

Body size in mammalian paleobiology

Estimation and biological implications

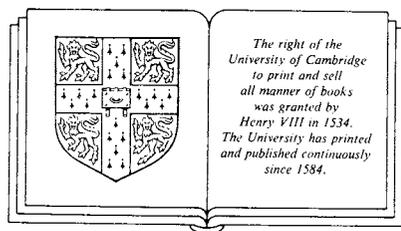
Edited by

JOHN DAMUTH

University of California, Santa Barbara

BRUCE J. MACFADDEN

Florida Museum of Natural History



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1

Introduction: body size and its estimation

JOHN DAMUTH AND BRUCE J. MACFADDEN

Body size in biology and paleobiology

In recent years there has been growing interest in the biological implications of body size in animals. Body mass is correlated with a host of metabolic and physiological variables; with ecologically relevant characteristics such as life history traits, diet, population density, population growth rate, home range size, and behavioral adaptations; and with larger-scale patterns in community structure and biogeography (Brown & Maurer 1989; Calder 1984; Damuth 1981, 1987; Eisenberg 1981, this volume; Emmons, Gautier-Hion, & Dubost 1983; Fleming 1973; Jarman 1974; McMahon & Bonner 1983; McNab, this volume; Peters 1983; Schmidt-Nielsen 1984).

At the same time, there has been increasing use of body size in a wide range of applications in vertebrate paleobiology. Studies of functional morphology often employ measurements that must be related to body size before functional interpretations can be applied to fossil species (e.g., Emerson 1985; Gantt 1986; Kay 1975; Thomason 1985). Inferences concerning the metabolism and energetics of fossil vertebrates often depend critically on body mass estimates of fossil species, and body size has figured prominently in evolutionary explanations of the evolution of vertebrate metabolic physiology (McNab 1987; Thomas & Olson 1980; Tracy, Turner, & Huey 1986; Turner & Tracy 1986). The evolution of body proportions and scaling relationships themselves, and the resulting functional implications, form an important area of paleobiological research (Fortelius 1985, this volume; Gingerich & Smith

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1985; Gould 1974, 1975; Jerison 1973; Kay 1975; Martin & Harvey 1985; Radinsky 1978; Scott 1985).

Body size plays a major role in studies of mammalian paleoecology. In fact, based upon modern knowledge, a mammal's body size may be the most useful *single* predictor of that species' adaptations. In addition to allowing reconstruction of trophic role and habitat preference, relationships between body size and ecological factors help us to make inferences about many more complex ecological characters of fossil mammals. For example, interpretations of life history characters and social behavior have played a part in explanations of the evolution of horns in ungulates (Janis 1982) and explanations of megafaunal susceptibility to extinction (Kiltie 1984; McDonald 1984). Faunal and community structure can be characterized in part by body size range and distribution, and has been used in studies of community evolution and energetics, and in the interpretation of climate and ancient vegetation (Andrews & Nesbit Evans 1979; Andrews, Lord, & Nesbit-Evans 1979; Collinson & Hooker 1987; Farlow 1976, 1987; Fleagle 1978; Janis 1982, 1984; Legendre 1986; Van Couvering 1980; Van Valkenburgh 1985, 1988).

The mammalian fossil record shows many examples of body size change within lineages, including the sometimes spectacular cases of gigantism and dwarfism on islands. Explanation of the island trends is still a challenge (Geist 1987; Hooijer 1967; Marshall & Corruccini 1979; Maiorana, this volume; Martin, this volume; Roth, this volume; Sondaar 1977, 1987; Thaler 1973).

Because body size is a character exhibited by every species, it potentially has an important role to play in studies of the tempo and mode of evolution (e.g., Gingerich 1976; Gould & Eldredge 1977; MacFadden 1987). Cope's rule – that size tends to increase within lineages or taxa – is one of the most widely discussed general macroevolutionary patterns (though until recently there were few studies that used actual body-mass estimates in quantitative studies of the phenomenon) (Gould 1988; MacFadden 1987; Newell, 1949; Rensch, 1959; Stanley 1973). At least the Pleistocene and Cretaceous mass extinction events have been notably size-selective among terrestrial vertebrates, affecting the larger species more strongly (Martin & Klein 1984; Padian & Clemens 1985). It has been suggested that frequent “megafaunal” extinctions or periods of size reduction may be characteristic of fossil vertebrate faunas, and may happen more locally and on a different time scale than the extinctions of the proposed long-term (i.e., 26 million years [myr]) global cycle

(Bakker 1977; Prothero 1985; Raup & Sepkoski 1984; Webb 1984). The presumed different extinction probabilities (and other ecological differences) exhibited by large and small vertebrates have implications for explaining the sorting of species in mammalian clades, but as yet this has not received much attention (but see Martin, this volume; Stanley 1973).

Finally, it is clear that many taphonomic processes operate upon vertebrate remains in a size-selective or size-dependent way (Behrensmeyer & Hill 1980; Behrensmeyer, Western & Dechant Boaz 1979; Voorhies 1969). Knowledge of body size can thus be a useful tool in the interpretation of mammalian fossil assemblages (Badgley 1986; Damuth 1982; Wolfe 1975).

Rationale and organization of this book

It may seem from the preceding sketch that body mass, having already been so widely used, must not be a problematic character to infer for fossil species. Certainly, size would appear to be one of the most straightforward characters that a fossil could exhibit. But the picture of satisfying accuracy and general compatibility that this widespread use suggests is misleading. We cannot measure body mass directly for fossil species, and must derive estimates from skeletal remains that are usually fragmentary and incomplete. Some taxa are represented by better fossil material than are others, and some have no living representatives. Some groups, such as the primates, have received far more detailed attention and have been analyzed by more sophisticated techniques than have others (e.g., Jungers 1985, this volume; Ruff, this volume). Estimates for species of different taxa typically derive from different regressions or other estimator techniques, and are based on different body parts. Studies vary considerably in the degree of precision they demand of body mass estimates. Some require only that relative masses be correct, some require only species averages, and some require accurate estimates for particular fossil specimens.

Workers have tended to develop and employ estimation techniques suited primarily to the study at hand, and intended to yield the level of accuracy that a particular study requires. Often, a skeletal element well represented among the fossil species is measured in a group of extant relatives and regressed upon body mass; a high correlation coefficient is taken as a sign of success and the regression equation is used to estimate fossil body masses. Too little attention has been paid in the

past to the choice of the reference sample of modern species, and to the range of probable error in the resulting estimates. As is shown by some of the contributions in this volume, regressions involving characters commonly used to estimate body masses of fossil species do not always produce what would be satisfactory results, even when reapplied to the extant species upon which the regression is based.

We sought several different kinds of chapters for this book. Some contributors work primarily with the modern fauna, investigating the significance of size. Others are here primarily concerned with the techniques of estimating mass in fossil mammals accurately. We decided to include this range of topics, so that there would be in one volume a compendium of techniques and basic practical information, and a source of ideas (including caveats) and signposts to the literature about the various applications of body size in paleobiological studies. The tables of Chapter 16 (Appendix) combine in one place, for the reader's convenience, the regression equations discussed in the preceding chapters. We have also included here additional regression equations provided by some authors, which are based on characters that may not be as reliable as those that the authors have judged to yield the "best" estimates of body mass for a particular group. Nevertheless, they may be of some value in cases where the "best" characters are not preserved for the fossils in question. We warn the reader not to use the equations of Chapter 16 uncritically, and also not to bypass the reading of the relevant chapter.

General conclusions

The general theme that emerged at the Gainesville workshop, and that runs through book, is that *body mass estimation and functional morphological interpretation are not separable*. The reason is that, in using data from modern species to derive estimation equations or other means of estimation, one must choose a set of modern species that exhibit a similar relationship between body parts and body mass. This requires identification of broad functional/morphological groupings, which may or (at least as often) may not fall within traditional taxonomic lines (Damuth; Fortelius; Janis; Van Valkenburgh, this volume). As Grand (this volume) reminds us, "body mass" is a composite character, whose components differ in animals pursuing different modes of life. The different ways the same anatomical element may be related to overall mass in different species can to some extent be predicted from functional considerations.

An analogous statement can be made for interpretations: Dividing the modern fauna into functional groups improves predictive power of body mass for both physiological and ecological variables (Eisenberg; McNab, this volume). In particular, diet is related to much of the variation found in both kinds of variables.

Practical conclusions and caveats

A number of general practical conclusions, recommendations, and cautions concerning body mass estimation in fossil mammals can be abstracted from the conference proceedings and the papers published here:

1. Estimates based upon certain limb measurements, if available, appear to be substantially more reliable than those based on cranial or dental measurements. However, much more comparative work needs to be done on the scaling of postcranial elements in modern forms before we can use limb measurements for most groups. Proximal limb elements are more reliable correlates of body mass than are distal elements in ungulates and primates (Ruff; Scott, this volume). The problem with using fossil limb elements, however, is that they first must be taxonomically assignable.
2. Because of their identifiability and preservability, teeth will continue to be of importance in body mass estimation. However, dental measures alone, even when restricted to functionally similar groups, may not be accurate enough for all purposes. Percent standard errors below 30 are rare in the dental regressions reported here.
3. In dealing with taxa with high ontogenetic dental variation (e.g., high-crowned horses), the worker must carefully consider which wear stage(s) should be used to predict body mass. Such variation differs among taxa and among different dental measures and among different teeth within the same species.
4. For ungulates, tooth length measurements are generally better predictors than widths or areas, as the latter vary more with diet.
5. Techniques using more than one morphological variable (e.g., multiple regression) can increase accuracy of predictions when feasible and appropriate. Particularly, combinations of dental and postcranial measures, including body length, can result in relatively accurate estimates for well-represented species (percent standard error < 30).

6. As in any other statistical prediction procedure, it is unwise to extrapolate regression predictions beyond the range of the available data for modern forms. There is no guarantee that relationships holding within this range will be applicable to smaller or larger forms (e.g., MacFadden & Hulbert, this volume). In such cases use of a more general regression (such as “all ungulate” or “all mammal” regressions), with the resulting loss of precision, may be preferable. This consideration adds particular uncertainty to our estimates of the very largest fossil species, which may lie beyond the size range of any living mammal; our sample of living megafauna is also highly restricted and composed of species exhibiting only a few body forms.
7. The use of general regression equations, even those with small standard errors, does not guarantee accuracy for every species. In particular, care should be taken to recognize fossil species that may be aberrant in one or more characters that for most species might yield good estimates (e.g., the enlarged third molars of suids, or the enlarged second molars of amynodonts).
8. Estimates remain only estimates. There are certainly numerous unrecognized sources of error for fossil species. The statistical errors reported here for regressions on living forms are underestimates of the actual inaccuracy in estimates for extinct species. To the extent that fossil species deviate from the average of the modern population used, inaccuracy will increase.

Future research directions

Some directions for future research in mammalian body-mass estimation are also evident. The need for broader investigation of the scaling of postcrania has already been mentioned. Craniodental and postcranial scaling relationships analogous to those presented here are unknown for many extant mammalian groups. These include most rodent taxa, insectivores, small marsupials, and various “oddball” groups such as the edentates. We need further refinement of functional groups among all of the mammals, as this could dramatically increase the accuracy of our predictions. Finally, there are extinct groups, such as the North American Merycoidodontidae (oreodonts), that exhibit what appear to be unique body proportions and craniodental relationships, but for which we have complete material for some members. Using the well-represented species, reliable body-mass estimates may be obtainable, and from these species correction factors could be derived for use on

the more fragmentary material representing the other members of the group.

In summary, we are just beginning to develop the empirical base and the analytical tools necessary for reliable reconstruction of the body masses of fossil species. Further refinement of body mass estimation techniques will make possible the reconstruction of a wide range of biological aspects of fossil species and faunas, and an exciting new dimension of time can be added to ecological and evolutionary studies that heretofore have had to rely primarily on patterns observed in the extant biota.

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