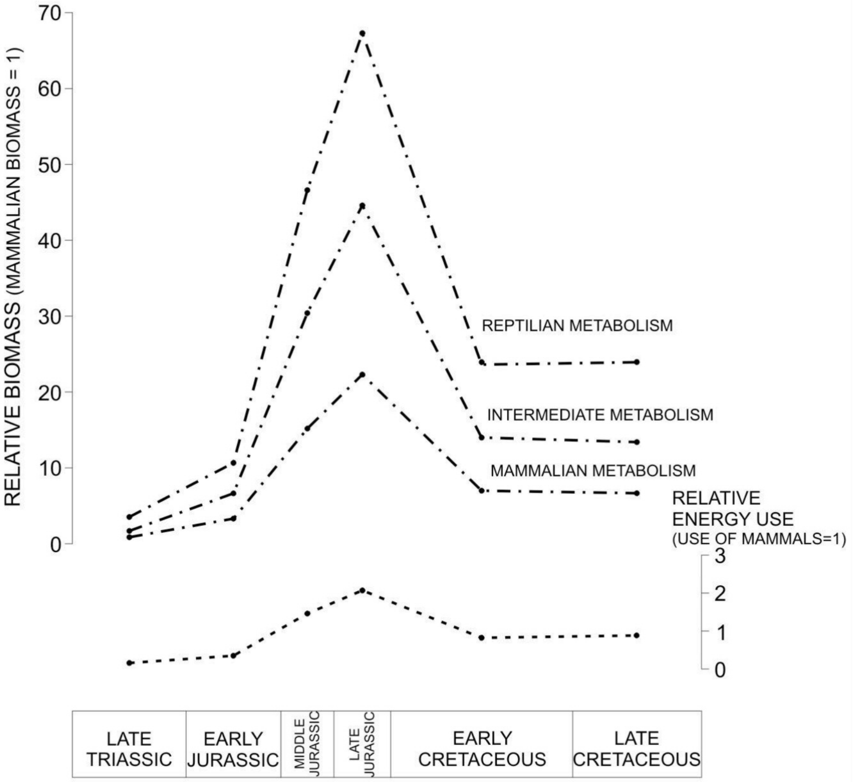
EPOCH	BIOMASS (10^{12} kg)	RELATIVE BIOMASS (MAMMALIAN BIOMASS=1)	MAMMALIAN METABOLISM		REPTILIAN METABOLISM	
			ENERGY USE (10^{12} J/sec)	RELATIVE ENERGY USE (MAMMALIAN USE=1)	ENERGY USE (10^{12} J/sec)	RELATIVE ENERGY USE (MAMMALIAN USE=1)
DINOSAURS						
LATE CRETACEOUS	2.00	6.66	1.316	0.88	0.368	0.245
EARLY CRETACEOUS	2.10	7.00	1.234	0.82	0.364	0.243
LATE JURASSIC	6.69	22.30	3.110	2.07	1.030	0.686
MIDDLE JURASSIC	4.56	15.20	2.187	1.46	0.714	0.476
EARLY JURASSIC	0.996	3.32	0.531	0.35	0.163	0.109
LATE TRIASSIC	0.255	0.85	0.237	0.158	0.057	0.038
QUATERNARY MAMMALS						
	0.300	1.0	1.5	1.0		1.0

Text-fig. 4. Estimated total global biomass and energy use of Quaternary mammals and Mesozoic terrestrial dinosaurs assuming that dinosaur species had mammalian-like population densities and geographic ranges, and either a mammalian- or reptilian-like metabolism. Estimates refer to instants of time

mostly a much larger global biomass (see also Farlow *et al.* 2010) and lower or only somewhat higher global energy use than Quaternary mammals. The relative biomass of dinosaurs (taking the mammalian biomass = 1) varied from 0.85 to 22.30, and the relative dinosaurian energy use (taking the use of mammals = 1) varied from 0.158 to 2.07 even when assuming mammalian-type densities, ranges and metabolism of dinosaurs (Text-figs 4 and 6). If the densities and ranges of dinosaurs and mammals were approximately the

EPOCH	RELATIVE BIOMASS (MAMMALIAN BIOMASS=1)		
	MAMMALIAN METABOLISM AND DENSITY	INTERMEDIATE (50% OF MAMMALIAN) METABOLISM, DOUBLED DENSITY	REPTILIAN METABOLISM AND DENSITY
DINOSAURS			
LATE CRETACEOUS	6.66	13.40	23.93
EARLY CRETACEOUS	7.00	14.00	23.62
LATE JURASSIC	22.30	44.60	67.29
MIDDLE JURASSIC	15.20	30. 40	46.62
EARLY JURASSIC	3.32	6.64	10.66
LATE TRIASSIC	0.85	1.70	3.53
QUATERNARY MAMMALS			
	1 (=0,3 x 10^{12} kg)	1	1

Text-fig. 5. Estimates of total global biomass of Mesozoic terrestrial dinosaurs with respect to the possible differing energy requirements of these animals depending on the kind of the metabolism assumed. Amount of energy consumed is the same for the three types of metabolism (specified in the column 'Mammalian metabolism. Energy use' in Text-fig. 4). Estimates refer to instants of time



Text-fig. 6. Estimates of total global biomass of Mesozoic terrestrial dinosaurs with respect to their possible differing energy requirements and of total dinosaurian global energy use compared to the entire world biomass and energy use of Quaternary mammals

same, but the dinosaurs had reptilian metabolic rates, then their relative energy use varied between 0.038 and 0.686 (Text-fig. 4).

For the same amount of food consumed, reptiles may attain higher densities and hence a larger biomass than mammals because of their lower energy requirements (e.g. Pough 1980; Farlow 1993; Farlow *et al.* 2010; Brown 1995; McNab 2009). Text-figs 5 and 6 show the estimates of total dinosaurian global biomass with respect to their possible differing energy requirements: mammalian, reptilian or intermediate (= 50% of metabolic rate of mammals). To produce approximate values of the global relative dinosaurian biomass assuming a reptilian metabolism, I multiplied the values of the relative biomass from Text-fig. 4 by the ratios of mammalian energy uses (Text-fig. 4) to the values of reptilian energy uses (Text-fig. 4). By analogy, to obtain values of dinosaurian biomass assuming an intermediate metabolism, I multiplied the values of relative biomass from Text-fig. 4 by two.

The relative biomass of dinosaurs from particular epochs (Text-figs 5 and 6) varied from 1.70 to 44.60, when they had an intermediate metabolism, and from 3.53 to 67.29 in the case of reptilian metabolic rates.

As a whole, dinosaurs used energy more efficiently than mammals. For the same amount of energy taken they produced much more biomass even if they had mammalian-type metabolic rates. For example, in the Late Jurassic, the consumption of 2.07 times more energy than Quaternary mammals resulted in the production of 22.30 times more biomass than mammals if they had a mammalian-type metabolism, or 67.29 times more biomass if they had a reptilian-type metabolism (Text-fig. 6). In the Late Cretaceous at 0.88 of mammalian energy use, dinosaurs produced 6.66 times more biomass than mammals when they were endotherms, or 23.93 times more biomass when they were ectotherms.

The results of calculations concerning the average body masses of individuals in particular epochs, the total number of individuals, and the average number of individuals per species are shown in Text-fig. 7. According to these estimates, the average masses of individuals were several thousand times higher in the case of dinosaurs than in the case of mammals. Moreover, dinosaurs were about one to several hundred times less numerous than mammals, depending on the epoch studied and the assumed density related to energy expendi-

EPOCH	AVERAGE MASS OF INDIVIDUAL (kg)	TOTAL NUMBER OF INDIVIDUALS (10^6)			AVERAGE NUMBER OF INDIVIDUALS PER SPECIES (10^6)		
		METABOLISM, ENERGY DEMAND AND DENSITY			METABOLISM, ENERGY DEMAND AND DENSITY		
		MAMMALIAN	INTERMEDIATE	REPTILIAN	MAMMALIAN	INTERMEDIATE	REPTILIAN
DINOSAURS							
LATE CRETACEOUS	4,567	438	876	1,573	1.26	2.52	4.52
EARLY CRETACEOUS	5,174	405	810	1,367	1.57	3.14	5.30
LATE JURASSIC	14,774	450	900	1,358	2.25	4.50	6.79
MIDDLE JURASSIC	15,189	300	600	920	1.94	3.88	5.94
EARLY JURASSIC	2,411	220	440	714	4.00	8.00	12.98
LATE TRIASSIC	1,085	230	460	956	4.04	8.08	16.77
QUATERNARY MAMMALS							
	0.85	170,000			33.00		

Text-fig. 7. Average body masses of individual, total and average numbers of individuals per species of Quaternary mammals and of Mesozoic terrestrial dinosaurs with respect to their possible differing energy requirements. The presented estimates refer to instants of time

ture (Text-fig. 7). Finally, the average number of individuals per dinosaur species was several to a dozen or so times lower than in the case of mammals, depending again on the epoch and the assumed energy demand.

DISCUSSION

I am aware that my methods are somewhat speculative and that the resulting estimates are necessarily coarse. At best they are order-of-magnitude estimates and hence should be treated with caution. These estimates are based, however, on ecological generalizations and tendencies and may be approximately true. When I varied the values of dinosaurian densities, ranges, numbers of species by ± 30%, this affected the values calculated for global biomass, energy use, number of individuals etc., but did not contradict the main conclusions presented above.

Farlow *et al.* (2010), in comparing life histories of the ostrich and the elephant argue that the clutch of oviparous dinosaurs might have been more numerous than the litter of viviparous mammals. The average body mass across the entire population of the ostrich represents 27% of the average adult body mass and 61.5% in the case of the elephant (Farlow *et al.* 2010). Similarly, young individuals may have comprised a much larger proportion of the population of dinosaurs than in mammals. If this is so, the values of dinosaurian relative biomass and relative energy use presented here (Text-fig. 4-6) are overestimated – approximately three times in the case of biomass and twice for energy use as recalculated using the ostrich versus elephant model of Farlow *et al.* (2010). I am not sure, however, if one may accept the ostrich versus elephant model as a general rule concerning all dinosaurs and mammals. For, differently than in the case of the ostrich versus elephant example, the clutch of oviparous birds, for instance of the vulture or the pigeon, may be less numerous than the litter of viviparous mammals like the dog or the boar. Usually many eggs (15–35) are found in the dinosaur nests (Chiappe *et al.* 2004), albeit fewer than in the ostrich nests (15–60). We do not know, however, how many dinosaur females have laid them.

It is not clear whether more efficient global production of biomass by large dinosaurs in comparison to the smaller mammals may be acknowledged as an evolutionary success of the dinosaurs, since the majority of evolutionary biologists and ecologists do not consider communities, ecosystems or systematic groups as functional units of ecology and evolution. Only some ecological modellers suggest that an evolutionary biological system tends to minimize its entropy production, selecting those organisms that tend to decrease entropy production, i.e. the mean specific metabolic rate (Prigodine and Wiame 1946; Lurié *et al.* 1983; Lurié and Wagensberg 1983; Han and Straskraba 2001). It is a fact that the evolutionary tendency to concentrate biomass in larger and larger bodies (Cope's rule) was much stronger among the Dinosauria than among the Mammalia. The body mass of the newly-appearing Cenozoic mammalian species was on average 9.1% larger than the mass of their ancestors (Alroy 1998). Among the dinosaurs, the mass of a new species was on average as much as 99% greater in comparison to the mass of its ancestral species (Hone *et al.* 2005; these authors point out a 25.7% change of length but such an increase in length corresponds to a 99% increase in mass).

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