

# Biological determinants of extinction risk: why are smaller species less vulnerable?

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## Abstract

It is becoming increasingly clear that species of smaller body size tend to be less vulnerable to contemporary extinction threats than larger species, but few studies have examined the mechanisms underlying this pattern. In this paper, data for the Australian terrestrial mammal fauna are used to ask whether higher reproductive output or smaller home ranges can explain the reduced extinction risk of smaller species. Extinct and endangered species do indeed have smaller litters and larger home ranges for their body size than expected under a null model. In multiple regressions, however, only litter size is a significant predictor of extinction risk once body size and phylogeny are controlled for. Larger litters contribute to fast population growth, and are probably part of the reason that smaller species are less extinction-prone. The effect of litter size varies between the mesic coastal regions and the arid interior of Australia, indicating that the environment a species inhabits mediates the effect of biology on extinction risk. These results suggest that predicting extinction risk from biological traits is likely to be a complex task which must consider explicitly interactions between biology and environment.

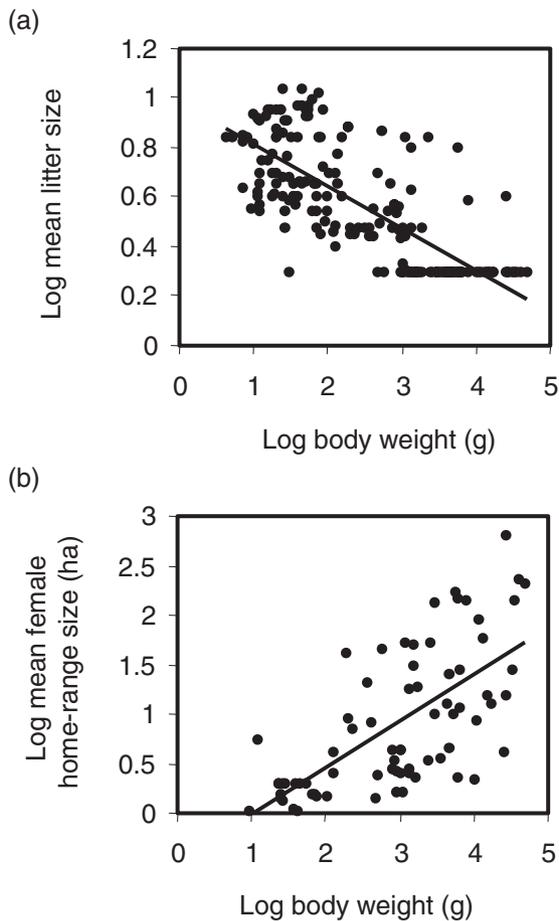
## INTRODUCTION

Recent extinctions and declines of species have been phylogenetically selective (Bennett & Owens, 1997; Gaston & Blackburn, 1997; Russell *et al.*, 1998; Purvis *et al.*, 2000a). This suggests that, in addition to external factors such as the degree of habitat loss, there are intrinsic traits which render some species particularly extinction-prone. A growing body of evidence indicates that body size is one such trait: smaller-bodied species seem to be less vulnerable to decline and extinction than larger species (Gaston & Blackburn, 1995; Smith & Quin, 1996; Bennett & Owens, 1997; Jennings, Reynolds & Mills, 1998; Purvis *et al.*, 2000b; Cardillo & Bromham, 2001). However, with two notable exceptions (Bennett & Owens, 1997; Purvis *et al.*, 2000b), previous studies have been based on univariate tests of association between body size and extinction risk, and beyond this little is known about why smaller size confers greater protection. On the one hand, it is possible that size directly determines a species' vulnerability: smaller species may, for instance, be less likely targets for

human hunters, or less common prey items for invasive predators. Alternatively, body size may simply be a surrogate for other life-history or ecological traits which influence vulnerability, such as reproductive output, mobility, energy requirements or population density. Furthermore, there may be tradeoffs between different traits; for example, smaller species may have an advantage in a higher reproductive output and higher population densities, but larger species may have an advantage in greater mobility and energetic efficiency. In addition, the relative importance of different traits, and hence the strength of the body-size effect on extinction risk, may depend on the type of environment a species inhabits. For example, traits which determine the efficiency with which energy is obtained and assimilated may be more critical to the survival of populations in low-productivity compared to high-productivity environments. Hence, the relationship between body size and extinction risk is potentially a complex one, and there is a need to investigate more closely why small body size has been associated with a lower risk of extinction. Specifically, it is necessary to move beyond simple univariate analyses to examine combined effects of different traits, and to test whether the relative effects of different traits on extinction risk vary depending on the type of environment a species inhabits.

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**Fig. 1.** Linear regression of female body weight against (a) mean litter size (d.f. = 194,  $r^2 = 0.56$ ,  $P < 0.0001$ ), and (b) mean female home-range size (d.f. = 71,  $r^2 = 0.28$ ,  $P < 0.0001$ ), across Australian indigenous terrestrial mammal species.

In this paper I investigate two life-history traits which may underlie the positive relationship between body size and extinction risk: reproductive output and home-range size. High reproductive output should generate faster population growth, and hence faster recovery from disturbances which reduce population size (Pimm, Jones & Diamond, 1988). Small home ranges suggest lower individual energetic requirements and higher population densities, so species with small home ranges may be better able to maintain viable populations in low-productivity environments or remnant habitat patches. In addition, species with larger home ranges may be more vulnerable to reserve edge effects (Woodroffe & Ginsberg, 1998).

The focus of the analysis is the terrestrial mammal fauna of Australia. Australian mammals are one of the best model assemblages for the study of processes underlying extinction risk, for several reasons. The decline and loss of mammal species from anthropogenic causes within the last few centuries has been higher in Australia than in any other continent (Short & Smith, 1994). Not only does this lend a particular urgency to the study of

extinction risk; it provides the largest sample of any continental mammal fauna with which to examine patterns and correlates of extinction. It has already been demonstrated that recent extinctions and declines among Australian terrestrial mammals have been size-selective: small species have been less vulnerable than medium-sized or large species (Smith & Quin, 1996; Cardillo & Bromham, 2001). Reproductive output and home-range size show strong correlations with body size in Australian mammals (negative and positive, respectively: Fig. 1), so provide potential explanations for the positive body size/extinction risk association in this fauna. Finally, Australia can be divided into a low-rainfall, low-productivity arid zone and a higher-rainfall, higher-productivity mesic zone, allowing examination of whether biological correlates of extinction risk differ between broad environmental types.

## METHODS

### Data set

This study is concerned with recent extinctions and declines (those which have occurred in the 200 years since European settlement) in the non-volant, terrestrial mammal fauna of mainland Australia and Tasmania. Offshore islands were excluded from the analysis as patterns of extinction, and underlying mechanisms, may differ substantially from those of the mainland. Non-native species were excluded. I assigned each species an extinction-risk classification ranging from 1 (secure) to 5 (extinct) based on Strahan (1992, 1995). Under these classifications, 25 species were counted as extinct (category 5) and 41 as extinct or endangered (category 4 plus category 5). Because islands are excluded, some of the species in category 5 are extinct from the mainland but still persist on some islands. To compare patterns of extinction and decline between the arid and mesic climatic zones, I also compiled separate lists of species inhabiting each zone (separated by the 500 mm isohyet, following Johnson, Burbidge & McKenzie (1989)), and separate extinction risk classifications within each zone. As a measure of reproductive output, I used mean litter size. Annual reproductive output is determined by number of litters per year as well as litter size, but data on number of litters per year are lacking for many species. Mean female mass (g), mean litter size and mean female home-range size (ha) for as many species as possible were recorded from Strahan (1995), and a number of primary sources (see Fisher, Owens & Johnson, 2001), and averages were used where different estimates were obtained for the same species. Litter-size estimates were available for 14 of the 25 'extinct' species, either because populations still exist on offshore islands or because extinction occurred recently enough that some biological study had already taken place. For home-range size, estimates were found for only four of the 'extinct' species, so analyses on these should be treated with some caution. All data are available from the author on request.

## Randomizations

I used randomization tests to examine whether the extinct and extinct + endangered species were non-random subsets of the continental fauna, with respect to litter size and home-range size. In order to examine the effects of litter size and home-range size independently of body size, I carried out the tests on the residuals of regressions of body size against litter size and body size against home-range size. I randomly selected the appropriate number of species from the continental species pool, and recorded the following statistics for litter-size residuals and home-range residuals: mean, mode, maximum, minimum, 1st quartile and 3rd quartile. This was done 2000 times to generate a null distribution of each statistic, and the positions of observed values within the null distributions were used to calculate exact *P*-values. The number of species selected varied with each randomization, depending on the number of extinct or extinct + endangered species for which I had data on body size, litter size and home-range size. The randomization tests were also performed separately for the arid zone fauna and the mesic zone fauna, to examine patterns within each zone.

## Independent contrast analyses

To test combined effects of body size, litter size and home-range size on extinction risk, I used multiple regression through the origin on phylogenetically independent contrasts, a method which controls for potential confounding effects of shared evolutionary history (Harvey & Pagel, 1991). To identify contrasts I constructed a composite species-level phylogeny of Australian mammals from published phylogenies (Watts & Aslin, 1981; Flannery, 1989; Watts *et al.*, 1992; Strahan, 1995; Watts & Baverstock, 1995; Kirsch, Lapointe & Springer, 1997; Krajewski, Buckley & Westerman, 1997; Blacket *et al.*, 1999). This is not an exhaustive list of phylogenetic studies of Australian mammals, but, in choosing studies, I favoured more recent and more comprehensive phylogenies, particularly those which synthesized results from several earlier studies. Contrasts were calculated using the CRUNCH algorithm in the CAIC program (Purvis & Rambaut, 1995), assuming equal branch lengths.

Regression analyses were performed separately for the continental, arid-zone and mesic-zone faunas. Inclusion of zone as a factor in the regression models was not possible because many species occupy both zones, and because many of the life-history contrasts incorporate information on species from both zones.

## RESULTS

Randomization tests indicate that the species classified as extinct (category 5) and extinct + endangered (categories 4 + 5) are non-random subsets of the continental fauna, with respect to both litter size and home-range size (Table 1). For the extinct species, residuals of litter size on body size have a significantly lower mean, mode and minimum than expected by chance, indicating that the extinct species had unusually small litters for their body size. Residuals of home-range size on body size have a significantly higher mean, mode, minimum, maximum, 1st quartile and 3rd quartile than expected, indicating that the extinct species had unusually large home-ranges for their body size. Similar patterns exist for the set of extinct + endangered species (Table 1).

These results do not necessarily imply a direct association between litter size and extinction risk or home-range size and extinction risk. One possible source of bias in litter size and home-range size may be differences between the arid and mesic zones. Mean extinction risk is significantly higher in the arid zone compared to the mesic zone (Wilcoxon 2-sample test:  $Z = 2.92$ ,  $P = 0.004$ ). There is no significant difference in litter size/body size residuals between the two zones ( $T$ -test:  $T = 0.35$ ,  $P = 0.72$ , d.f. = 136), but there is a significant difference in home-range size/body size residuals ( $T = 2.06$ ,  $P = 0.04$ , d.f. = 51), indicating that arid-zone species have larger home-ranges for their body size than do mesic-zone species. To examine this further I repeated the randomizations within each zone. Within each zone, the patterns are weaker than for the continental test and fewer of the results are strongly significant, but there is still a tendency for litters to be smaller and home-ranges larger among both the extinct and extinct + endangered species (Tables 2 & 3). Therefore it is unlikely that geographic differences are the sole cause of the bias in litter size and home-range size among extinct and endangered species.

**Table 1.** Results of randomization tests to examine whether extinct and endangered species are non-random subsets of the continental fauna, with respect to litter size and home-range size. Tests are done on the residuals of litter size and home-range size from regressions against body size. The number of species (*n*) varies depending on the numbers of species for which the appropriate data were available. The table shows whether observed values fell within the upper (+) or lower (–) tail of the null distributions, and the probability that the values were no different from those for sets of species drawn randomly from the null distributions: \* $P \leq 0.1$ ; \*\* $P \leq 0.05$ ; \*\*\* $P \leq 0.01$ .

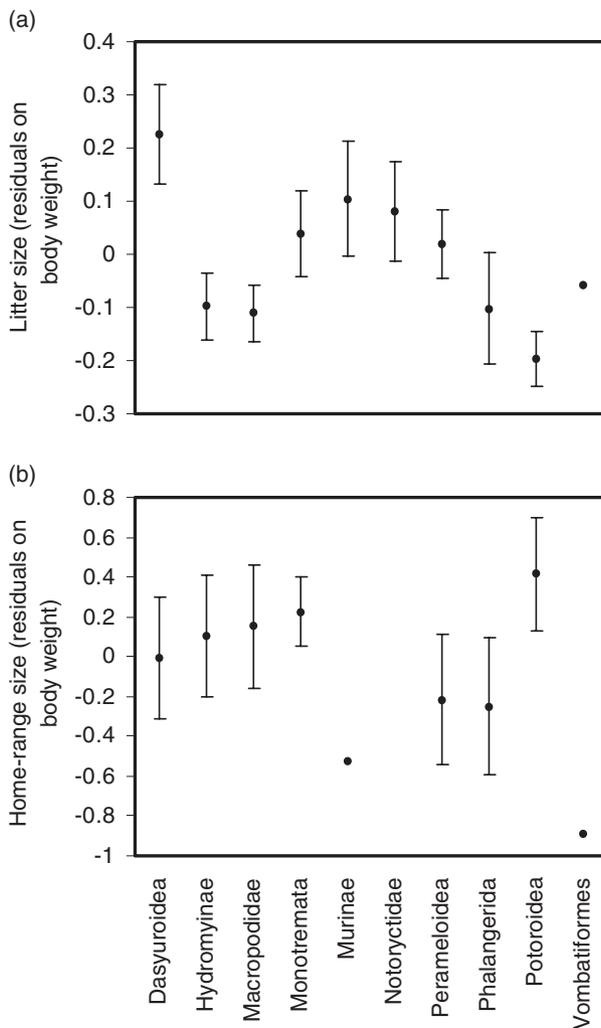
	<i>n</i>	mean	mode	max.	min.	1st quartile	3rd quartile
Extinct species							
Litter size	14	–**	–***	–	–***	–	–
Home-range size	4	+***	+***	+***	+***	+***	+***
Extinct + endangered species							
Litter size	28	–**	–***	–	–***	–	–*
Home-range size	12	+**	+	+***	+	+**	+

**Table 2.** Results of randomization tests for the arid-zone fauna (see Table 1 for explanation).

	<i>n</i>	mean	mode	max.	min.	1st quartile	3rd quartile
Extinct species							
Litter size	24	-	+*	_*	_***	_*	-
Home-range size	13	+	+	+***	+	+	+
Extinct + endangered species							
Litter size	29	_*	+*	_*	_***	-	-
Home-range size	14	-	+	+***	+	+	-

**Table 3.** Results of randomization tests for the mesic zone fauna (see Table 1 for explanation).

	<i>n</i>	mean	mode	max.	min.	1st quartile	3rd quartile
Extinct species							
Litter size	14	-	_***	+*	_***	-	-
Home-range size	4	+**	+	+***	+	+*	+***
Extinct + endangered species							
Litter size	28	-	_***	+	_***	-	-
Home-range size	12	+*	+	+***	+	+	+

**Fig. 2.** Mean and standard errors of (a) mean litter size and (b) mean female home-range size, for each of ten higher taxa of Australian indigenous terrestrial mammals. Values shown are residuals from regressions against mean female body weight.

A second potential confounding effect is phylogeny. If those taxonomic groups which account for many of the extinct and endangered species have unusually small litters or large home ranges, this could explain the results of the randomization tests. The taxa with the largest numbers of extinct and endangered species are the Hydromyinae and the Macropodidae, which together account for 16 of the 25 extinct species and 21 of the 41 extinct + endangered species. Both taxa have smaller litter sizes than would be predicted from their body sizes (Figure 2(a)). Both taxa also have slightly larger home ranges than would be predicted, though not unusually large (Figure 2(b)). This suggests a possibility that phylogeny contributes to the bias in litter size and home-range size among extinct and endangered species.

Finally, I used multiple regression through the origin on independent contrasts to examine combined effects of body size, litter size and home-range size on extinction risk, in a way which controls for phylogeny. Body size alone shows a positive association with extinction risk, though not a significant one ( $F = 2.77$ ,  $P = 0.09$ ). This trend disappears when litter size and home-range size are controlled for; litter size is the only significant factor in a model containing all variables (Table 4(a)). With home-range size removed, the model explains 12.3% of the variance in extinction risk (Table 4(b)). Independently of phylogeny and body size, therefore, extinction risk is associated with litter size but not with home-range size. However, this result is not consistent across regions. Within the arid zone, neither body size, litter size nor home-range size is a significant predictor of extinction risk (Table 5). Within the mesic zone, litter size is the only significant predictor of extinction risk (Table 6).

## DISCUSSION

In this study I have used the Australian terrestrial mammal fauna to test two hypotheses (higher reproductive

**Table 4.** Results of multiple regression through the origin on phylogenetically independent contrasts, for the continental fauna. (a) Body size, litter size and home-range size included ( $r^2 = 0.20$ ,  $P = 0.03$ ,  $n = 66$ ); (b) body size and litter size only ( $r^2 = 0.13$ ,  $P = 0.0001$ ,  $n = 187$ ). The number of contrasts varies between models because only species with data on home-range size were included in model (a). Results are for Type 1 sums of squares.

(a)			
Variable	Slope	<i>F</i>	<i>P</i>
Body size	-1.58	0.55	0.46
Litter size	-7.93	6.52	0.01
Home-range size	0.23	0.32	0.58
(b)			
Variable	Slope	<i>F</i>	<i>P</i>
Body size	0.05	0.08	0.78
Litter size	-2.24	25.88	0.0001

**Table 5.** Results of multiple regression through the origin on phylogenetically independent contrasts, for the arid-zone fauna. ( $r^2 = 0.01$ ,  $P = 0.97$ ,  $n = 26$ ).

Variable	Slope	<i>F</i>	<i>P</i>
Body size	-0.22	0.01	0.92
Litter size	-0.91	0.04	0.84
Home-range size	0.3	0.17	0.69

**Table 6.** Results of multiple regression through the origin on phylogenetically independent contrasts, for the mesic-zone fauna. (a) Body size, litter size and home-range size included ( $r^2 = 0.07$ ,  $P = 0.23$ ,  $n = 63$  contrasts); (b) body size and litter size only ( $r^2 = 0.06$ ,  $P = 0.007$ ,  $n = 162$ ).

(a)			
Variable	Slope	<i>F</i>	<i>P</i>
Body size	-0.84	0.28	0.6
Litter size	-5.57	4.05	0.04
Home-range size	0.05	0.02	0.89
(b)			
Variable	Slope	<i>F</i>	<i>P</i>
Body size	0.16	0.69	0.41
Litter size	-1.63	9.62	0.002

output and smaller home ranges), explaining why smaller body size is often associated with a lower risk of extinction. There is strong evidence that higher reproductive output contributes to lower extinction risk. Not only did extinct and endangered species have smaller litters than expected by chance, but litter size was a significant predictor of extinction risk in multiple regression models, and a weak positive association between body size and extinction risk disappeared when litter size was included in the model. These results suggest that at least part of the reason smaller species are less vulnerable is because they have a higher reproductive output. On the other hand, the evidence for an effect of home-range size on extinction risk is less compelling: although extinct and endangered species did have larger home ranges

than expected by chance, home-range size was not a significant predictor in regression models.

A negative relationship between mean litter size and the risk of extinction is consistent with suggestions that a faster reproductive rate should allow populations to recover more quickly from disturbances which reduce population size, and thus be less vulnerable to stochastic extinction (Pimm *et al.*, 1988). Several previous studies have made a similar finding (Laurance, 1991; Smith & Quin, 1996; Purvis *et al.*, 2000b), although only two (Bennett & Owens, 1997; Purvis *et al.*, 2000b) used methods which control for shared phylogenetic history among species. The results presented here are also consistent with a recent discovery by Johnson (2002) that the so-called 'megafaunal' extinctions of the late Pleistocene were closely associated with low reproductive rates, but not with body size once reproductive rate is controlled for. This suggests that current and historical extinctions may share at least some common causes.

Litter size is, however, only one component of total reproductive output. Although sufficient data were not available to test the number of litters per year, which also contributes to total reproductive output, it is possible that doing so would improve the amount of variation in extinction risk explained. However, I assume that mean litter size is at least a reasonable proxy for reproductive output, and that differences in reproductive output are therefore part of the explanation for phylogenetic selectivity in recent extinctions and declines of Australian mammal species. For example, the Dasyuroidea and Hydromyinae are two of the most speciose taxa of Australian mammals. Despite covering a similar distribution of body sizes, the Dasyuroidea have suffered significantly fewer recent extinctions and declines than expected by chance, while the Hydromyinae have suffered significantly more than expected (Cardillo & Bromham, 2001). This is probably partly because the Dasyuroidea have unusually large litters for their body size and the Hydromyinae have unusually small litters for their body size (Fig. 2). Of course, it is likely that other factors are also important. Burbidge & McKenzie (1989), for example, suggested that the use of torpor as an energy-conserving strategy by many small marsupials (such as Dasyuroidea), but not by rodents (such as Hydromyinae), may explain why small marsupials have been less extinction-prone than small rodents in the low-productivity environments which characterize most of Australia. A proper statistical test of this hypothesis, however, would require multiple independent cases where torpor has evolved along one branch of a phylogeny but not another; a single comparison of marsupials and rodents does not represent an adequate test.

Although home range sizes of extinct and endangered species were unusually large, home range was not a significant predictor of extinction risk in multiple regressions. It is possible that this is simply a result of a small sample size. Although sufficient data on home-range sizes were available for 66 independent contrasts overall, this included home-range data for only four category

5 species (those extinct from the mainland), which may have compromised the power of tests to detect any association between home-range size and extinction risk. However, even if this is the case, the lack of an association detectable with the data available suggests that home-range size is unlikely to be a strong determinant of extinction risk in Australian terrestrial mammals. This result is consistent with that of Purvis *et al.* (2000b) for carnivores and primates, but differs from that of Woodroffe & Ginsberg (1998), who demonstrated that populations of carnivore species with large home ranges are more threatened because they are more likely to encounter threatening processes at reserve edges. If large home ranges are a liability in fragmented landscapes, as Woodroffe & Ginsberg (1998) suggest, then lack of a home-range-size effect in Australian mammals may suggest that landscape fragmentation is perhaps a less important threat to mammal species in Australia than processes operating throughout a species' range, such as predation by introduced species. It may also be possible that any advantages of smaller home ranges are offset by larger home ranges conferring greater access to refuges such as rocky outcrops, which are believed to play an important role in the survival of many Australian mammal species (Burbidge & McKenzie, 1989; Smith & Quin, 1996).

When the multiple regression analyses were repeated within each of the two climatic zones, the significant effect of litter size on extinction risk was only present in the mesic zone; there was no litter-size effect within the arid zone. This suggests that the mechanisms underlying decline and extinction may differ depending on the type of environment a species inhabits. Most of the Australian arid zone still largely retains its original vegetation structure, albeit modified by domestic stock-grazing. In the arid zone the threat to native mammal species is primarily from introduced predators such as cats and foxes (Morton, 1990; Short & Smith, 1994). Throughout much of the mesic east, southeast and southwest of Australia, on the other hand, native habitat loss and fragmentation have been extensive, in addition to high densities of introduced predators. The contrasting results in the two climatic zones seem counter to expectations, as we might expect reproductive rate to be a more important determinant of extinction risk where predation is the primary source of threat (Owens & Bennett, 2000), as species with higher reproductive rates can sustain higher rates of predator-driven mortality. One possibility is that reproduction is more strongly seasonal in mesic compared to arid regions, for many groups. Among arid-zone species, therefore, litter size may be a weaker proxy for annual fecundity than in mesic species, which could explain the lack of a litter-size effect in the arid zone. Whatever the explanation, it seems clear that in order to get an accurate picture of how a species' biology determines its vulnerability, it will be important to consider not only the combined effects of different traits and different sources of threat, but also the type of environment the species inhabits.

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