Body Size and Risk of Extinction in Australian Mammals

MARCEL CARDILLO* AND LINDELL BROMHAM

Department of Zoology and Entomology, University of Queensland, Brisbane 4072, Australia

---

Abstract: *The link between body size and risk of extinction has been the focus of much recent attention. For Australian terrestrial mammals this link is of particular interest because it is widely believed that species in the intermediate size range of 35–5500 g (the "critical weight range") have been the most prone to recent extinction. But the relationship between body size and extinction risk in Australian mammals has never been subject to a robust statistical analysis. Using a combination of randomization tests and phylogenetic comparative analyses, we found that Australian mammal extinctions and declines have been nonrandom with respect to body size, but we reject the hypothesis of a critical weight range at intermediate sizes. Small species appear to be the least prone to extinction, but extinctions have not been significantly clustered around intermediate sizes. Our results suggest that hypotheses linking intermediate body size with high risk of extinction in Australian mammals are misguided and that the focus of future research should shift to explaining why the smallest species are the most resistant to extinction.*

Tamaño del Cuerpo y Riesgo de Extinción en Mamíferos Australianos

Resumen: *El vínculo entre el tamaño del cuerpo y el riesgo de extinción ha sido el centro de mucha atención reciente. Para los mamíferos terrestres australianos este vínculo es de particular interés debido a que se cree ampliamente que las especies en un rango intermedio de tamaño de 35–5500 g (el rango de peso crítico) ha sido el más susceptible a extinciones recientes. Sin embargo, la relación entre extinciones, el tamaño y el riesgo de extinción en mamíferos australianos nunca ha sido sometida a un análisis estadístico robusto. Usando una combinación de pruebas aleatorizadas y análisis filogenéticos comparativos, encontramos que las extinciones y disminuciones de mamíferos australianos han sido no aleatorias con respecto al tamaño del cuerpo, pero rechazamos la hipótesis de un rango crítico a tamaños intermedios. Las especies pequeñas aparentan ser las menos susceptibles de extinción, pero las extinciones no se han agrupado significativamente alrededor de tamaños intermedios. Nuestros resultados sugieren que la hipótesis que vincula el tamaño intermedio de cuerpo con un alto riesgo de extinción en mamíferos australianos está mal planteada y que el centro de la investigación a futuro deberá enfocarse a explicar el porqué las especies más pequeñas son las más robustas a la extinción.*

Introduction

Some taxonomic groups have suffered higher rates of recent extinctions than others, suggesting that certain heritable traits may predispose species to becoming endangered and extinct (Bennett & Owens 1997; Russell et al. 1997; Purvis et al. 2000). Among the traits implicated are population variability, reproductive rate, population density, trophic level, and dispersal ability (Terborgh & Winter 1980; Karr 1982; Pimm et al. 1988; Gaston & Blackburn 1995; Lawton 1995; Bennett & Owens 1997). Because many of these traits correlate with body size, and body size is more reliably measured and available for a greater range of species, the association between body size and extinction risk has been the focus of much recent attention. Many studies suggest that larger-bodied species are more extinction-prone than smaller species (Wilcox 1980; Karr 1982; Gaston & Blackburn 1995; Ben-

*email mcardillo@zoology.uq.edu.au

Paper submitted July 5, 2000; revised manuscript accepted February 14, 2001.

nett & Owens 1997). There are exceptions (Pimm et al. 1988; Bennett & Owens 2000), however, and the precise nature of the relationship between body size and extinction risk is still poorly understood (Lawton 1995).

Australian mammals are an ideal group with which to explore the link between body size and extinction risk for two reasons. First, Australia has suffered a higher rate of mammal extinctions than any other continent in the past 200 years. Seventeen species of Australian terrestrial mammals have gone extinct, representing nearly half of the world's recent mammal extinctions (Short & Smith 1994). Second, the link between body size and extinction risk is of particular interest in Australian mammals, because it appears that extinctions have been biased with respect to body size in an unusual way. Burbidge and McKenzie (1989) observed that most of the recently extinct species of nonvolant, terrestrial mammals in Australia fall within an intermediate body weight range of 35–5500 g, which they termed the "critical weight range" (CWR), whereas smaller and larger species have been relatively unaffected. The CWR pattern has become widely accepted: it is discussed in the introduction to the major reference work on Australian mammals (Strahan 1995), and it has generated several hypotheses that explicitly link high extinction risk to intermediate body size. For example, it has been suggested that a combination of high daily metabolic requirements and low mobility may leave medium-sized species more vulnerable (Burbidge & McKenzie 1989; Morton 1990) and that medium-sized species fit the preferred prey-size range of introduced predators (Short & Turner 1994; Smith & Quin 1996).

It is surprising, therefore, that the CWR pattern has never been tested within a rigorous statistical and phylogenetically explicit framework. This is important because it is possible that the pattern is simply an artifact of the underlying frequency distribution of species' body sizes. Because most Australian nonvolant terrestrial mammals (128 out of 210 species) fall within the critical weight range of 35–5500 g (Fig. 1), most extinct species would be expected to fall within this range even if extinction risk is random with respect to body size. Furthermore, even if extinct species are biased toward a certain size class, this may not be due to a direct effect of body size on extinction risk; phylogenetic biases could create an incidental association. Geographic biases could have the same effect. The arid interior of the Australian continent has suffered a higher rate of mammal extinctions than the mesic regions (Short & Smith 1994), so if the representation of body sizes or phylogenetic groups differs between the arid and mesic zones, a spurious association between body size and extinction risk may result.

We present a test of the critical-weight-range hypothesis, with the aim of clarifying the link between body size and extinction risk in the Australian terrestrial mammal fauna. We considered extinction the endpoint on a continuum of rarity, so we analyzed patterns both for recently extinct species and for species highly threatened with extinction. We combined a null-model approach and phylogenetic comparative methods to determine (1) whether extinct and endangered species are a nonrandom subset of the continental fauna with respect to body size, and, if so, whether medium-sized species are the most vulnerable; (2) whether the body-size bias in extinctions is due to confounding phylogenetic effects; and (3) whether the body-size bias in extinctions is due to confounding geographic effects.

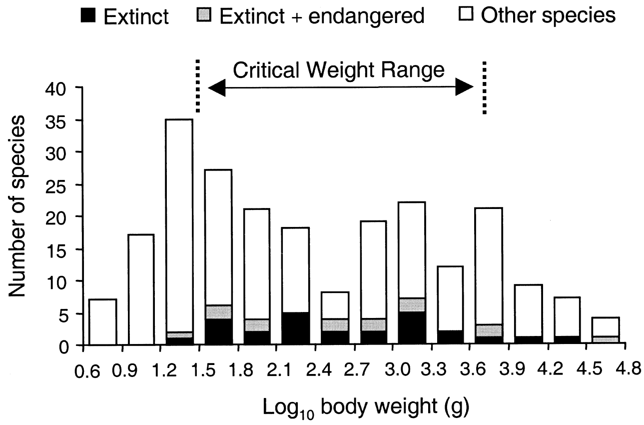

Figure 1. Body-size frequency distribution of the Australian terrestrial mammal fauna, with distributions for the 25 extinct species and 41 extinct + endangered species superimposed (see text for definitions).

Methods and Results

Data

We restricted our analysis to nonvolant terrestrial native mammals of mainland Australia, including Tasmania. We did not include the dingo or other recently introduced species. We did not include the two island endemic species, the Kangaroo Island dunnart (*Sminthopsis aitkeni*) and Bramble Cay melomys (*Melomys rubicola*), because their susceptibility to extinction may be heavily influenced by island effects such as small geographic range, lack of immigration from other populations, or absence of introduced predators. Mean adult body sizes were compiled from Strahan (1995) and additional primary sources. Each species was assigned to a category of extinction risk following Strahan (1992, 1995): 5, extinct or probably extinct; 4, endangered; 3, possibly endangered; 2, vulnerable; 1, secure or probably secure. We considered a species recently extinct if it had disappeared from a recorded mainland or Tasmanian distribution within the last 200 years. We counted as extinct those species previously found on the mainland but now persisting only on offshore islands. Under this classification, 25 species were counted as extinct (category 5) and 41 species as either extinct or endangered (categories 4 and 5). In addition, we compiled lists of species occurring (or formerly occurring) in the arid and mesic zones and assigned separate arid and mesic extinction-risk classifications for each species based on its status within each zone. The boundary between the two zones was the 500-mm isohyet, following Johnson et al. (1989).

Tests for Nonrandom Body-Size Distributions in Extinct and Endangered Species

If extinctions have selectively affected species in the critical weight range, the 25 extinct species should be more clustered toward intermediate body sizes than expected by chance, with smaller and larger species relatively underrepresented. To test this, we constructed a null distribution of body sizes for extinct species. We sampled 25 species at random from the continental species pool and recorded the mean, mode, maximum, minimum, first and third quartiles, interquartile range, and range of the log-transformed body sizes. This was repeated 2000 times, and we compared the parameters of the observed body-size distribution of extinct species with the resulting null distributions to obtain exact p values. We repeated this for the 41 extinct and endangered species and for the arid- and mesic-zone faunas separately.

The randomization tests showed that extinct species were not a random subset of the continental fauna with respect to body size (Table 1). The interquartile range of body sizes of extinct species was significantly narrower than expected by chance, and the minimum, first quartile, and mode were significantly higher than expected. This indicates that small species are underrepresented among the extinctions. The third quartile and maximum were no different than expected by chance. Therefore, these results reject the CWR hypothesis: although small species have suffered the fewest extinctions, extinctions have not been significantly clustered around intermediate sizes. Similar results were obtained for the extinct and endangered species at the continental level. At the regional level, neither the arid-zone nor the mesic-zone results supported the CWR hypothesis (Table 1). In the arid zone, patterns of nonrandomness were similar to those at the continental level: among extinct and endangered species, small species were underrepresented, but there were no fewer large species than expected. In the mesic zone, extinct and endangered species had a higher minimum body size than expected, but were otherwise random with respect to body size.

Tests for Phylogenetic Bias

We next tested whether the nonrandomness of extinct and endangered species with respect to body size is due to phylogenetic bias at higher taxon or species levels. To test for bias among higher taxonomic groups (typically families or subfamilies; Table 2), we used a variation of a method presented by Bennett and Owens (1997). This method tests whether extinct species are distributed nonrandomly among higher taxa and thus whether some taxa have a greater or lesser share of the extinctions than expected. We selected 25 species at random from the continental pool and calculated the proportion of this sample taken up by each higher taxon. This was repeated 2000 times, and the mean proportions were used to create a null distribution of extinct species among higher taxa. We compared this to the observed distribution of extinct species among higher taxa with a chi-square goodness-of-fit test (groups with a low expected number of extinct species were pooled to satisfy the requirements of the test). This procedure was repeated for the 41 extinct and endangered species. The distribution of ex-

Table 1. Parameters of the distributions of log body size (g) for all species, extinct species, and extinct + endangered species of terrestrial Australian mammals.[†]

Group of species	n	*Minimum*	*1st quartile*	*Mode*	*Mean*	*3rd quartile*	*Maximum*	*Interquartile range*	*Range*
Continental									
all species	226	0.63	1.48	0.85	2.39	3.20	4.69	1.73	4.06
extinct	25	1.26^{**}	2.00^{*}	3.18^{*}	2.57	3.18	4.40	1.18^{*}	3.14
extinct + endangered	41	1.26^{***}	1.94^{**}	3.18^{*}	2.58	3.18	4.51	1.24^{**}	3.26
Arid zone									
all species	105	0.63	1.30	0.85	2.23	3.18	4.69	1.88	4.06
extinct	31	1.00^{**}	2.3^{***}	3.18^{**}	2.73^{***}	3.18	4.51	0.88^{***}	3.51
extinct + endangered	36	1.00^{**}	2.13^{***}	3.18^{**}	2.65^{***}	3.18	4.51	1.04^{**}	3.51
Mesic zone									
all species	186	0.63	1.6	1.20	2.52	3.39	4.69	1.79	4.06
extinct	17	1.26	1.72	1.72	2.68	3.26	4.40	1.54	3.14
extinct + endangered	30	1.26^{*}	1.81	1.72	2.71	3.26	4.51	1.44	3.26

[†] *Values for the extinct and extinct + endangered species that are significantly different from those expected under randomly generated null models are indicated as follows:* $^{*}p \leq 0.05$, $^{**}p \leq 0.01$, $^{***}p \leq 0.001$.

Table 2. Numbers of extinct and extinct + endangered species in higher taxa of Australian mammals compared with the mean number expected under randomly generated null models.[†]

		Number extinct		*Number extinct + endangered*	
Taxon	*Total species*	*expected*	*observed*	*expected*	*observed*
Dasyuroidea	62	7.05	2**	11.19	6*
Hydromyinae	54	5.91	10*	9.72	13
Macropodidae	44	4.94	6	7.92	8
Phalangerida	27	3.10	0***	4.93	3
Perameloidea	13	1.84	4*	2.54	5*
Potoroidea	11	1.64	3*	2.24	5**
Murinae	8	1.42	0	1.79	0
Vombatiformes	4	1.17	0	1.32	1
Monotremata	2	1.05	0	1.11	0
Notoryctidae	1	1.00	0	1.00	0

[†] *Observed values significantly different from those expected under randomly generated null models are indicated as follows:* *$p \le 0.05$, **$p \le 0.01$, ***$p \le 0.001$.

tinct species among higher taxa was significantly different from random ($\chi^2 = 13.65$, df = 3, $p < 0.0001$), although for extinct + endangered species the difference was not as strong ($\chi^2 = 8.46$, df = 4, $p = 0.08$).

We then tested each higher taxon separately to identify taxa with a disproportionately high or low number of extinct species. For each taxon, we randomly sampled (2000 times) the appropriate number of species from the continental species pool and compared the actual number of extinct species in the taxon with the number expected if extinction is random with respect to phylogeny. The results (Table 2) suggest that it is unlikely that phylogenetic bias at the higher-taxon level has contributed to an indirect association between body size and extinction risk. For example, the Dasyuroidea (carnivorous marsupials) and Hydromyinae (water rats and hopping mice) have similar numbers of species and together accounted for a large proportion of the total mammal diversity. Although these two groups cover a similar body size range, they differed in overall extinction risk. Dasyuroidea had fewer extinct species than expected, whereas Hydromyinae had more than expected. The Phalangerida (possums and gliders) also had fewer extinct species than expected, whereas the Potoroidea (potoroos and bettongs) and Perameloidea (bandicoots and bilbies) had more extinct species than expected. For the remaining higher taxa, the numbers of extinct species were not significantly different from a random expectation. These patterns were similar for extinct + endangered species.

To test for an association between body size and extinction risk at the species level, we used the program CAIC (Purvis & Rambaut 1995) to calculate phylogenetically independent comparisons from a composite phylogeny (based on Watts & Aslin 1981; Flannery 1989; Watts et al. 1992; Strahan 1995; Watts & Baverstock 1995; Kirsch et al. 1997; Krajewski et al. 1997; Blacket et al. 1999). We analyzed the data in two ways. First, treating body size as a continuous variable, we used regression through the origin (Harvey & Pagel 1991) to test associations between body size and extinction risk. Because the CWR hypothesis predicts a unimodal relationship between body size and extinction risk, we also performed regressions separately for smaller and larger species. We used the median body weight of 150 g to distinguish between small and large species (the midpoint of the range of log body sizes gave similar results). There was no significant association between body size and extinction risk for the continental fauna as a whole, for separate analyses of large species, or for the arid or mesic fauna. For small species (<150 g) there was a weak positive association (94 comparisons, $r^2 = 0.04$, $p = 0.06$). Next, we treated body size as a categorical variable. Phylogenetically independent comparisons between species within the CWR (i.e., 35–5500 g) and closely related species outside the CWR (both larger and smaller) revealed that CWR species have a higher risk of extinction in 19 out of 26 comparisons (sign test, $p < 0.01$). But this result was due almost entirely to smaller species having a lower extinction risk than CWR species (13 out of 16 comparisons, $p = 0.03$). There was no significant difference in extinction risk between CWR and larger species (6 out of 10 comparisons, $p = 0.4$).

Tests for Geographic Bias

It is possible that the strong geographic bias in recent extinctions of Australian terrestrial mammals contributed to the results of our randomization tests. The arid zone has had a higher rate of extinctions (31 out of 105 species) than the mesic zone (17 out of 186 species), and the mean extinction risk for arid species (2.49 ± 0.17) was significantly higher than for mesic species (1.81 ± 0.13; Wilcoxon signed-ranks test: $z = 2.92, p = 0.004$, two-tailed). If mean body size is larger in the arid zone, this could be an indirect cause of smaller species appearing less extinction-prone on a continental scale. The opposite is true, however: mean body size for the arid fauna (170 g) is significantly lower than for the mesic fauna (347 g; $z = 2.26$, $p = 0.006$, two-tailed). It is therefore unlikely that geographic bias in extinction risk is an indirect cause of small species being underrepresented among recent extinctions.

Discussion

By showing that extinction risk in Australian mammals is nonrandom with respect to body size, our study contributes to recent efforts to describe the influence of body size on a species' risk of extinction (Wilcox 1980; Karr 1982; Laurance 1991; Gaston & Blackburn 1995; Bennett & Owens 1997, 2000). In particular, our finding that the smallest species are the least extinction-prone is consistent with other null-model-based, phylogenetically controlled analyses of the relationship between body size and extinction risk (Gaston & Blackburn 1995; Bennett & Owens 1997). But we reject the widely held belief that Australian mammal species of intermediate size have been the most extinction-prone, which appears to be largely an artifact of the underlying body-size distribution of the continental fauna. This suggests that hypotheses that attempt to establish an explicit link between high extinction risk and intermediate body size (Burbidge & McKenzie 1989; Morton 1990; Short & Turner 1994; Smith & Quin 1996) may be misguided. Instead, it seems that the real pattern requiring explanation is the relative resistance to extinction of the smallest species.

There are a number of reasons to expect smaller-bodied species to be less vulnerable to extinction than larger species. Smaller species have lower individual energy requirements, allowing them to maintain higher average population densities than larger species (Damuth 1981). This would make smaller species more robust to disturbances than lower population sizes and hence less vulnerable to stochastic extinction. Smaller species also have a higher reproductive potential, which may reduce the time to recovery of populations lowered by disturbances (Gaston & Blackburn 1995; Bennett & Owens 1997). Hypotheses such as these could be tested by choosing appropriate summary measures of reproductive output (e.g., litter size) and energy requirements (e.g., home-range size) and applying similar comparative analyses to those used here. Such data are limited at present, but preliminary analyses suggest that, when body size is controlled for, endangered Australian mammal species have both smaller litters and larger home ranges than would be expected by chance (M. Cardillo & D. Fisher, unpublished analyses).

If life-history traits such as reproductive output or energy requirements influence extinction risk, there should be a positive association between body size and extinction risk across the entire range of body sizes. But the positive relationship between body size and extinction risk we describe is restricted to smaller species; there is no relationship among larger species. One possible explanation for this is that the megafaunal extinction event at the end of the Pleistocene acted as an "extinction filter" for large species. Between 60,000 and 15,000 years ago, most of Australia's mammal species of 10 kg or more went extinct (Flannery 1990). It is possible, therefore, that the more extinction-prone of the larger species were culled from the fauna in prehistoric times, removing any contemporary relationship between body size and extinction risk among larger species. It would be interesting to test whether other faunas that were subject to late-Pleistocene extinctions show similar patterns.

Our results show that the relationship between body size and extinction risk in Australian mammals varies geographically: the association is much stronger in the arid zone than the mesic zone. This could be consistent with an intriguing recent finding of Bennett and Owens (2000) that the form of the body size–extinction risk relationship in birds depends on the particular source of threat. They found that extinction risk incurred through habitat loss affects small-bodied species more strongly than large species, whereas extinction risk incurred through introduced predators and direct human persecution affects large-bodied species more strongly. Could this explain the different regional extinction patterns in the Australian mammals? In the arid zone, where introduced predators have had a far greater impact on native mammals than direct habitat loss, we found that small-bodied species are less threatened than large and medium-sized species. The mesic zone has suffered both from widespread habitat loss and introduced predators; in this zone we found much less evidence of a body-size bias among extinct and endangered species.

Acknowledgments

We extend many thanks to I. P. F. Owens, D. O. Fisher, P. B. Cassey, and C. N. Johnson for helpful comments and suggestions.

Literature Cited

Bennett, P. M., and I. P. F. Owens. 1997. Variation in extinction risk among birds: chance or evolutionary predisposition? Proceedings of the Royal Society of London B, Biological Sciences **264:**401–408.

Bennett, P. M., and I. P. F. Owens. 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. Proceedings of the National Academy of Sciences of the United States of America **97:**12144–12148.

Blacket, M. J., C. Krajewski, A. Labrinidis, B. Cambron, S. Cooper, and M. Westerman. 1999. Systematic relationships within the Dasyurid marsupial tribe Sminthopsini: a multigene approach. Molecular Phylogenetics and Evolution **12:**140–155.

Burbidge, A. A., and N. L. McKenzie. 1989. Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. Biological Conservation **50:**143–198.

Damuth. 1981. Population density and body size in mammals. Nature **290:**699–700.

Flannery, T. F. 1989. Phylogeny of the Macropodoidea: a study in convergence. Pages 1–46 in G. Grigg, P. Jarman, and I. Hume, editors. Kangaroos, wallabies and rat-kangaroos. Surrey Beatty & Sons, Sydney.

Flannery, T. F. 1990. Pleistocene faunal loss: implications of the aftershock for Australia's past and future. Archaeology in Oceania **25:** 45–67.

Gaston, K. J., and T. M. Blackburn. 1995. Birds, body size and the threat of extinction. Philosophical Transactions of the Royal Society of London B, Biological Sciences **347:**205–212.

Harvey, P. H., and M. D. Pagel. 1991. The comparative method in evolutionary biology. Oxford University Press, Oxford, United Kingdom.

Johnson, K. A., A. A. Burbidge, and N. L. McKenzie. 1989. Australian Macropoidea: status, causes of decline, and future research and management. Pages 641–657 in G. Grigg, P. Jarman, and I. Hume, editors. Kangaroos, wallabies, and rat-kangaroos. Surrey Beatty and Sons, Sydney.

Karr, J. R. 1982. Population variability and extinction in the avifauna of a tropical landbridge island. Ecology **63:**1975–1978.

Kirsch, J. A., F. J. Lapointe, and M. S. Springer. 1997. DNA-hybridization studies of marsupials and their implications for metatherian classification. Australian Journal of Zoology **45:**211–280.

Krajewski, C., L. Buckley, and M. Westerman. 1997. DNA phylogeny of the marsupial wolf resolved. Proceedings of the Royal Society of London B, Biological Sciences **264:**911–917.

Laurance, W. F. 1991. Ecological correlates of extinction proneness in Australian tropical rainforest mammals. Conservation Biology **5:**79–89.

Lawton, J. H. 1995. Population dynamic principles. Pages 147–163 in J. H. Lawton and R. M. May, editors. Extinction rates. Oxford University Press, Oxford, United Kingdom.

Morton, S. R. 1990. The impact of European settlement on the vertebrate animals of arid Australia: a conceptual model. Proceedings of the Ecological Society of Australia **16:**210–213.

Pimm, S. L., L. Jones, and J. Diamond. 1988. On the risk of extinction. The American Naturalist **132:**757–785.

Purvis, A., and A. Rambaut. 1995. Comparative analysis by independent contrasts (CAIC): an Apple MacIntosh application for analysing comparative data. Computer Applied Biosciences **11:**247–251.

Purvis, A., P.-M. Agapow, J. L. Gittleman, and G. M. Mace. 2000. Nonrandom extinction and the loss of evolutionary history. Science **288:**328–330.

Russell, G. J., T. M. Brooks, M. L. McKinney, and C. G. Anderson. 1997. Present and future taxonomic selectivity in bird and mammal extinctions. Conservation Biology **12:**1365–1376.

Short, J., and A. Smith. 1994. Mammal decline and recovery in Australia. Journal of Mammalogy **75:**288–297.

Short, J., and B. Turner. 1994. A test of the vegetation mosaic hypothesis: a hypothesis to explain the decline and extinction of Australian mammals. Conservation Biology **8:**439–449.

Smith, A. P., and D. G. Quin. 1996. Patterns and causes of extinction and decline in Australian conilurine rodents. Biological Conservation **77:**243–267.

Strahan, R. 1992. Encyclopaedia of Australian animals: mammals. Angus and Robertson, Sydney.

Strahan, R., editor. 1995. The mammals of Australia. Reed New Holland, Sydney.

Terborgh, J., and B. Winter. 1980. Some causes of extinction. Pages 119–133 in M. E. Soulé and B. A. Wilcox, editors. Conservation biology: an evolutionary-ecological perspective. Sinauer Associates, Sunderland, Massachusetts.

Watts, C. H. S., and H. J. Aslin. 1981. The rodents of Australia. Angus & Robertson, Sydney.

Watts, C. H. S., and P. R. Baverstock. 1995. Evolution of the Murinae (Rodentia) assessed by microcomplement fixation of albumin. Australian Journal of Zoology **43:**105–118.

Watts, C. H. S., P. R. Baverstock, J. Birrel, and M. Kreig. 1992. Phylogeny of the Australian rodents (Muridae): a molecular approach using microcomplement fixation of albumin. Australian Journal of Zoology **40:**81–90.

Wilcox, B. A. 1980. Insular ecology and conservation. Pages 95-117. in M. E. Soulé and B. A. Wilcox, editors. Conservation biology: an evolutionary-ecological perspective. Sinauer Associates, Sunderland Massachusetts.