

# The size of the largest marsupial and why it matters

Stephen Wroe<sup>1\*</sup>, Mathew Crowther<sup>1</sup>, Joe Dortch<sup>2</sup> and John Chong<sup>1</sup>

<sup>1</sup>School of Biological Sciences A08, University of Sydney, Sydney, NSW 2006, Australia

<sup>2</sup>Archaeology, A14, University of Sydney, Sydney, NSW 2006, Australia

\* Author for correspondence (swroe@bio.usyd.edu.au).

Recd 22.06.03; Accptd 04.08.03; Online 18.09.03

**We show that at 2786 kg, the largest known marsupial, *Diprotodon optatum*, was much larger than has previously been suggested. Our results contradict the conclusion that the maximum attainable body mass of an Australian marsupial has been constrained by low productivity.**

**Keywords:** body mass; *Diprotodon optatum*; productivity

## 1. INTRODUCTION

Body mass is fundamental to interpretations of biological patterns and its reliable prediction for fossil species has become increasingly important in the analysis of past ecosystems (Janis 1990; Van Valkenburgh 1990; Alexander 1998; Fariña *et al.* 1998; Wroe *et al.* 2003a). Historically, estimates for body mass in fossil taxa have been determined subjectively, often producing widely divergent figures that can vary by an order of magnitude (Wroe 2002; Wroe *et al.* 2003a). Consequently, palaeoecologists have increasingly turned to quantitative approaches. Empirical methods, commonly based on regressions of craniodental and body mass data in extant taxa, are now available for many fossil placentals (Janis 1990; Van Valkenburgh 1990; Christiansen 1999a). In recent years, predictive equations for fossil marsupials have also been developed (Myers 2001; Wroe *et al.* 2003a). However, because living marsupials do not exceed *ca.* 85 kg, the efficacy of methods derived from craniodental data is questionable where this figure is much surpassed (Wroe *et al.* 2003a). This is especially problematic regarding the largest known marsupial, *Diprotodon optatum*, and the body mass of this species is of particular significance because it strongly impacts on interpretations of Australian prehistory and ecology (Milewski & Diamond 2000; Burness *et al.* 2001; Wroe *et al.* 2003a,b).

A recent study wherein the body masses of the single largest herbivore and carnivore species on various landmasses were regressed against landmass area, found that *D. optatum* was unexpectedly small (Burness *et al.* 2001). This finding incorporated a subjectively determined estimate for mean body mass of 1175 kg. Burness *et al.* (2001) concluded that uniquely low productivity had probably constrained the maximal body mass attainable by an Australian marsupial, a proposition first made by Flannery (1994), who further posited that low productivity had generally limited mammalian body masses on the island conti-

nent. Body mass also correlates negatively with population size and fecundity, both of which impact on assessments of vulnerability to climatically or anthropogenically driven extinction (Johnson 2002).

Subjective inferences of body mass and comparisons of general morphology in *D. optatum* range widely, from comparisons with bullocks (Long *et al.* 2003) to rhinoceroses (Archer *et al.* 1994). A mounted Australian Museum specimen has a head-body length of 3.7 m (A. Musser, personal communication). In life, this animal would have exceeded 4 m because cartilaginous tissue, which is lost in fossils, amounts to *ca.* 20% of pre-sacral vertebral column length (Finch & Freedman 1986). However, even 3.7 m exceeds the head-body length of any extant bovid (Nowak & Paradiso 1983). *Diprotodon* was massive, and *Hippopotamus* or rhinoceros species are more appropriate analogues. Maximal head-body length and body mass in the hippopotamus (*Hippopotamus amphibius*) are 4.6 m and 4500 kg, respectively (Nowak & Paradiso 1983). For the largest rhinoceros (the white rhinoceros, *Ceratotherium simum*), these dimensions are 3.77 m and 3600 kg (Groves 1972). The mean body masses are 1405 kg for *H. amphibius* (Smithers 1983) and 2000 kg for *C. serum* (Bourlière 1965). With a mean body mass of 1000 kg, the black rhinoceros, *Diceros bicornis*, is closest to the estimate used by Burness *et al.* (2001). This smaller species has a head-body length of 2.80–2.90 m, and a maximum body mass of 1300 kg (Happold 1987; Hillman-Smith & Groves 1994).

## 2. MATERIAL AND METHODS

Body mass predictions founded on minimum mid-shaft circumferences of the femur and humerus ( $C_{h+f}$ ) offer greater accuracy than those using craniodental data and are less constrained by phylogenetic differences (Anderson *et al.* 1985). To estimate mean body mass in *D. optatum*, we measured  $C_{h+f}$  in 18 quadrupedal marsupials of known body mass and combined these data with those taken for 32 placentals that ranged up to 5879 kg (Anderson *et al.* 1985; see electronic Appendix A available on The Royal Society's Publications Web site). We then generated a predictive equation using Model I regression and holding body mass as the dependent variable (figure 1). A smearing estimate (SE) was calculated to correct log-transformed results for transformation bias (Smith 1993). To test for phylogenetic effects, we also compared the relationship between  $C_{h+f}$  and body mass in 17 quadrupedal marsupials with that of 15 placentals within the same size range (less than 44 kg). Slopes derived from the regressions of log-transformed marsupial and placental data were compared using Student's *t*-test (Zar 1984). Our estimate of mean body mass in *D. optatum* ( $n = 17$ ; see electronic Appendix B) was compared with predicted maximal mean body mass (MMBM) for endothermic herbivores based on landmass area, i.e. MMBM (endothermic herbivore) =  $0.47 \times (\text{landmass area})^{0.52}$  (Burness *et al.* 2001).

## 3. RESULTS

The mean  $C_{h+f}$  for *D. optatum* was 530 mm (s.e.m. = 1.05). At 2786 kg, our resultant prediction of mean body mass greatly exceeds that of previous estimates (95% CI of 3417 kg to 2272 kg). The average  $C_{h+f}$  in *D. optatum* was much larger than that of the two closest individual extant placentals, an *H. amphibius* ( $C_{h+f} = 417$  mm, body mass = 1950 kg) and an American bison (*Bison bison*) ( $C_{h+f} = 359$  mm, body mass = 1179 kg). This is also much greater than mean  $C_{h+f}$  for *C. simum* (455 mm,  $n = 7$ ; see Christiansen 1999b), an animal with an average adult body mass of 2000 kg.

Slopes were significantly different between marsupials and placentals with masses of less than 44 kg ( $t = 3.389$ , d.f. = 29,  $p < 0.005$ ). Because the slope for marsupials was

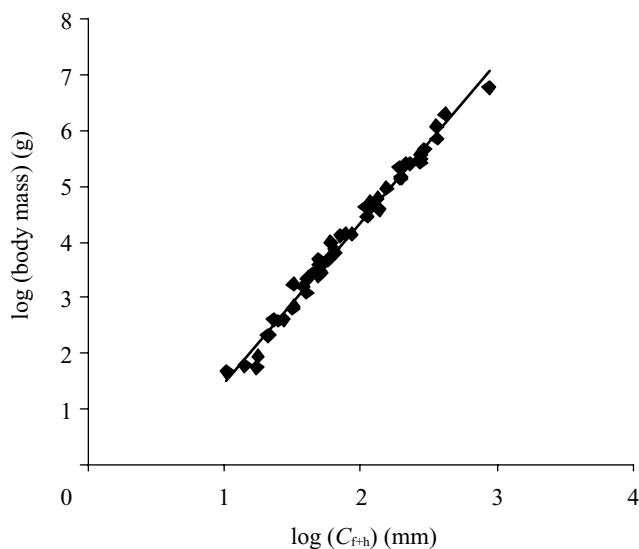


Figure 1. Regression of body mass with minimum circumferences of the humerus and femur ( $C_{f+h}$ ) in 32 placental and 18 marsupial quadrupeds;  $\log(\text{body mass}) = -1.42 + 2.89 \log(C_{f+h})$ ;  $r^2 = 0.99$ .

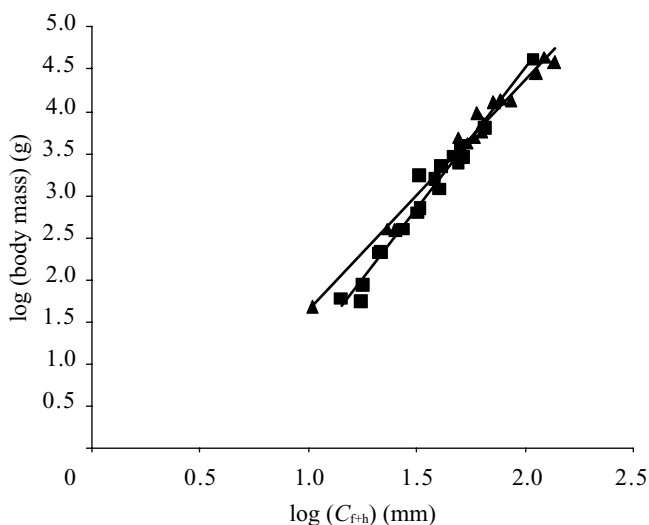


Figure 2. Regressions of body mass with minimum circumferences of the humerus and femur ( $C_{f+h}$ ) for 18 marsupials (squares) and 15 placentals (triangles), all with body masses of less than 44 kg. The slope is significantly greater for marsupials (3.32) than for placentals (2.74);  $r^2$  values are 0.97 and 0.99, respectively.

higher (3.32 versus 2.74), we infer that methods incorporating data from placentals, such as those presented here, may underestimate body mass in marsupials (figure 2).

The predicted MMBM for an Australian endothermic herbivore based on landmass area (7 682 000 km<sup>2</sup>) was 1788 kg. Marsupials consume *ca.* 20% less food than placentals of equal body mass (Burness *et al.* 2001). Correcting for this lower food intake gives a predicted MMBM of 2235 kg for Australian marsupials. After allowing for lower consumption, *D. optatum* is 25% larger than expected. Operating on the same premise, consideration of 95% confidence limits places the mean body mass in *D. optatum* at between 53% and 2% higher than predicted on the basis of landmass area.

#### 4. DISCUSSION

We conclude that body mass in the Late Pleistocene giant, *D. optatum*, has previously been underestimated. These findings contradict the assertion that uniquely low productivity has constrained the MMBM attainable by Australian marsupials, but marginally strengthen the correlation between MMBM of endothermic herbivores and landmass area ( $r^2$  changes from 0.74 to 0.75).

The relationship between productivity and body mass is not necessarily simple or linear. Large body mass can be a response to highly seasonal, relatively unproductive conditions (Owen-Smith 1988). Similarly, the relationship between species richness and productivity can be linear, bimodal or unimodal (Wroe 2002). Discovering whether productivity or other uniquely Australian influences have more generally limited the body masses of the continent's marsupials will require further empirical tests.

#### Acknowledgements

Funding has been provided to S. Wroe through a U2000 Postdoctoral Research Fellowship (University of Sydney) and from the Institute of Wildlife Research (University of Sydney). For comment on earlier drafts the authors thank G. Blackwell, C. Dickman, R. Fullagar, A. Milewski, F. Seebacher and R. Shine.

- Alexander, R. M. 1998 All-time giants: the largest animals and their problems. *Palaeontology* 4, 1231–1245.
- Anderson, J. F., Hall-Martin, A. & Russell, D. A. 1985 Long-bone circumference and weight in mammals, birds, and dinosaurs. *J. Zool. (Lond.)* 207, 53–61.
- Archer, M., Hand, S. J. & Godthelp, H. 1994. In *History of the Australian vegetation* (ed. R. S. Hill), pp. 80–103. Cambridge University Press.
- Bourlière, F. 1965 Densities and biomass of some ungulates in Eastern Congo and Rwanda with notes on population structure and lion/ungulate ratios. *Zool. Afr.* 1, 99–107.
- Burness, G. P., Diamond, J. & Flannery, T. F. 2001 Dinosaurs dragons, and dwarfs: The evolution of maximal body size. *Proc. Natl Acad. Sci. USA* 98, 14 518–14 523.
- Christiansen, P. 1999a What size were *Arctodus simus* and *Ursus spelaeus* (Carnivora: Ursidae)? *Ann. Zool. Fenn.* 36, 93–102.
- Christiansen, P. 1999b Scaling of mammalian long bones: small and large animals compared. *J. Zool. (Lond.)* 247, 333–347.
- Fariña, R. A., Vizcaino, S. F. & Bargo, M. S. 1998 Bodymass estimations in Lujanian (Late Pleistocene–Early Holocene of South America) mammal megafauna. *Mastozoöl. Neotrop.* 5, 87–108.
- Finch, M. E. & Freedman, L. 1986 Functional morphology of the vertebral column of *Thylacoleo carnifex* Owen (Thylacoleonidae: Marsupialia). *Aust. J. Zool.* 34, 1–16.
- Flannery, T. F. 1994 *The future eaters*. Sydney: New Holland Publishers.
- Groves, C. P. 1972 *Ceratotherium simum*. *Mamm. Species* 8, 1–6.
- Happold, D. C. C. 1987 *The mammals of Nigeria*. Oxford University Press.
- Hillman-Smith, A. K. K. & Groves, C. P. 1994 *Diceros bicornis*. *Mamm. Species* 455, 1–8.
- Janis, C. M. 1990 Correlation of cranial and dental variables with body size in ungulates and macropodoids. In *Body size in mammalian paleobiology* (ed. J. Damuth & B. J. MacFadden), pp. 255–300. Cambridge University Press.
- Johnson, C. N. 2002 Determinants of loss of mammal species during the late Quaternary 'megafauna' extinctions: life history and ecology, but not body size. *Proc. R. Soc. Lond. B* 269, 2221–2227. (DOI 10.1098/rspb.2002.2130.)
- Long, J., Archer, M., Flannery, T. & Hand, S. 2003 *Prehistoric mammals of Australia and New Guinea*. Sydney: UNSW Press.
- Milewski, A. V. & Diamond, R. E. 2000 Why are very large herbivores absent from Australia? A new theory of micronutrients. *J. Biogeogr.* 27, 957–978.
- Myers, T. J. 2001 Marsupial body mass prediction. *Aust. J. Zool.* 49, 99–118.
- Nowak, R. M. & Paradiso, J. N. 1983 *Walker's mammals of the world*, vol. II. 4th edn. Baltimore, MD: John Hopkins University Press.
- Owen-Smith, R. N. 1988 *Megaherbivores: the influence of very large body size on ecology*. Cambridge University Press.

- Smith, R. J. 1993 Logarithmic transformation bias in allometry. *Am. J. Phys. Anthropol.* **90**, 215–228.
- Smithers, R. H. N. 1983 *The mammals of the Southern African sub-region*. Pretoria University Press.
- Van Valkenburgh, B. 1990 Skeletal and dental predictors of body mass in carnivores. In *Body size in mammalian paleobiology* (ed. J. Damuth & B. J. MacFadden), pp. 181–205. Cambridge University Press.
- Wroe, S. 2002 A review of terrestrial mammalian and reptilian carnivores ecology in Australian fossil faunas and factors influencing their diversity: the myth of reptilian domination and its broader ramifications. *Aust. J. Zool* **50**, 1–24.
- Wroe, S., Myers, T. J., Seebacher, F., Kear, B., Gillespie, A., Crowther, M. & Salisbury, S. 2003a An alternative method for predicting body mass: the case of the Pleistocene marsupial lion. *Paleobiology* **29**, 404–412.
- Wroe, S., Field, J., Fullagar, R. & Jermiin, L. 2003b Megafaunal extinction in the Late Quaternary and the global overkill hypothesis. *Alcheringa* (In the press).
- Zar, J. H. 1984 *Biostatistical analysis*. Englewood Cliffs, NJ: Prentice-Hall.

Visit <http://www.pubs.royalsoc.ac.uk> to see electronic appendices to this paper.