Body mass of late Quaternary mammals

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Introduction

Body mass is the most obvious, and arguably, the most fundamental characteristic of an organism, impacting many important attributes of life history, ecology and evolution.� The range and mode of body mass for a taxonomic group reflects underlying allometeric, phylogenetic and ecological constraints.� Yet, how these factors and selective forces interact to determine the characteristic body sizes seen in animals is unclear and remains a major area of study in biology.

This paper documents the development of a body mass dataset created as part of a National Center for Ecological Analysis and Synthesis (NCEAS) working group.� Our purpose in compiling these data was to explore the body mass similarities and differences of mammals across the taxonomic hierarchy, broad geographic space, and evolutionary time.� We have used these data to compare, for example, the body mass distributions of terminal Pleistocene mammals on each continent prior to the arrival of man.� Our analyses suggest they were remarkably similar and that anthropogenic hunting activities, not climate change, resulted in the differences seen today (Lyons et al., *in revision*). In other work, we have investigated the heritability of body mass across the taxonomic hierarchy and across space and time.� We found a very high correlation of body mass among congeners, except for the very smallest size classes.� For those species under about 10g, body mass of sister species tends to be very diverse (Smith *et al, in revision*).� Moreover, the body mass patterns seen across the taxonomic hierarchy are also recapitulated across geographic space and evolutionary time.� The broad spectrum of body mass seen today was established early in the Cenozoic and has been maintained despite enormous taxonomic turnover.

Our dataset consists of the updated version of Wilson and Reeder�s (1993) taxonomic list of all known mammals of the world (N=4629 species) to which we added status, distribution, and body mass estimates compiled from the literature.� Mammals occurring on more than one continent have multiple records; continent-specific masses were used when available. Moreover, for four of the continents (Africa, North and South America and Australia), we included the mammalian species that went extinct at the late Pleistocene (an additional 230 species).� Overall, we have 5731 rows of data.� We defined �late Pleistocene as approximately 11 ka for Africa, North and South America, and at 50 ka for Australia, because these times predate anthropogenic impacts on mammalian fauna (e.g., Klein 1984; Martin 1984; Kurten 1988; Lessa and Farina 1996; Flannery and Roberts 1999; Martin and Steadman 1999 and Stuart 1999). About half the records in our dataset are derived from previous compilations (Silva and Downing 1995; Marquet and Cofre 1999; Jones et al. 2003); the remainder are largely drawn directly from the primary literature.�����

The dataset is fairly comprehensive for oceanic mammals, and for those occurring on four of the continents (Africa, Australia, South America, and North America), but is less complete for Eurasian and

insular species (Table 1). We have been able to obtain mass estimates for 4361 of the 5731 rows of data; 1372 are missing values. Most, if not all missing species are poorly studied and tend to be rare, cryptic or both.• Body mass was estimated using an algorithm that prioritized in the following order:• 1)• A gender-specific estimate obtained by averaging values reported from across geographic localities, these were then averaged to obtain an overall species value, 2) When no geographic information was provided, gender-specific values were averaged for an overall species body mass estimate, 3) If both male and female masses were not available, male mass was used preferentially, averaging over geographic localities if such information was available, 4) If only female body mass was available, it was used, again averaging over geographic localities as available. In no instance did we use generic means as a proxy for a species average.• Body mass estimates for extinct species were gathered from the primary literature, from personal communications, estimated from regressions of teeth measurements (e.g., Damuth and MacFadden 1990), or obtained from web databases.• The source for each datum is listed in the reference column of the dataset.• All extant mammalian orders are represented, and we include several archaic groups present in the late Pleistocene.• By compiling such data from geographically and historically isolated areas, we were able to compare similarities and differences in mammal body mass across continents differing in species composition, current and past environments and geographic history.• Moreover, we were able to examine the impact of early humans on patterns of mammalian diversity across disparate regions.

Because our studies have focused on broad macroecological patterns, we have ignored the often substantial geographic body mass variation that may exist for a species.• Estimates contained within this dataset thus represent a generalized species value, averaged across gender and geographic space.• Consequently, care should be taken if these values are used to represent species at a particular locality and/or time.

Metadata

Class I. Data Set Descriptors
A. Data set identity:
•••••••••••••• **Title**: Macroecological Database of Mammalian Body Mass
B. Data set identification code
•••••••••••••• **Suggested Data Set Identity Code**: MOM v3.3
C. Data set description
•••••••••••••• **Principal Investigators**:

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Abstract:
The purpose of this dataset was to compile body mass information for all mammals on Earth so that we could investigate the patterns of body mass seen across geographic and taxonomic space and evolutionary time. We were interested in the heritability of body size across taxonomic groups (How conserved is body mass within a genus, family and order?), in the overall pattern of body mass across continents (Do the moments and other descriptive statistics remain the same across geographic space?), and over evolutionary time (How quickly did body mass patterns iterate on the patterns seen today? Were the Pleistocene extinctions size specific on each continent and did these events coincide with the arrival of man?). These data are also part of a larger project that seeks to integrate body mass patterns across very diverse taxa (NCEAS Working Group on *Body size in ecology and paleoecology: linking pattern and process across space, time and taxonomic scales*). We began with the updated version of Wilson and Reeder's (1993) taxonomic list of all known Recent mammals of the world (N=4629 species) to which we added status, distribution, and body mass estimates compiled from the primary and secondary literature. Whenever possible, we used an average of male and female body mass, which was in turn averaged over multiple localities to arrive at our species body mass values. The sources are line referenced in the main dataset, with the actual references appearing in a table within the metadata. Mammals have individual records for each continent they occur on. Please note that our dataset is more than an amalgamation of smaller compilations. Although we relied heavily a dataset for Chiroptera by K.E. Jones (N=905), the CRC handbook of Mammalian Body Mass (N=688), and a data set compiled by for South America by P. Marquet (N=505), these total less than half the records in the current database. The remainder are derived from more than 150 other sources (see reference table). Furthermore, we include a comprehensive late Pleistocene species assemblage for Africa, North and South America and Australia (an additional 230 species). Late Pleistocene is defined as approximately 11 ka for Africa, North and South America, and at 50 ka for Australia, because these times predate anthropogenic impacts on mammalian fauna. Estimates contained within this dataset represent a generalized species value, averaged across gender and geographic space. Consequently, these data are not appropriate for asking population-level questions where the integration of body mass with specific environmental conditions is important. All extant orders of mammals are included, as well as several archaic groups (N=4859 species). Because some species are found on more than one continent (particularly Chiroptera), there are 5731 entries. We have body masses for the following: Artiodactyla (280 records), Bibymalagasia (2 records), Carnivora (393 records), Cetacea (75 records), Chiroptera (1071 records), Dasyuromorphia (67 records), Dermoptera (3 records), Didelphimorphia (68 records), Diprotodontia (127 records), Hydracoidea (5 records), Insectivora (234 records), Lagomorpha (53 records), Litopterna (2 records), Macroscelidea (14 records), Microbiotheria (1 record), Monotremata (7 records), Notoryctemorphia (1 record), Notoungulata (5 records), Paucituberculata (5 records), Peramelemorphia (24 records), Perissodactyla (47 records), Pholidota (8 records), Primates (276 records), Proboscidea (14 records), Rodentia (1425 records), Scandentia (15 records), Sirenia (6 records), Tubulidentata (1 record), and Xenarthra (75 records).

D. Keywords:

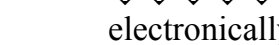
Keywords: body mass, extinct mammals, macroecology, taxonomy, late Quaternary

Class II. Research origin descriptors

A. Overall project description

Identity: NCEAS Working Group on *Body Size in Ecology and Paleoecology: Linking pattern and process across space, time, and taxonomic scale.*
Originator: Felisa A. Smith
Period of Study: 1999-continuing
Objectives: To understand the processes and factors which lead to the macroecological patterns seen across taxonomic and geographic space and through evolutionary time.
Abstract: This research project, initiated in 1999, endeavors to compile body mass, life history, geographic range, and other data for a broad range of taxonomic groups including plants, mammals, birds, reptiles, mollusks for use in investigating macroecological patterns. This work is the outcome of a working group funded by the National Center for Ecological Analysis and Synthesis.
Source(s) of funding: National Center for Ecological Analysis and Synthesis

B. Specific subproject description

Site description: Data were obtained from species from a variety of habitats, geologies, hydrologies, etc. Although this is a global database, entries are more comprehensive for oceanic species and those residing on North America, South America, Australia, and Africa. All mammals of the world, and their continental, status and taxonomic affiliations are included, regardless of whether a body mass estimate was obtained.
Experimental or sampling design: Most data were obtained from published literature sources. A few body mass values were obtained by examining museum specimens or by personal communication with scientists working on the species in question.
Research Methods:
 Field/Laboratory: Data were collected from published sources written by experienced mammalogists. A species specific body mass was obtained using an algorithm that prioritized the procedure in the following order: 1) A gender-specific estimate obtained by averaging male or female values reported from across different geographic localities, these were then averaged to obtain an overall species value, 2) When no geographic information was provided but gender-specific values were available, these were averaged for an overall species body mass estimate, 3) If both male and female masses were not available, male mass was used preferentially, averaging over geographic localities if such information was available, 4) If only female body mass was available, it was used, averaging over geographic localities as available. When museum records were utilized, averages were obtained for each gender across their range, and these were again averaged to obtain an overall species-specific value. The source of the value is line referenced in the dataset. In no instance did we use generic means as a proxy for a species average. Equal weight was given to male and female estimates; we did not use a weighted average to account for possible differences in sample size. For bats, if body mass estimates were not available for both females and males, female mass was used preferentially (i.e. the order of numbers 3 and 4 above were switched).
 Taxonomy: Taxonomy follows Wilson and Reeder (1993), as updated electronically (4 June 2002; *www.nmnh.si.edu/msw*),
Project Personnel: n/a

Class III. Data set Status and Accessibility

A. Status

Latest Update: April 20, 2003
Latest Archive date: April 20, 2003

Metadata status: April 22, 2003, metadata is current
Data verification: Data has undergone substantial data quality and assurance checking, though this is an on-going process.• Histograms of the body masses of each order were produced, and values at the tails were double-checked for accuracy.• When multiple sources of information were available for a species, or new sources encountered, we used those with higher sample sizes and gender-specific information.

B. Accessibility

Storage location and medium: Original data file exists on primary author•s personal computer in Microsoft Excel format.
Contact person: Felisa A. Smith, Department of Biology, University of New Mexico 87131, phone: 505.277.6725, fax: 505.277.0304, email: fasmith@unm.edu
Copyright restrictions: None
Proprietary restrictions: None
Costs: None, author believes scientific data should be free for scientific use.

Class IV. Data Structural Descriptors:

A. Data Set File

Identity: MOMv3.3.txt
Size: 5731 records, not including header row.
Format and Storage mode: Ascii text, tab delimited. No compression schemes used.
Header information: Headers are given here as header name followed by more information such as measurement units or other basic descriptor. More information on the variable definitions can be found in Section B, variable information. Continent (SA, NA, EA, insular, oceanic, AUS, AF), Status (extinct, historical, introduction, or extant), Order, Family, Genus, Species, Log Mass (grams), Combined Mass (grams), Reference.
Alphanumeric attributes: Mixed
Special characters/fields: -999 denotes lack of information for that field.
Authentication procedures: The number of records for each continent and for extant and extinct species should match the values reported in Table 1.• The following are sums (excluding missing values) for the overall numeric columns: Log Mass = 10,828.71; Combined Mass (g) = 879,113,624. Sums for log Mass (excluding missing values) by continent are:• AF = 1,839.66; AUS = 934.58; EA = 1560.16; Insular = 2,118.89; NA = 1,655.91; Oceanic = 439.14; SA = 2,280.37.

B. Variable definitions

Variable Name	Variable Definition	Units	Storage Type	Range Numeric Values (-999 not incl.)	Missing Value codes
Continent	Continent that a species resides on. If species resides on more than one continent, a continent specific body mass is reported when available.• Thus, some mammals have multiple entries. The division between North and South	N/a	Character	N/a	-999

	America occurs at the isthmus of Panama.				
Status	Whether species is currently present in the wild (extant); extinct as of late Pleistocene (extinct), extinct within the last 300 years (historical); or an introduction (introduction); Note these do not necessarily follow CITES or IUCN categories.	N/a	Character	N/a	-999
Order	Taxonomic order of species	N/a	Character	N/a	-999
Family	Taxonomic family of species	N/a	Character	N/a	-999
Genus	Taxonomic genus of species	N/a	Character	N/a	-999
Species	Species epithet	N/a	Character	N/a	-999
Log Mass	Log10 transformation of Combined Mass	Grams	Floating Point	0.26 to 8.28	-999
Combined Mass	Adult body mass averaged across males and females and geographic locations.	Grams	Floating point	1.8 to 190,000,000	-999
Reference	Reference source for body mass information and/or status for that species; the updated electronic version of Wilson and Reeder (1993)  (6 June 2002; *www.nmnh.si.edu/msw*) serves as the status reference for all extant species.	N/a	Alphanumeric	N/a	-999

C. Data set references

The numbers listed in the reference column of the MOMv3.3 dataset refer to the following citations:

Reference number	Citation
1	Anderson, E. 1984. Who  s who in the Pleistocene: A mammalian bestiary. In *Quaternary extinctions: a prehistoric revolution* (P.S. Martin and R.G. Klein, eds.), pp. 40-89. Tucson, AZ: University of Arizona Press.
2	Klein, R.G. 1984. Mammalian extinctions and stone age people in Africa. In *Quaternary extinctions: a prehistoric revolution* (P.S. Martin and R.G. Klein, eds.), pp. 553-573. Tucson, AZ: University of Arizona Press.
3	Flannery, T. and Schouten, P. 2001. *A gap in nature: discovering the world  s extinct*

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4	MacPhee, R.D.E. and Flemming, C. 1999. Requiem ternam: The last five hundred years of mammalian species extinctions. In *Extinctions in near time: causes, contexts, and consequences* (R.D.E. MacPhee, ed.), pp. 333-372. New York: Kluwer Academic/Plenum Press.
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Class V. Supplemental descriptors

A. **Data acquisition**

Data forms: n/a

□□□□□□□□□□□□□□ Location of completed data forms: n/a

B. Quality assurance/quality control procedures

Data were entered directly from source material into the computer file and values were double checked upon entry. After complete entry of data, data points were randomly selected and checked against original source material until approximately 50% of values had been checked against source material. After the initial data-checking phase was complete, the body mass of species within each mammalian order were plotted and values lying outside the bulk of the distribution were re-examined against the source material. If there was a discrepancy or if there was reason to believe the original data source may have contained an error, an attempt was made to find additional body mass estimates for the taxon.□ If values could not be reconciled, no body mass value was reported (i.e., initial value was replaced with □999).

C. Related material: n/a

D. Computer programs and data processing algorithms: n/a

E. Archiving: n/a

F. Publications and results:

To date, these data have been used in several manuscripts currently under review:

Ernest, S.K.M., Enquist, B.J., Brown, J.H., Charnov, E.L, Gillooly, J.F., Savage, V.W., White, E.P., Smith, F.A., Hadly, E.A., Haskell, J.P., Lyons, S.K., Maurer, B.A., Niklas, K.J., and Tiffney, B.□ Thermodynamic and metabolic effects on the scaling of production and abundance.□ *Nature*, in review.

Smith, F.A., Brown, J.H., Haskell, J.P., Lyons, S.K., Alroy, J., Charnov, E.L., Dayan, T., Enquist, B.J., Ernest, S.K.M., Hadly, E.A., Jablonski, D., Jones, K.E., Kaufman, D.M., Marquet, P.A., Maurer, B.A., Niklas, K.J., Porter, W.P., Roy, K., Tiffney, B., and Willig, M.R. Similarity of mammalian body size across the taxonomic hierarchy and across space and time. *American Naturalist, revision under review*

Lyons, S.K., Smith, F.A., and Brown, J.H. Of mice, mastodons, and men: human caused extinctions on four continents. *Evolutionary Ecology Research*, *in revision*.

G. History of data set usage

Data request history: The data have been disseminated among the ~20 members of the working group; additionally, we have provided it to a number of other researchers as requested. These projects are still in early stages of completion.

Data set update history:
������������ A major overhaul of the data set, which was formerly known as "MOM-mammals", occurred during June 2002. At this time, each value was double checked for accuracy and all entries were cross-checked against the Smithsonian website." A second overhaul occurred in October and November 2002, with the addition of continental affiliations for ~1300 mammals not included earlier, the inclusion of body mass estimates for a number of rare species, and the inclusion of all extinct mammals from the late Pleistocene on North America, South America, Africa and Australia." In October and November 2002, line by line error checking on the entire dataset was conducted by S.K.M. Ernest, S.K. Lyons and F.A. Smith. "A third major overhaul of the data occurred during February-April 2003 when the orders Chiroptera and Cetacea were added (thus making it a global database of all mammals), and a major literature search effort resulted in the inclusion of body mass values for many Eurasian and insular species."

Review history: n/a
Questions and comments from secondary users: n/a

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Table 1.&#65533; Continental affiliations of mammals included in dataset.

	Overall			Extant*			Extinct		
Continent	**Total spp**	**Total&#65533; with mass**	**Total missing mass**	**Total spp**	**Total with mass**	**Total missing mass**	**Total spp**	**Total with mass**	**Total missing mass**
Africa	1034	736	298	1017	719	298	17	17	0
Australia	346	338	8	278	270	8	68	67	1
Eurasia	1033	612	421	1027	608	419	6**	4	2
Insular* **	1484	954	530	1405	916	489	79**	38	41
North America	779	715	64	700	636	64	79	79	0
Oceanic	78	75	3	78	75	3	0**	0	0
South America	977	930	47	900	854	46	77	76	1
TOTAL	**5731**	**4361**	**1372**	**5405**	**4078**	**1327**	**326**	**281**	**45**

*Introductions are not excluded from the extant total.
**Only a small number of extinct species from the terminal Pleistocene are included; no effort was made to develop a comprehensive late Pleistocene faunal list for Eurasia, insular or oceanic species. However, the species list *is* comprehensive for Africa, Australia, North and South America.
***A small number of species that primarily occur on North or South America, but are also found on adjacent islands, may be missing records in the insular category.

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