Ann. Zool. Fennici 28:201–216
Helsinki 19 February 1992

ISSN 0003-455X

Scaling of reproductive turnover in archosaurs and mammals: why are large terrestrial mammals so rare?

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Received 26 March 1990, accepted 10 October 1990

Following an idea originally expressed by Björn Kurtén (1953), we here investigate the notion that differences in the scaling of reproductive output could be responsible (at least in part) for the differences in body sizes (both mean and maximum) attained by dinosaurs and terrestrial mammals. Using terrestrial non-passerine birds as "dinosaur analogs" we show that birds exhibit little or no decline in a variety of reproductive life history parameters with increasing body size, in contrast to terrestrial mammals. Extending this argument to dinosaurs, we suggest that large dinosaurs would have had a greater potential for reproductive turnover than similarly sized mammals and would thus have had a much greater capacity for rebuilding populations following environmental perturbations. This difference in reproductive strategies, which has its basis in ovoparity (dinosaur) versus viviparity plus lactation (mammals), may have resulted in a differential in the ability for dinosaurs and mammals to evolve and sustain large-bodied species over evolutionary time. We also compare terrestrial mammals to cetaceans and show that marine mammals show a lesser decline in the scaling of reproductive output with body size. We suggest that differences in the costs of gestation and lactation, related to the richer available diet in the marine environment, may in part explain the greater sizes obtained by marine mammals in comparison to terrestrial ones.

1. Introduction

In the summer of 1988 the senior author was reading the collected works of Björn Kurtén (1988), following a request to review the book (Janis 1989). She was struck by a comment imbedded in his 1953 paper, "On the variation and population dynamics of fossil and recent mammal populations" about possible differences in life history strategies between mammals and dinosaurs, and their consequences for evolutionary trends (Kurtén 1953). He pointed out that limits to increasing body size for any taxon might not only be related to mechanical constraints (e.g., Huxley 1943) or physiological constraints resulting from problems of heat loss (e.g., Benedict 1938), but might also be related to the scaling of reproductive parameters and life history variables. He noted that, as gestation length and interbirth intervals in mammals scale with body size, at some critical body mass there will come a point where the gestation period is greater than one year (about 300–500 kg adult body mass), and that this might pose a "threshold" that would be difficult to cross in evolutionary terms. Past this body mass, interbirth interval would increase to every other year (or more), and the taxa that "made it through" this threshold (only large herbivores in present times) would do so at the expense of a decrease in total numbers and population density due to the concommittant increase in generation time. Such taxa might also be more vulnerable to extinction (see later discussion of Kiltie 1985). Kurtén also briefly expressed the idea that this "threshold" effect might not apply so severely, if at all, to dinosaurs, as a result of their habit of laying eggs rather than bearing live young.

While dinosaurs were the dominant large tetrapods of the Mesozoic and mammals the dominant large tetrapods of the Cenozoic, there has been surprisingly little careful analysis of the modes in which they might represent "niche analogs," nor consideration of the differences in general paleobiology between the two groups [aside from blanket assertions for the necessity, by analogy, of endothermy in dinosaurs (e.g. Bakker 1986)]. Various simplistic attempts to compare dinosaurs directly with mammals have often been erroneous. For example, certain later ornithischian dinosaurs (hadrosaurs and ceratopsians) have been seen as comparable to mammalian ungulate herbivores; but attempts to model their jaw mechanics by analogy with the type of translation of the lower jaw seen in mammals have been shown to be incorrect, and the mode of occlusion was in fact quite different from anything devised within the class Mammalia (see discussion in Norman & Weishampel 1985).

There appears to be no a priori reason to assume that, within the laws of biomechanics and physiology, terrestrial mammals would be incapable of routinely attaining the size of larger dinosaurs. Alexander (1989) points out that most dinosaurs had a body mass that was within the size range of living (or at least, Pleistocene) mammals. Furthermore, the giant extinct "giraffe-rhino", *Indricotherium*, has been estimated as having a body mass of around 20 000 kg (Economos 1981), and thus is of a comparable size to most sauropod dinosaurs (Alexander 1989). Although Economos (1981) suggests that *Indricotherium* represents the largest-size animal that could withstand terrestrial gravity, the brachiosaurid sauropods were considerably bigger than this; a conservative body mass estimate for the largest brachiosaur is 50 000 kg (Paul 1988).

Originally, at least the sauropod dinosaurs were thought to have been semi-aquatic in order to support their body mass (Marsh, 1883). Bakker (1971) showed that the anatomy of sauropod dinosaurs was better suited to an "elephant" analogue than to a "hippo" analogue, and further argued for a fully terrestrial existence by showing that there was no reason to suppose that their bones were not scaled in an appropriate fashion to support their body weight on land. He further mustered taphonomic evidence to support a paleobiological interpretation of sauropods as fully terrestrial, high-plain, high-level browsers, a view that now appears to be universally accepted (e.g. Dodson et al. 1980). Subsequent arguments in recent years to explain the larger size of dinosaurs all implicitly assume that they had an ectothermic type of physiology (see Alexander 1989 for review). The question of why large dinosaurs were generally bigger than large mammals deserves reevaluation.

Mammals *do*, of course, attain body sizes comparable to large dinosaurs in the aquatic environment. It is common knowledge that the largest animal that ever existed is the present day blue whale, *Balaenoptera musculus,* with a body mass of 140 000 kg. However, it is also true that, while whales are "large" in comparison with most other mammals [the smallest cetacean has a body mass of 40 kg (Nowack & Paradiso 1983)], very few whale taxa fall outside of the estimated range of body masses for dinosaurs. Thus, the common explanation that most whales can attain such large body sizes because the constraints of gravity are relaxed in the aquatic environment can only apply to the largest taxa, not to the majority of cetaceans which, although considerably bigger than most terrestrial mammals, are not bigger than large dinosaurs.

In this paper, we explore and extend the original ideas of Kurtén (1953) to examine the hypothesis that the difference in observed maximum sizes of mammalian and dinosaurian taxa (as well as the mean differences in average sizes) may be based in the difference in the reproductive strategies of the two taxa, and in the scaling of reproductive parameters, rather than in constraints imposed by structural materials or metabolic physiology. We also address the question of why whales can routinely attain larger body sizes than terrestrial mammals.

2. Materials and methods

As dinosaurs are extinct, it is impossible to make direct comparison between the life history strategies of dinosaurs and mammals. Yet, two alternatives exist as models for dinosaurs. Birds might provide a good model, as the direct descendants of dinosaurs (e.g. Gauthier 1986), especially if the study were restricted to terrestrial, non-passerine birds (as passerines have a higher metabolic rate than other birds). But birds are endothermic and, despite the recent furor on the state of dinosaur physiology (see Bakker 1986), the metabolic status of dinosaurs remains uncertain. Alternatively, crocodiles are the extant group of ectothermic archosaurs, the sister group to both birds and dinosaurs, and might serve as a better model for dinosaur life history strategy and reproductive behavior. Unfortunately, comparative data for crocodiles are difficult to obtain. This is at least in part because crocodiles cannot be said to have a fixed "adult body mass" to use in comparative studies because, unlike birds or mammals, they experience indeterminate growth throughout life. The data that we have been able to obtain suggest that dinosaurs may be more analogous to birds than to crocodiles in reproductive strategy. Although small dinosaurs, such as *Orodromeus*, have a larger number of offspring per clutch than birds of equivalent size, they have a much smaller clutch than is typical of crocodiles (Table 1).

We thus decided to use terrestrial non-passerine birds as a "dinosaur analog" for comparison with mammals, although dinosaurs can be included with birds for certain variables. Note that the total reproductive output of the one crocodile species for which we could obtain an estimate is an order of magnitude greater than that obtained for any bird (Table 1). Thus, in picking birds rather than crocodiles as "dinosaur analogs", we can only be erring on the side of the conservative, and we do not consider that our conclusions would be influenced for the worse if dinosaurs were indeed ectothermic (like crocodiles) rather than endothermic (like birds). The ideal birds to use as "dinosaur analogs" would be those that were flightless (predominantly ratite birds); however, there are simply not enough extant ratites to use in a statistical study for comparison with mammals. Thus, we extended our comparative data base to include birds that were primarily terrestrial, regardless of the capacity for flight, from the families Anatidae, Apterygidae, Ardeidae, Casuariidae, Ciconiidae, Dinornithidae (extinct), Dromaiidae, Gruidae, Otitidae, Pelecaniidae, Phasianidae, Phoenicopteridae, Rheidae, Rhynochetidae, Otididae, Sagittariidae, Struthionidae and Threskiornithidae. We restricted the entire study to vertebrates with a body mass of greater than approximately 1 kg, as this probably represents the size of the smallest dinosaur (Bakker 1986).

We obtained the following average variables from a wide variety of literature sources (see annotations in the references): adult body mass, body mass of single offspring, number of offspring per litter (clutch), litters (clutches) per year, age at sexual maturity, and total lifespan. From a compounding of these variables, we obtained numbers for the following variables: total mass of litter (clutch) expressed as a percentage of adult body mass, total number of offspring produced per year, potential reproductive lifespan, and total (potential) reproductive output (see explanation in legend to Table 1). We examined the scaling relationships of the following variables: number of offspring per litter (clutch), litters (clutches) per year, total potential number of offspring per year, total potential reproductive output and total mass of litter (clutch) as a percentage of adult body mass. This was performed by regressing these variables against adult body mass in a double logarithmic plot; the least squares method of regression was employed as we assumed that the variables were ultimately dependent on the body mass, and that, relative to the range of body sizes included, errors in the estimation of body mass were negligible. Figures 1 to 5 show the scaling relationships, and the values of the various scaling parameters are listed in Table 2. We also performed tests of significance for differences in slopes and intercepts of

Table 1. Life history variables used in analyses.

	ABM	OBM	NOL	POM	LPY	TOY	SXM	LFS	RLS	TRO
DINOSAURS										
Maiasaura peeblesorum	6 000	1.05	24	0.42	–	–	–	–	–	–
Hypselosaurus priscus	5 300	3.3	20	0.44	–	–	–	–	–	
Protoceratops andrewsi	177	0.5	27	7.6	–	–	–	–	–	–
Orodromeus malekai	21	0.44	20	41.9	–	–	–	–	–	–
CROCODILES										
Crocodylus palustris	–	–	12	–	1	12	–	–	–	–
Crocodylus porosus	–	0.1	50	–	1	50	–	–	–	–
Alligator mississippiensis	–	–	35	–	1	35	9	86.5	77.5	2 713
TERRESTRIAL BIRDS										
Dinornis maximus	250	7.0	1.5	4.2	–	–	–	–	–	–
Struthio camelus	128	1.35	6.5	2.01	1	6.5	3	20	17	130
Megalapteryx hectori	93	0.5	1.5	0.8	–	–	–	–	–	–
Casuarius casuarius	85	–	5	–	1	5	4.5	21	16.5	82.5
Dromaius novaehollandiae	45	0.6	9	12	1	9	2.5	15	12.5	112.5
Rhea americana	22.5	0.61	14	37.9	1	14	2.5	13	10.5	147
Ardeotis kori	18.1	0.14	4	3.09	1.5	6	–	–	–	–
Pterocnemia pennata	13	0.53	13	53	1	13	2.5	–	–	–
Argusianus argus	10.8	–	2	–	1	2	–	30	–	–
Cygnus olor	10.8	0.08	6.5	4.8	1	6.5	4	26	22	143
Pelecanus onocrotalus	10.3	0.18	2	3.5	1	2	3.5	10	6.5	13
Otis tarda	9.5	0.14	3	4.42	1	3	4	–	–	–
Meleagris gallopavo	7.6	0.07	11.1	10.2	1	11.1	2	–	–	–
Eupodotis afra	6.9	0.05	2.5	1.81	1	2.5				
Leptoptilos crumeniferus	6.4	0.14	2.5	5.47	1	2.5	4	25	21	52.5
Neotis denhami	6.3	0.13	1.5	3.1	1	1.5				
Grus grus	5.5	0.2	2	7.3	1	2	3.5	–	–	–
Pelecanus rufescens	5.5	0.12	2	4.4	1	2	3	10.0	7.0	14.0
Anthropoides virgo	5.0	0.13	2	5.2	1	2	2	–	–	–
Sagittarius serpentarius	4.0	6.13	2.5	8.1	1	2.5	–	–	–	–
Balearica pavonina	3.6	–	3	–	1	3	4	–	–	–
Ciconia ciconia	3.4	0.11	3.5	11.3	1	3.5	4	26	22	77
Phoenicopterus ruber	3.0	0.14	1	4.67	1	1	4.5	40	35	35
Tetrao urogallus	3.0	0.05	8	13.3	1	8	1	18	17	136
Apteryx australis	2.5	0.45	1.5	27	1	1.5	5.5	–	–	–
Rhynochetos jubatus	1.8	0.07	1	3.9	–	–	2	21	19	–
Phoeniconaias minor	1.8	0.12	1	6.67	1	1	4	20	16	16
Platalea alba	1.8	0.07	3	11.7	1	3	4	–	–	–
Ardea cinerea	1.4	0.06	4.5	19.3	1	4.5	2	–	–	–
Botaurus stellaris	1.3	0.04	5	15.4	1	5	1	8	7	35
Anas platyrhynchos	1.2	0.05	11	45.8	1	11	–	23	–	–
Netta rufina	1.1	0.06	10	54.6	1	10	1.5	–	–	–
Phasianus colchicus	1.0	0.03	9	27	1	9	1	–	–	–
Aythya marila	0.9	0.06	10	66.7	1	10	1	20	19	190
TERRESTRIAL MAMMALS										
Loxodonta africana	4200	105	1	2.5	0.28	0.28	12.5	55	42.5	11.9
Elephas maximus	3865	100	1	2.6	0.28	0.28	7.5	55	47.5	13.3
Ceratotherium simum	2950	60	1	1.7	0.33	0.33	5.5	45	39.5	13
Rhinoceros unicornis	2625	55	1	2.1	0.33	0.33	5	30	25	8.25
Hippopotamus amphibius	2550	40	1	1.6	1	1	10	35	25	12.5
Diceros bicornis	1490	27.5	1	1.9	0.33	0.33	6.5	35	28.5	9.4
Giraffa camelopardalis	1115	59	1	5.3	0.6	0.6	4.5	23	18.5	11.1
Bubalis bubalis	837	–	1	–	1	1	2.5	25	22.5	22.5
Dicerorhinus sumatrensis	800	23	1	2	0.33	0.33	7	32	25	8.3
Bos gaurus	746	–	1	–	0.75	1	2.5	22	19.5	14.6
Bison bison	668	30	1	4.5	0.75	1	3	20	17	17
Bos grunniens	614	18	1	2.9	0.75	1	2.5	25	22.5	22.5
Taurotragus oryx	603	29	1	4.8	1	1	3	23	20	20
Camelus dromedarius	550	–	1	–	0.5	0.5	5	50	45	22.5
Syncerus caffer	473	38	1	8	0.6	0.6	3.5	19	15.5	9.3
Alces alces	447	13.5	2	6	1	2	2	23.5	21.5	43
Ursus maritimus	398	0.8	2.5	0.5	0.4	2.2	5.5	30	24.5	53.9
Equus caballus	350	32	1	9.1	0.75	0.75	3	30	27	20.25
Ovibos moschatus	305	11.5	1	3.8	0.75	0.75	2	23	21	15.8
Tapirus terrestris	263	8.6	1	3.3	0.5	0.5	3	32.5	29	14.5
Equus zebra	249	32.4	1	13	0.75	0.75	2	25	23	17.3
Choeropsis liberiensis	228	4.9	1	2.2	0.7	0.7	4.5	36.5	32	22.4
Ursus arctos	222.5	0.3	2.3	0.3	0.5	1.15	5	30	25	28.8
Connochaetes taurinus	212	17	1	8	1	1	2	21	19	19
Cervus elaphus	185	16.5	1	8.9	1	1	2.3	26	23.7	23.7
Panthera tigris	183	1.36	2.5	1.9	0.5	1.25	3.5	15	11.5	14.4
Panthera leo	175.5	1.35	2.5	1.9	0.5	1.25	3	13	10	12.5

	ABM	OBM	NOL	POM	LPY	TOY	SXM	LFS	RLS	TRO
Oryx dammah	155	10.9	1	7	1	1	3	20	17	17
Ailuropoda melanoleuca	129	0.1	1.5	0.12	1	1.5	6.5	26	19.5	29.3
Panthera onca	97	0.8	2	1.7	0.5	1	3	22	19	19
Rangifer tarandus	95.5	7.45	1.5	11.7	1	1.5	3	13	10	15
Dama dama	88	4.5	1.2	6.1	1	1.2	1.3	15	13.7	16.4
Ammotragus lervia	86.9	4.12	1.5	7.1	2	3	1.5	20	18.5	55.5
Phacochoerus aethiopicus	84.5	0.89	2.5	2.6	1	2.5	1.4	18	16.6	41.5
Tragelaphus imberbis	77.5	–	1	–	1	1	2.4	25	22.6	22.6
Selenarctos tibetanus	71	–	1.5	–	1	1.5	3	33	30	45
Puma concolor	66.5	0.34	3.5	1.8	0.75	1.75	2.5	19	16.5	28.9
Ovis canadensis	61.4	3.5	1.5	8.6	1	1.5	2.25	16	13.75	20.6
Hydrochoerus hydrochaeris	55.5	1.35	4.5	11	1.5	6.75	1.25	10	8.75	59.1
Crocuta crocuta	55.3	1.48	2	5.4	1	2	3	25	22	44
Tragelaphus scriptus	52.3	3.45	1	6.6	1.3	1.3	1	10	9	11.7
Odocoileus virginianus	49.6	2.5	2	10.1	1	2	2	10	8	16
Potamochoerus porcus	47.7	–	3.5	–	1	3.5	3	20	17	59.5
Hyaena hyaena	41	0.7	2.4	4.1	1	2.4	2.5	24	21.5	51.6
Canis lupus	38.3	0.43	6	6.7	1	6	2	16	14	84
Antilocapra americana	38	2.9	1.75	20.25	1	1.75	1.3	10	8.7	56.6
Gulo gulo	22	0.1	1.5	0.68	1	1.5	2.5	13	10.5	15.8
Gazella dorcas	21.4	1.35	3	18.9	1.3	3.9	0.7	17	16.3	63.6
Hystrix cristata	20	–	1.5	–	1.75	2.63	1	13.5	12.5	32.9
Civettictis civetta	14	0.68	2.5	12.1	2	5	1	15	27	70
Hyemoschus aquaticus	12.5	–	1	–	1	1	1.5	13	11.5	11.5
Dolichotis patagonum	12	0.43	1	3.6	4	4	0.8	10	9.2	36.8
Felis rufus	9.7	0.33	3.5	11.9	1	3.5	1.25	17	15.75	55.1
Pudu pudu	8.5	0.5	1.98	11.7	1.5	2.97	1	15	14	41.6
Agouti paca	8.2	0.71	1.5	13	2	3	1	16	15	45
Taxidea taxus	8	0.12	2	3	1	2	0.3	14	13.7	27.4
Tragulus napu	7.8	0.37	1.5	7.1	1.5	2.25	0.4	10	9.6	21.6
Myocastor coypu	7.7	0.23	4	12	2.2	8.8	0.4	6.2	5.8	51
Vulpes vulpes	7.5	0.11	4.6	6.8	1	4.6	0.8	6	5.2	23.9
Cerdocyon thous	6.5	0.14	4.5	9.7	1.3	5.85	0.75	6	5.25	30.7
Erethizion dorsatum	6.1	0.48	1	7.9	1	1	2	13.5	11.5	11.5
Dolichotis salinicola	5.7	0.19	1.5	5	3.25	4.88	0.8	10	9.2	44.9
Procyon lotor	5.3	0.07	1	1.3	1	1	1	16	15	15
Madoqua kirkii	5.1	0.61	1	12	2	1	1.2	10	8.8	8.8
Nesotragus moschatus	4.5	–	1	–	1	1	0.5	8	7.5	7.5
Nasua nasua	4.4	0.18	3.5	14.3	1	3.5	2	7	5	17.5
Capromys pilorides	4.3	0.22	2	10.2	2	4	0.8	11.3	10.5	42
Ailurus fulgens	3.75	0.2	2	10.7	1	2	1.6	13	11.4	22.8
Neotragus pygmaeus	3.5	–	1	–	1	1	0.5	8	7.5	7.5
Oryctolagus cuniculus	3.1	0.04	3.5	4.5	2	7	2	5	3	21
Dasyprocta agouti	2.7	0.18	1.5	10	2	3	0.8	10	9.2	27.6
Tragulus javanicus	2.5	0.38	1.5	23	1.5	2.25	0.4	10	9.6	21.6
Genetta genetta	2.0	0.07	2.5	8.8	0.8	2	4	13	9	18
Martes martes	1.3	0.03	4	9.2	1	4	2	10	8	18
Sylvilagus floridanus	1.2	0.04	5	16.6	4	20	0.5	1.4	0.9	18
WHALES										
Balaenoptera musculus	140 000	2 000	1	1.4	0.42	0.42	27	100	73	30.7
Balaenoptera physalus	60 000	1 800	1	3	0.42	0.42	8	100	92	38.6
Balaena mysticetus	60 000	–	1	–	0.42	0.42	4	40	36	15.1
Megaptera novaeangliae	45 000	–	1	–	0.5	0.5	9	80	71	35.5
Eschrichtius robustus	28 000	500	1	1.8	0.5	0.5	8	70	62	31
Physeter catodon	16 500	1 000	1	6	0.33	0.33	9	70	61	20.1
Balaenoptera acutorostrata	10 000	–	1	–	0.5	0.5	7.5	47	39.5	19.8
Orcinus orca	5 500	180	1	3.3	0.15	0.15	9	75	66	9.9
Hyperoodon ampullarus	2 500	–	1	–	0.5	0.5	9	37	28	–
Delphinapterus leucas	1 360	80	1	5.9	0.42	0.42	5.5	33	27.5	11.6
Monodon monoceros	1 100	80	1	7.3	0.33	0.33	5	35	30	10
Globicephala melaena	800	–	1	–	0.33	–	–	40	–	–
Tursiops aduncus	175	10.5	1	6	0.5	0.5	8.5	30	21.5	10.8
Stenella attenuata	110	–	1	–	0.33	0.33	6	46	40	13.2
Delphinius delphis	67	–	1	–	0.42	0.42	4	20	16	6.72
Phocoena phocoena	58	5	1	11.6	0.75	0.75	3.5	11	7.5	5.63
Pontoporia blainvillei	50	–	1	–	1	1	2.5	16	13.5	13.5

Key: ABM = adult mass (kg.); OBM = body mass of single offspring (kg.) NOL = number of offspring per litter (clutches); POM = weight of offspring expressed as percentage of adult body mass [100 × (OBM × NOL) / ABM]; LPY = litters (clutches) per year; TOY = total (potential) offspring per year (NOL × LPY); SXM = age at sexual maturity (years); LFS = lifespan (years); RLS = reproductive lifespan (years) (LFS – SXM); TRO = total (potential) reproductive output (TOY × RLS). Note that the calcultaion of total potential reproductive output does not take into account the fact that maximum life expectancy increases with incrasing size (Calder, 1984), and should be trated as a theoretical maimum rather than as a generally realised potential.

Table 2. Values of parameters derived from scaling equations. Significance levels for slope and correlation are given. Key to variable abbreviations as for Table 1.

	NOL	LPY	TOY	TRO	POM
All birds					
n	34	31	31	14	31
r^2	0.002	0.09	0.02	0.08	0.30^{b}
Slope	–0.023	–0.020	0.08 1	0. 173	-0.413^{b}
Intercept	0.571	0.015	0.563	1.630	1.258
Extant birds only					
n	32	31	31	14	29
r^2	0.02	0.09	0.02	0.08	0.21^{b}
Slope	0.089	–0.020	0.081	0.173	-0.402^{b}
Intercept	0.513	0.015	0.563	1.630	1.256
Dinosaurs					
n	4				4
r^2	0.003				0.998^{b}
Slope	0.003				-0.821^{b}
Intercept	1.346				2.714
All birds plus dinosaurs					
n	38				35
r^2	0.14				0.426^{a}
Slope	0.171				-0.387^{a}
Intercept	0.465				1.279
Extant birds plus dinosaurs					
n	36				35
r^2	0.25				0.442
Slope	0.229				–0.394
Intercept	0.446				1.276
All mammals					
n	92	92	91	90	74
r^2	0.28^{a}	0.56^{a}	0.57^{a}	0.03	0.20^{b}
Slope	-0.101^{a}	-0.173^{a}	-0.267^{a}	–0.038	-0.165^{a}
Intercept	0.380	0.271	0.639	1.40	1.008
All terrestrial mammals					
n	75	75	75	75	65
r^2	0.24^{a}	0.56^{a}	0.55^{a}	0.07^{c}	0.22^{a}
Slope	-0.119^{a}	-0.196^{a}	-0.30^{a}	-0.072^{c}	-0.216^{a}
Intercept	0.421	0.323	0.721	1.479	1.067
Smaller terrestrial mammals (Mass < 130 kg.)					
n	47	47	47	47	40
r^2	0.01	0.151^{b}	0.09	0.09	0.09
Slope	–0.039	-0.122^{b}	-0.161^{c}	0.145^{c}	–0.174
Larger terrestrial mammals (Mass >40 kg)					
n	44	44	44	44	41
r^2	0.29^{a}	0.55^{a}	0.63^{a}	0.28^{a}	0.06
Slope	-0.174^{a}	-0.271^{a}	-0.422^{a}	-0.214^{a}	–0.174
Intercept	0.555	0.516	1.028	1.817	1.057
Whales					
n	17	17	16	15	9
r^2	NA	0.08	0.08	0.65^{a}	0.73^{a}
Slope	NA	–0.042	–0.042	0.167^{b}	-0.222^{b}
Intercept	NA	–0.227	0.227	0.613	1.431

[a] = significant at the $P < 0.001$ level or greater; [b] = significant at the $P < 0.01$ level; [c] = significant at the $P < 0.05$ level. NA = not applicable.

the regression lines obtained separately for different taxonomic groups, and these results are presented in Table 3. [Although we did not correct for the fact that these data were log transformed (e.g., LaBarbera 1989), we considered that, as we were interested in relative rather than absolute differences between the taxonomic groups, this additional step would not yield significantly more robust information]. All statistical calculations were performed with an IBM mainframe SAS statistical package.

Despite the extensive literature on bird reproduction, our bird data were limited by the difficulty of obtaining adult body masses and lifespans for birds. Our problem with the non-cetacean mammals was the converse, with the ensuing difficulty that a regression line based on all available mammal data was liable to be biased by a heavy emphasis on small mammals (see discussion of this scaling problem in Economos 1983). To compensate for this, we included only a size-selected range of mammals in the data set, in order to achieve a roughly even distribution of mammalian body sizes on a logarithmic scale. Few mammal taxa exist with a body mass of greater than 1000 kg, so all available taxa in this range were included. For mammals with a body mass of less than this, we selected taxa by body mass based on the divisions of the logarithmic scale: no more than three taxa were selected per intervals of 100 kg in the range of 100–1000 kg; per intervals of 10 kg in the range of 10–100 kg; and per intervals of 1 kg in the range of 1–10 kg. In each case, the three taxa selected (if available) represent a diverse distribution of families or orders so as to avoid taxonomic bias (Table 1).

Because of the differences in reproductive strategies in the different mammalian subclasses, only eutherian mammals were included in the mammal data. But we excluded eutherian mammals that had either abnormally low metabolic rates for their body size (edentates and hyracoids) or abnormally high metabolic rates (sciurid or muroid rodents). Primates were also excluded due to their "abnormally" low reproductive turnover. We also, separately, included data on whales. (Because the data on terrestrial birds and whales were extremely limited, there was no need to perform this type of "logarithmic size culling" on these data.) The dinosaur data represent those currently available from the literature, as summarised by Dunham et al. (1989). We also note that the only "reliable" dinosaur data are for the genera *Maiasaura* and *Orodromeus;* only in these cases have X-rays of the eggs confirmed that the fossilized clutches actually do belong with the associated adults (Horner & Weishampel 1988).

In addition to making direct comparisons between birds and terrestrial (and/or all) mammals, we further examined the differences between birds and "smaller mammals" (those within the size range of extant birds, with a body mass of less than 130 kg). Likewise, in the comparison of terrestrial mammals with whales, we compared whales with terrestrial mammals in the same size range (body masses greater than 40 kg). This was done in order to control for bias in comparing regression lines derived from a differing order of magnitude in the spread of the data points along the x-axis of body mass. While we included the data available (from fossilized clutches) for the extinct birds, *Dinornis* and *Megalapteryx*, in the regression line for birds, we also examined the regression line obtained for extant birds only, in deference to the fact that data obtained for fossil organisms might not be as reliable as those obtained for the living ones. The two lines (when applicable) were compared separately with the regression lines derived from the mammal data.

Table 3. Comparisons between regression lines derived from scaling equations. Key to variable abbreviations as for Table 1. S = slope, I = intercept.

Mammals:	all		terrestrial		smaller		larger	
	S	I	S	I	S	I	S	I
All birds								
NOL	*NS*	**	*NS*	**	*NS*	**		
LPY	**	*NA*	**	*NA*	*	*NA*		
TOY	**	*NA*	**	*NA*	*NS*	*NS*		
TRO	*NS*	**	*	*NA*	*NS*	**		
POM	*	*NA*	*NS*	*NS*	*NS*	*NS*		
Extant birds								
NOL	*	*NA*	*	*NA*	*NS*	**		
LPY	**	*NA*	**	*NA*	*	*NA*		
TOY	**	*NA*	**	*NA*	*NS*	*NS*		
TRO	*NS*	**	*	*NA*	*NS*	**		
POM	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*		
All birds & dinosaurs								
NOL	**	*NA*	**	*NA*				
POM	**	*NA*	**	*NA*				
Whales								
NOI							**	*NA*
LPY							**	*NA*
TOY							**	*NA*
TRO							**	*NA*
POM							*NS*	*NS*

** = significant at the $P < 0.01$ level; * = significant at the $P < 0.05$ level. *NS* = not significant. *NA* = not applicable.

We acknowledge that, as shown in Table 2, the r^2 values for the regression lines are often very low (although many are statistically significant). It is certainly true that there is a lot of scatter in the data presented, and that the data were gathered with the intention of examining an interesting hypothesis rather than to attempt a rigorous "proof". However although the data might be limited and flawed, it is unlikely that they are biased in any systematic fashion. We present tentative conclusions that can be "eyeballed" from the figures, and that additionally stand up to statistical testing. We freely admit that our primary intention is to provide stimulation for both a potential audience and ourselves.

3. Results

Neither birds nor dinosaurs show a significant change in number of young per clutch with change in body mass. There is a significant increase if birds and dinosaurs are lumped together, but this probably reflects the fact that neither archosaur taxon shows a decrease in the number of offspring with increasing size, and that dinosaurs produced a larger clutch for their size than birds. For terrestrial mammals, all mammals, and "larger mammals" (body mass greater than 40 kg), there is significant decrease in number of young per litter with increasing body mass, but this is not true for "smaller mammals" (body mass less than 130 kg). Slopes of regression lines for extant birds, or for all birds plus dinosaurs, are significantly different from the slope for all mammals and terrestrial mammals. The slopes are not significantly different between birds and terrestrial mammals if extinct birds are included, but in this case the intercepts are significantly different. Whales show no change in the number of offspring

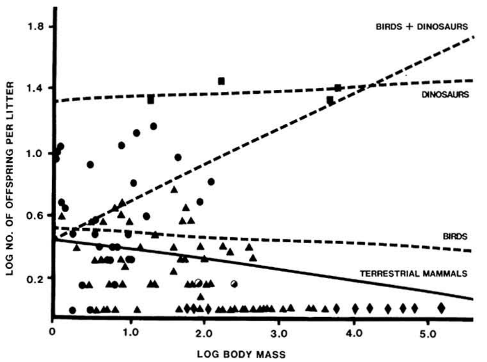

Fig. 1. Scaling of number of offspring per litter/clutch with body mass. — Circles = birds (half-filled circle = extinct birds); squares = dinosaurs; triangles = terrestrial mammals; diamonds = whales. Regression lines for birds and dinosaurs are dotted; lines for mammals are solid.

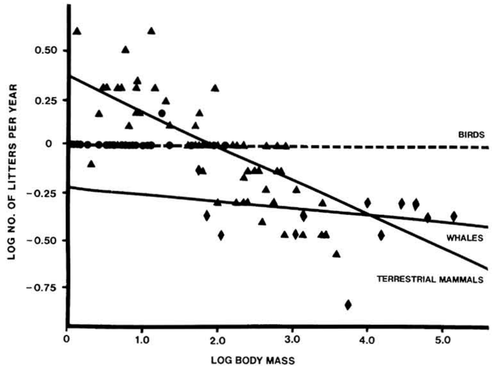

Fig. 2. Scaling of litters/clutches per year with body mass. Key as for Fig. 1.

per litter with body mass, which is different from terrestrial mammals of equivalent size, which show a significant decrease with body mass (Fig. 1).

Birds show no significant change in number of clutches per year with body mass. Mammals (terrestrial or aquatic) of all size ranges show a significant decrease in numbers of litters a year with increasing body mass. Thus birds are significantly different from all types of mammals. Whales are different from terrestrial mammals of equivalent size in having a significantly shallower slope to the relationship between numbers of litters per year and body mass (Fig. 2).

Birds exhibit no significant change in total number of offspring per year with increasing body mass. But all classes of terrestrial mammals (but not whales) do show a significant decrease in total number of young produced per year with increasing body mass. Thus, birds have a significantly different scaling of this variable from all mammals or from terrestrial mammals, even thought their number of offspring per year is not significantly different from smaller mammals (that is, mammals of a comparable size range to extant birds). Larger mammals show a significantly greater decrease in number of young per year with increasing body mass than do whales (Fig. 3).

Birds show no significant change in total reproductive output with change in body mass. (This is also true if the pelicans, which appear to have an "abnormally" short lifespan, are removed from the data analysis.) Large terrestrial mammals, and all terrestrial mammals considered together, do show a significant decrease in total reproductive output with increasing body mass. Small mammals show a marginally significant increase, and whales show a more significant increase, with a slope significantly different from that of larger mammals. Thus all terrestrial mammals have relationships different from birds, which show a greater potential reproductive output at large body sizes than mammals in general. (Fig. 4).

All vertebrates exhibit a decrease in total mass of the litter or clutch expressed as a percentage of adult body mass with increasing body mass; tests of this relationship prove significant, although there are problems of regressing the reciprocal of a variable (adult body mass) against itself. Birds alone do not show a significant difference in the scaling of percent clutch mass from terrestrial mammals, but birds lumped with dinosaurs show a significantly greater decrease with body mass than mammals (probably because the larger dinosaurs greatly increase the range of body mass in this comparison). Whales appear to have somewhat larger young for their body size than larger terrestrial mammals, but this difference is not significant (Fig. 5). Note, however, that in Fig. 5 almost all of the whale data lie above those for terrestrial mammals; the lack of statistical significance may reside in the scatter of the data for terrestrial mammals rather than in the lack of absolute differences between terrestrial mammals and whales.

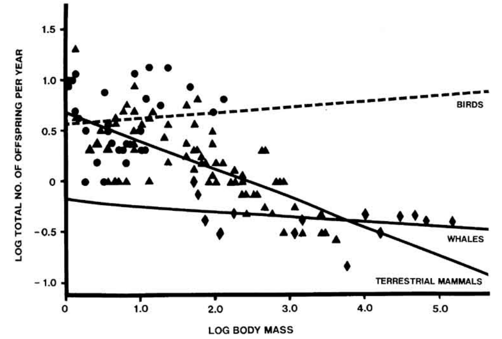

Fig. 3. Scaling of total (potential) number of offspring per year with body mass. Key as for Fig. 1.

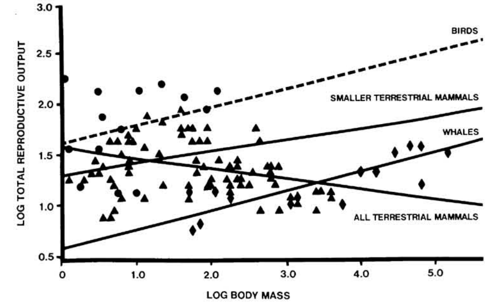

Fig. 4. Scaling of total (potential) reproductive output with body mass. Key as for Fig. 1.

Because all these single variables are correlated with each other, as well as with body mass, we also attempted a principal components analysis of these data. Analysis of the simple variables alone yielded no separation between birds and mammals, a surprising result in light of the bivariate analyses. However, an analysis that included both simple and compounded variables (see previous explanation) produced an interesting result (although we acknowledge that this is not strictly the correct use of principal components analysis). Not only were birds distinguished from terrestrial mammals to a certain extent, but additionally whales tended to group with birds rather than with terrestrial mammals.

The first three components accounted for 85 % of the variance in the data. The first component (accounting for 49 % of the variance) appeared to reflect primarily body size (see Table 4). Birds and whales separated out along the axes of both component 2 (accounting for 26 % of the variance) and component 3 (accounting for 10 % of the variance). Component 2 had high loadings for number of offspring per litter/clutch and total reproductive output, and low loadings for number of litters/clutches per year. Component 3 had high loadings for number of litters per year and total number of offspring per year, and low loadings for number of offspring per litter/clutch and total reproductive output. Fig. 6 is a scatter plot of principal component 2 against principal component 3.

In summary, birds differ from terrestrial mammals in terms of life history or reproductive strategy as follows: they show no significant change with respect to body mass in number of offspring per clutch, number of clutches per year or total number of offspring per year, whereas mammals show a significant decrease of all these variables with increasing body mass. [Note that this is not necessarily true of all birds. The California condor (not considered in this paper) has an extremely low reproductive turnover, and population maintenance is apparently dependent on extreme longevity (Mertz 1971).] If birds and dinosaurs are lumped together, there is a significant increase in number of offspring per clutch with body mass; however, this lumping may not be appropriate, as the data suggest that dinosaurs may scale differently from birds in this variable (see Fig. 1).

Table 4. Loadings for the first three principal components of reproductive scaling data in mammals and birds. Key to variable abbreviations as for Table 1. LFS = absolute lifespan; TOM = total offspring mass.

Variable	Comp. 1	Comp. 2	Comp. 3
ABM	0.3334	0.2927	0.3405
OBM	0.3522	0.2885	0.2878
NOL	−0.2473	0.4637	−0.2239
LPY	−0.2526	0.0402	0.7624
TOY	−0.2903	0.3884	0.2610
SXM	0.3867	0.1610	−0.0024
LFS	0.4100	0.1842	−0.0943
RLS	0.3925	0.1827	−0.1043
TRO	−0.1823	0.4900	−0.2429
TOM	−0.2260	0.3612	−0.1522

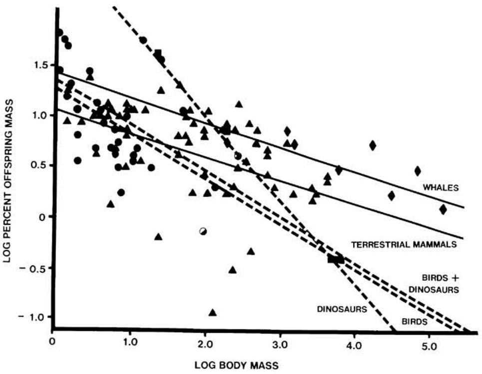

Fig. 5. Scaling of total offspring mass expressed as a percentage of maternal mass with body mass. Key as for Fig. 1.

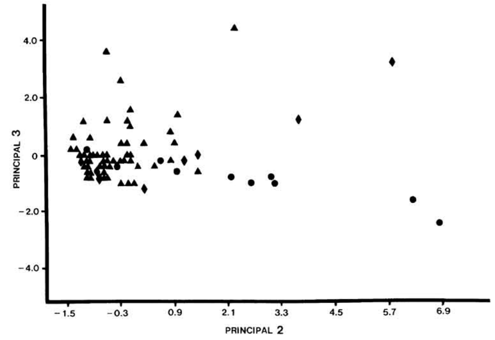

Fig. 6. Plot of principal component 3 against pricipal component 2 from principal components analysis on all reproductive variables. Key as for Fig. 1.

As a result of these factors, birds have a greater overall total (potential) reproductive output than mammals of equivalent body size, and also do not show the decrease in total reproductive output with body size that is typical of terrestrial mammals. (Note that we have not factored into this equation the fact that individuals may experience a decline in reproductive potential with advancing years.) Both groups show a similar decrease in relative weight of the offspring (expressed as a percentage of adult body mass) with increasing body mass, and the difference between mammals and archosaurs is significant if birds and dinosaurs are lumped together (with a significantly greater decrease in slope in archosaurs).

Thus the general archosaur strategy in comparison with mammals is as follows: archosaurs maintain the same number of clutches per year, and number of offspring per clutch, regardless of body size. This gives them a potentially greater total lifetime reproductive output than mammals, which show a decrease in both variables with increasing body size. (Note that the data in Table 1 suggest that the reproductive lifespans of birds and mammals of equivalent masses are similar, so this difference in total reproductive output is not related to a longer lifespan in birds, but rather just to the total number of offspring produced per year.) However, the "archosaur strategy" at large body sizes may be at the expense of reducing both the size of the individual young and the total weight of the clutch to a greater extent than is seen in large mammals (see later discussion of potential design constraints on egg-laying tetrapods).

Terrestrial mammals show significant differences from cetaceans in the scaling of number of offspring per litter, number of litters per year and total number of offspring per year, with cetaceans representing a "leveling off" in the negative allometry that characterizes terrestrial mammals. This results in whales having a significantly greater total reproductive output than other mammals of equivalent body size (indeed, one that shows a positive allometric scaling rather than a negative one). This may be related to the fact that whales appear to produce offspring that are relatively larger than those of equivalently sized terrestrial mammals, although this difference could not be shown to be statistically significant in this study.

3. Discussion

The salient difference between birds and mammals is the greater total potential reproductive output of birds, which does not decrease with increasing body size. Could dinosaurs be considered to be similar to birds in this aspect of life history strategy, producing a similarly large number of offspring every year? All known dinosaurs produced a larger number of eggs per clutch than is seen in present day birds (Fig. 1), although the offspring of the larger dinosaurs were more altricial than those of the smaller ones (at least among those that have been available for study) (Horner & Weishampel 1988). This corresponds with the observation here that the total mass of the clutch in larger dinosaurs is a smaller percentage of adult body mass than is true of the smaller ones. As the number of clutches per year does not decrease with increasing body size in birds (at least in the range of body sizes of birds considered here), and the slope of the lines for the relative percentage mass of the clutch is virtually identical for birds considered alone or for birds and dinosaurs lumped together (Fig. 5), would it be fair to assume that even large dinosaurs laid a clutch every year?

The fossilized nests and young of the hypsilophodontid *Orodromeus* appear to have been laid down in a seasonal fashion (Horner 1982), although we have no way of knowing if this "season" in fact corresponded to a single year. However, even in the absence of a possible shorter interbirth interval, given the fact that the lifespan of all taxa tends to increase with increasing body size (Peters 1983), and that theoretical calculations suggest that *Maiasaura* could not have had a greatly delayed onset of sexual maturity (as is typical for many ectothermic vertebrates) (Dunham et al. 1989), it is a reasonable assumption that the total potential reproductive output of dinosaurs might actually show an increase with increasing body size (as appears to be true for cetaceans among mammals, in this case achieved by an increased potential lifespan; see Fig. 4).

How do these issues relate to the possibly divergent modes of life history strategies, and subsequent evolutionary patterns, in dinosaurs as opposed to mammals? Eisenberg (1981) points out that, for mammals, the average potential output of offspring for a female of any taxon is around 12, with a near equivalence over the range of size classes [although Calder (1984) suggests that the actual output in nature is around 2.6]. A compensation is achieved for the decrease in litter size and interbirth interval in larger taxa by an increase in the lifespan, plus the greater life expectancy at birth relative to lifespan. If archosaurs were to have a greater average total reproductive output than mammals, as we suggest here, this might not in fact have any effect on population sizes at equilibrium. One could interpret the data as meaning that archosaurs are typical "*r*-strategists," producing larger numbers of more immature offspring and experiencing greater rates of juvenile mortality. In contrast, larger mammals, at least, could be seen as being typical "*K*-strategists" producing smaller numbers of offspring that were more likely, on average, to survive to maturity (see MacArthur & Wilson 1967, Pianka 1970).

However, this type of simplistic view of ecological/evolutionary strategies between different taxonomic groups has been criticized by Stearns (1977), who points out that design constraints may mean that different taxa may not be able to respond in the identical fashion to what may be perceived as similar selection regimes. We propose that the differences observed between mammals and dinosaurs are the results of design constraints imposed by the initial reproductive modes of the smaller, ancestral taxa (as detailed below), not due to different selection pressures on life history strategies. Such differences would not be apparent at smaller body sizes: both a mammalian or archosaurian taxon (bird or dinosaur) could be expected to have a similar production of offspring per year at a body mass of about 5 kg — probably around six to ten offspring produced in one or perhaps two litters or clutches. But with increasing body size, a profound divergance would become apparent.

Larger mammals, especially large herbivores, can usually produce no more than a single offspring per litter (although the moose regularly produces twins, and twins are also rarely seen in some other large ungulates, like the horse). Eisenberg (1981) suggests that this is due to the constraints imposed by lactation, that pose a particular problem for herbivores. A large herbivore, with a diet of structural carbohydrates and low nitrogen content, has a problem in providing sufficient protein in the milk for rapid postnatal growth. As nutrients are more easily transferred across the placenta than via the milk, a compensatory evolutionary strategy appears to be the production of highly precocial young and correspondingly short periods of lactation. Lactation costs are also much greater than gestation costs in mammals, especially in herbivores (Clutton-Brock et al. 1989). However, it is apparently impossible for a large herbivore to produce more than one highly precocial offspring, perhaps because of gravitational and size-packing constraints on the pregnant female, or again maybe related to the fact that protein transference across the placenta might still be a limiting factor during prenatal growth. In contrast, carnivorous mammals have a lesser problem: even larger carnivores usually produce multiple offspring per litter, and these young are fairly altricial. A consequence of this in terms of total life history strategies is that mammalian carnivores have, on average, shorter lifespans than herbivores of equivalent size (Eisenberg 1981).

Eisenberg (1981) also extends this argument to cetaceans, pointing out that whale milk has a high fat content, and that whales have rapid postnatal growth; thus they can afford to have offspring that are less precocial (at least in terms of developmental stage, although note that our data suggest that whales actually have relatively larger offspring than terrestrial mammals), and can breed at more frequent intervals. The data we present here support this view, showing that cetaceans represent a "leveling off" in the negative allometry of the scaling of life history parameters in large mammals.

Although Read & Harvey (1989) recently produced evidence to show that body size alone cannot account for interordinal differences in mammalian reproductive life-history strategies, their concern was primarily to illustrate that many smaller mammals may show the reproductive strategy of a low reproductive turnover, combined with a long lifespan (such taxa were dropped from our analysis, as previously detailed). It remains true that no large mammal (body mass of greater than 200 kg) adopts the "opposite strategy" of producing large numbers of small young, even though intertaxon variation in life history strategies may still exist. (The relatively large litters of bears, combined with altricial young, are a case in point here.)

What were the constraints imposed on dinosaurs? Viviparity via egg retention (as seen in certain squamate reptiles) may be impossible for birds because of endothermy (Dunbrack & Ramsey 1989), and may also have been impossible for dinosaurs. In contrast, mammal ancestors may have achieved this evolutionary step via egg size reduction accompanied by lactation (Dunbrack & Ramsey 1989). One absolute constraint must be the size of the egg than can be laid, due to scaling considerations of both the support of the egg contents by the shell and the rate of diffusion of oxygen into the egg (Peters 1983). Calder (1984) suggests that the size of the largest known terrestrial bird, the extinct *Aepyornis*. may have been limited by constraints on eggshell strength. However, the data in Table 1 suggest that, while large birds such as *Dinornis* and *Struthio* (the ostrich) tend to have a fairly small number of relatively large eggs, dinosaurs had a larger number of relatively small eggs. (In fact, the individual eggs of *Maiasaura* are smaller than those of the ostrich.) This strategy of producing a large number of altricial young is usually correlated with high infant mortality in non-mammalian tetrapods (Peters 1983). Although this may well have been the case in dinosaurs, it must also be remembered that, unlike most living reptiles, there is considerable evidence that *Maiasaura,* at least, provided parental care of the young (Horner & Makela 1979, Horner 1984), perhaps even to the extent of providing the young with a diet of relatively high protein content (Hunter & Janis 1992).

The conclusion that larger mammals and dinosaurs had different types of reproductive strategies, with dinosaurs having a greater number of young but experiencing a greater rate of juvenile mortality, might not seem to have great evolutionary importance viewed over *ecological* time. However, we propose that when viewed over *evolutionary* time, the presumed greater reproductive output of dinosaurs might make them less vulnerable to environmental perturbations than large mammals, and hence less vulnerable to extinction. This would provide an explanation for the observation that large dinosaur taxa were commonly seen in the Mesozoic while mammalian taxa of equivalent size were very rare in the Cenozoic.

Consider the potential effect of environmental change on a population of large mammals. Kiltie (1985) points out that virtually all the ungulates that survived the late Pleistocene extinctions in the higher latitudes were those with a gestation period of less than one year (corresponding, more-or-less, to a body mass of at most 300 to 500 kg). He argues that a change in environmental conditions will not only affect the length of the favorable season for birth but also its predictability. A mammal with a gestation period of even slightly greater than a year might be pushed from an interbirth interval of around fifteen months to one of every two or three years, thus greatly reducing the reproductive turnover of the species. Although under many conditions this decrease in reproductive turnover is matched by the longer life-span and greater life expectancy of larger species, so population levels are maintained, large mammals are more vulnerable to disasters, because they cannot rapidly rebuild populations (see Owen-Smith 1988).

Kiltie's argument encompasses only a consideration of gestation length and interbirth interval. We might assert that it is likely that large dinosaurs would have shorter interbirth intervals than mammals of equivalent size, but this cannot be proven. However, consideration must also be paid to the absolute number of offspring that individuals of a species can produce at any one time. Although under normal conditions one might expect most dinosaur juveniles to die before reaching maturity, if an environmental perturbation disrupted reproductive cycles, or even led to a high level of adult mortality, the capacity would still exist for a dinosaur taxon to rebuild population levels rapidly, irrespective of the normally "expected" survival of these offspring. This would be an impossibility for a large mammal, which can produce only a single offspring at a time. To extend Kiltie's argument of the effect of the late Pleistocene climatic change on larger taxa, large mammals might be especially vulnerable to even small, transitory environmental changes because of long interbirth intervals and slow capacity for reproductive turnover. However, large dinosaurs would be considerably less vulnerable, because the interbirth interval was possibly shorter and because of the capacity to produce large numbers of offspring (an order of magnitude greater than mammals of equivalent size). Thus, in addition to Kurtén's (1953) "threshold" of difficulty of evolving a mammal over around 500 kg in body mass, there might be a further "threshold" of around 5000 kg beyond which any mammalian taxon would be too large to survive, at least in a stochastic sense, normal types of environmental perturbations that exist over evolutionary time. The very terrestrial few mammals that have exceeded this body size in the fossil record (a classic example being the indricotheriine rhinos) are known only from a very short period of geological time.

This argument might also be extended to a comparison of the range of body sizes between terrestrial mammals and cetaceans. As previously noted, very few whales fall outside of the size range characteristic of dinosaurs. It might be possible for a mammal to attain a larger size in the aquatic environment for two reasons other than the usual argument of structural constraints due to gravitational forces (which cannot be the limiting factor if dinosaurs could achieve such large sizes on land). Firstly, the marine environment might be less subject to the type of perturbation experienced in the terrestrial realm. The other reason, more likely in our view; is that both the predictability and the high-protein content of the diet available in the marine habitat, whales are not as limited in their capacity for reproductive turnover as large, terrestrial mammals, and hence can more easily evolve into taxa of very large body size.

One way to test this hypothesis, which is outside of the scope of this paper, would be to determine if large mammal species had a shorter longevity in the fossil record than dinosaur species of equivalent size and of apparently similar ecological habits (ceratomorphs could be compared with ceratopsians, for example). This type of test could be extended to see if there were differences in longevity between small and large mammalian species, or small and large dinosaur species, within any given clade. One outstanding problem, in our eyes, in this comparison of terrestrial mammals with cetaceans and dinosaurs is the absence of large terrestrial mammalian carnivores. The largest living fully terrestrial carnivore specialists among present day mammals are the large cats, with body masses in the range of 200 kg, and the largest known fossil carnivore, the mesonychid *Andrewsarchus* (which may have been more bear-like in its habits), was no bigger than a bison and could not have weighed much more than 700 kg. This is in stark contrast to the condition seen in dinosaurs, where the carnosaur taxa appear to be routinely as large as the ornithischian herbivore taxa, and also to the condition in present day cetaceans (the largest specialist carnivore is the sperm whale, *Physeter,* at 16 500 kg). We do not know if this difference might also be explained by some factor related to reproductive turnover and life history strategy.

Another possible factor might be the scaling of biomechanical properties in quadrupedal mammals that need to maintain a certain limb posture to retain agility for predation [200 kg represents a transition point in posture in living mammals, from a more flexed-limb stance to a more pillar-like stance (Biewener 1989, Bertram & Biewener 1990).] Such constraints might not have applied in the same fashion to the bipedal carnivorous dinosaurs. We hope that the ideas expressed here will encourage speculation in other researchers.

5. Conclusion

Kurtén (1953) originally suggested that mammals and dinosaurs might face different types of constraints on the size that taxa could attain in evolution because of differences in reproductive strategies. Using terrestrial birds as a model for dinosaurs (incorporating dinosaur data where available) we show that dinosaurs most likely differed profoundly from mammals in their total reproductive output. Dinosaurs probably produced much greater numbers of young per lifetime than mammals; additionally, it is likely that this capacity for reproductive output did not decline with increasing body size, as is true for mammals. Differences in life history strategies between dinosaurs and mammals reside in the respective design constraints inherent in laying eggs versus bearing life young. While such constraints would probably not result in great apparent differences at small body sizes (under 10 kg), profound differences would be seen at larger body sizes, especially at body masses of greater than 5000 kg.

We suggest that it is these differences in life history strategies and reproductive behavior, rather than any constraints of structural design, that lie behind the observed differences in body sizes commonly attained by dinosaurian versus mammalian taxa. Large dinosaur species, by virtue of their ability to produce large numbers of young (resulting from a reproductive strategy of oviparity rather than viviparity) would have the capacity to rebuild population levels rapidly following environmental perturbations. They might thus be less vulnerable to extinction than mammal species of similar size; large mammals can only produce a single young at a time, and the evidence of the late Pleistocene extinctions illustrates the vulnerability of large mammals to ecological change (Kiltie 1985). Previous studies on the effect of reproductive turnover on vulnerability to extinction at large body size principally consider gestation length and interbirth interval as the critical variables (e.g., Kiltie 1985). Although we consider it likely that dinosaurs had relatively shorter interbirth intervals than large mammals, our main argument is concerned only with the total numbers of offspring produced. While the majority of these offspring would die under normal ecological circumstances, dinosaurs still must have had a higher intrinsic rate of reproduction than mammals, with the resultant capacity for rapid population regeneration. While this hypothesis cannot be proven in a rigorous fashion, we note that there is currently no competing explanation for the reason why large dinosaur taxa were commonly seen in the Mesozoic, whereas terrestrial mammalian taxa of comparable size were extremely rare in the Cenozoic.

However, a few other factors might be considered here. The more stable climate of the Mesozoic (in comparison with the Cenozoic) might have resulted in a more equable environment for the evolution of large body sizes in dinosaurs. Additionally, the Mesozoic "Age of Dinosaurs", from the late Triassic to the end of the Cretaceous (approximately 150 million years) was a much longer time than the Cenozoic "Age of Mammals" of around 65 million years. By Cope's Rule alone (see Stanley 1973) dinosaurs may have had a longer time to evolve large body sizes. However, we note that large sauropodomorphs were known from the Jurassic and late Triassic, and that large body sizes (on the order of several hundred kilograms) were attained by Paleocene pantodonts. Thus absolute differences in body sizes cannot be solely accounted for by the time taken for their evolution.

Although very large terrestrial mammals are rare, large body sizes are commonly attained among the Cetacea. However, with the exception of the very largest mysticetes, constraints imposed by gravitational forces cannot be the only answer to this observed difference, since dinosaurs were able to attain body masses on land of up to 50 000 kg. We suggest that life history strategies and reproductive limitations may play a role here too. Whales are apparently less limited in reproductive turnover than terrestrial mammals of similar body size, and this may be due to the easier access to high-protein diets, allowing for proportionally lower costs of both gestation and lactation.

Acknowledgments. We thank Drs. D. Bruning, D. Carrier, V. Maiorana, D. Morse, and L. Van Valen for help in obtaining life history variables on birds, Drs. W. Coombs, M. Ramsey, and J. Waage for useful suggestions and additional references, J. Hunter and Drs. D. Carrier, J. Damuth, D. Fastovsky, M. Labarbera, V. Mairorana, J. Sepkoski, L. Van Valen and an anonymous reviewer for critical editorial comments on the manuscript, and P. Wilhelm and Drs. J. Schmidt and J. Sepkoski for statistical help and advice. Finally, thanks to Dr. M. Fortelius for his continuing advice and support. This project was supported in part by a Brown Biomedical Research Grant (B.R.S.G., no. PHS 2 507 RR07085-24) to the senior author, and by Brown University Independent Study student funds to the junior author.

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