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Body mass and extinction risk in Australian marsupials: The 'Critical Weight Range' revisited

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Abstract Australian mammals have suffered an exceptionally high rate of decline and extinction over the last two hundred years. Body mass is linked to extinction risk in Australian mammals, but the nature of this association is controversial. A widely held view is that species of intermediate body mass (between 35 and 5500 g, the 'critical weight range', CWR) have declined most severely. However, the existence of the CWR has been disputed. In this paper we clarify the relationship of decline status and body mass in Australian marsupials. We show that the form of this relationship differs for ground-living *versus* arboreal species, and for species from low *versus* high rainfall areas. Among ground-living species and those from low-rainfall areas, declines were strongly size-selective and concentrated on species within the CWR. For the remaining species, decline was only weakly related to body mass with no evidence of heightened risk for species of intermediate size. We conclude that for terrestrial species in low rainfall areas, species within the CWR are most at risk of decline and extinction.

Key words: exotic predator, extinction selectivity, feral cat, marsupialia, population decline, red fox.

INTRODUCTION

Extinction risk in mammals generally increases with body size. This relationship holds both for species currently threatened with extinction (Cardillo *et al.* 2005, 2006) as well as many species that went extinct in prehistory (Martin & Steadman 1999). The relationship is probably due to ecological factors such as low population density, and life-history traits such as low fecundity and long generation time, that predispose species to extinction and that are themselves strongly related to body size (Purvis 2001; Johnson 2002; Cardillo *et al.* 2005). Cardillo *et al.* (2005) also demonstrate that while present-day extinction risk in small mammals is explained mainly by environmental factors, for large mammals environmental factors interact with intrinsic biological traits to amplify extinction risk.

Australian mammals may provide an exception to this rule. Many Australian mammals have declined over the last two hundred years, but most extinctions have been of medium-sized species (Burbidge & McKenzie 1989; Johnson *et al.* 1989, 2002; Morton 1990). This pattern has been used to define a 'critical weight range' (CWR) between approximately 35 and 5500 g, within which extinction risk has been, and is predicted to remain, high (Burbidge & McKenzie 1989). There is growing historical and experimental evidence of a significant role for predation by the introduced red fox *Vulpes vulpes* and feral cat *Felis catus* in the decline of many Australian mammals (Dickman 1996a,b; Smith & Quinn 1996; Short 1998; Kinnear *et al.* 2002; Johnson 2006; Johnson *et al.* 2007). Small species are likely to be resilient to predation because of higher population growth rates, while intensities of fox and cat predation are relatively low for large species. The CWR is therefore consistent with the impact of predation by foxes and cats.

However, the existence of the CWR has been disputed. Cardillo and Bromham (2001) found that although very small species had the lowest extinction risk, extinction risk did not significantly decline again among the largest-bodied species. In their analysis the high number of extinct and threatened species between 35 and 5500 g is explained by the fact that the majority of recent Australian mammals fall within this size range, not because such species have suffered exceptionally high rates of decline in comparison with larger species (Cardillo & Bromham 2001). Chisholm and Taylor (2007) repeated part of Cardillo and Bromham's analysis using a more sensitive test statistic and concluded that there was evidence for higher extinction risk in medium-sized species. However, Chisholm and Taylor did not consider phylogeny in their analysis. This may be important, given that another study, Fisher *et al.* (2003), found no effect of body mass on the pattern of decline among marsupials when phylogenetic non-independence of species was taken into account.

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The analyses by Cardillo and Bromham (2001) and Fisher *et al.* (2003) suggest that there may be no simple and general correlation of body mass and extinction risk in Australian mammals, other than that the smallest species tend to persist better. In particular, they imply that invoking a concentration of extinction risk among species of intermediate size may not help us to either understand the causes of recent declines, or to halt future declines. In this paper we re-evaluate the relationship between body mass and extinction risk in Australian marsupials, and provide new tests for the existence of the CWR. Our analyses differ from previous studies in that we explicitly consider the possibility that the relationship of body mass to extinction risk is affected by interactions with two other factors that are themselves strongly related to extinction risk. First, we distinguish ground-dwelling from arboreal species. There have been no extinctions of arboreal marsupials, but sixteen ground-dwelling taxa (species and subspecies) have declined to extinction on the mainland (Maxwell *et al.* 1996), and many more have disappeared from large proportions of their mainland range (Johnson 2006). Foxes and cats are predominantly terrestrial predators, so if predation affects middle-sized marsupials this should be most apparent in ground-dwelling species. Second, we consider climate. All previous surveys of the pattern of loss of Australian mammals indicate that declines have been greatest for species from low-rainfall regions, most notably the semi-arid and arid areas south of the tropics (e.g. Short & Turner 1994; McKenzie *et al.* 2007). These species may have been more vulnerable because the sparse vegetation of those regions afforded them little cover from predation. In that case, we predict that the concentration of losses among middle-sized species should be strongest in low-rainfall regions, but weak or absent in mesic regions.

The hypothesis tested in our analysis is, therefore, that if the CWR exists for Australian marsupials, and is primarily driven by predation pressure from foxes and cats, it should be most evident for the subset of species that lived on the ground and/or in low-rainfall regions, while being weak or absent for other species.

METHODS

We followed the taxonomy of Australian marsupials used by Maxwell *et al.* (1996) and treated subspecies as separate taxonomic units. Different subspecies of marsupials often have contrasting conservation status, so they can be considered independent for the purpose of this analysis. Our dataset was restricted to 165 mainland Australian marsupials (including extinct taxa). We excluded taxa which occur(ed) on Tasmania and other offshore islands as they have generally been immune from the mammal declines that affected much of the mainland (Burbidge & Manly 2002), probably because of fewer introduced predators.

We measured conservation status as 'persistence', defined as the current range on mainland Australia as a proportion of the range at the time of European arrival. High values represent species that have suffered little or no decline, low values indicate taxa that have declined severely or gone extinct. Persistence values were subjected to the Anscombe transformation, following Fisher *et al.* (2003) (this produces maximum values that exceed 1). Persistence values were calculated from past and present range maps in Strahan (1995) and Maxwell *et al.* (1996). Areas were estimated by transcribing distributions onto gridded base maps, in which grid squares were 1:250 000 map sheets (as used in Maxwell *et al.* 1996; Johnson *et al.* 2007), and by overlaying maps and counting grid squares. Taxa were considered to be arboreal if they fed and denned predominantly in trees ($n = 32$); all other taxa were classed as ground-living, with no distinctions made for those that used burrows or sheltered in rock piles ($n = 133$). For each taxon, we recorded mean annual rainfall in the geographic centre of the original range. The range centre was defined by the mid-points of the latitudinal and longitudinal ranges of the taxon's distribution, and mean annual rainfall obtained for the nearest Bureau of Meteorology weather station. Rainfall in the centre of the range does not measure the intensity of rainfall experienced by a taxon throughout its range, but it is a useful measure for capturing the extent of overlap with low-rainfall regions. We used it to divide taxa into two categories of low *versus* high-rainfall, depending on whether they were below or above the mean rainfall for all species.

All regressions of persistence on body mass were calculated using both the raw data, and phylogenetically independent contrasts to evaluate their robustness to non-independence due to phylogeny. For the contrasts analysis, a species-level phylogeny was constructed in PDTREE (Version 5), an extension of the program PDAP (Garland *et al.* 2003), by pruning the marsupial supertree (Cardillo *et al.* 2004a). Geographic subspecies were classed as sister taxa and added to the tree. Each of the variables used in the analysis was assessed for phylogenetic signal using the program PHYSIG.M in MatLab (Blomberg *et al.* 2003). All traits showed a strong phylogenetic signal and independent contrasts were calculated in PDAP.

RESULTS

Persistence and body mass

The relationship of persistence to body mass in all taxa is shown in Figure 1. There was a weak tendency for

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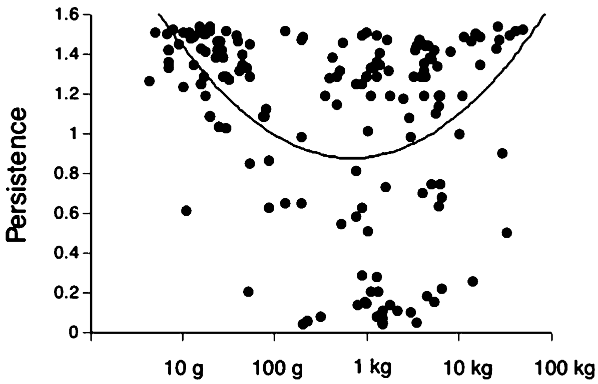

Fig. 1. Relationship of persistence to body mass in Australian marsupials. The curve is a quadratic fit (see Table 1 for significance tests).

taxa with low persistence to be concentrated in the middle of the body-mass range. In a multiple regression model of persistence on logMass and $(\text{logMass})^2$, both expressions of mass had significant effects (Table 1). This showed that both the tendency for persistence to fall with increasing body mass among relatively small taxa (described by the negative coefficient of logMass), and to increase with body mass among larger taxa (described by the positive coefficient of logMass^2), were supported. These results also held for the analysis of phylogenetically independent contrasts in mass and persistence (Table 2).

Interactions between body mass, arboreality and rainfall on persistence

We tested for effects of ground-living and rainfall on the form of the relationship between persistence to body mass, by including all variables in ANOVA models and examining the significance of interactions with logMass and $(\text{logMass})^2$. In analysis of the raw data, there were significant interactions of ground-living with both logMass ($t = 2.05$, $P < 0.06$) and $(\text{logMass})^2$ ($t = -1.95$, $P = 0.05$). Similarly, interactions with logRainfall were significant for both expressions of mass (respectively, $t = 2.87$, $P < 0.01$; $t = -2.29$, $P < 0.05$). In analysis of independent contrasts, there was a significant interaction of logRainfall with $(\text{logMass})^2$ ($t = 2.02$, $P < 0.05$), but no significant interaction of ground-living with mass.

Among ground-living and low-rainfall species there was a significant quadratic (U-shaped) relationship between persistence and body mass (Fig. 2a,b, Tables 1,2). No such relationship was found for arboreal or high rainfall species (Fig. 2c,d, Tables 1,2). The U-shaped relationship between persistence and body mass was most significant among species that were both ground-living and occupied low-rainfall regions (Fig. 3, Tables 1,2).

DISCUSSION

This study demonstrates that Australian mainland marsupials between approximately 100 g and 5 kg are most extinction prone. This range corresponds approximately with the CWR originally defined by Burbidge and McKenzie (1989), except that their review included rodents and probably for this reason they placed the lower boundary of the CWR at a smaller body mass (35 g). The boundaries between high and low persistence in this group of marsupials are not sharp. Rather, they appear to reflect continuous variation in the probability of severe decline in relation to body mass. We also provide evidence that those species which are primarily ground-dwelling and occupy low rainfall areas are most at risk of population decline and extinction.

Why are mid-sized marsupials more at risk?

Body size is a predictor of conservation status and extinction risk in a variety of mammal groups, because it is related to a number of life history traits, including lifespan and reproductive rate, which influence extinction risk (Cardillo *et al.* 2005). However, in most eutherian mammals studied so far, extinction risk increases linearly with body size, while in Australian marsupials extinction risk appears to increase with body size up to a point, but then declines in the largest species. The factors contributing to the persistence of smaller species have been discussed in detail elsewhere (e.g. Cardillo 2003); higher population growth rates of smaller species allow them to recover more quickly from declines and to absorb higher levels of predation. These factors may explain the resilience of small species, but the apparent resilience of the largest marsupials is unusual.

In our dataset 84% (21 out of 25) of species above our observed CWR threshold of 5 kg were large macropods (the other species were the three wombats *Vombatus ursinus, Lasiorhinus latifrons* and *L. krefftii* and the spot-tailed quoll *Dasyurus maculatus*). Two factors might explain relatively high persistence in these species. Most obviously, they fall above the preferred prey size for cats and foxes. While foxes are known to predate smaller macropods and can have an impact on juvenile survival in the larger species (Banks *et al.* 2000), the population impacts of this predation is generally low. Second, many large mammals which have declined elsewhere have been carnivores (Cardillo *et al.* 2004b, 2005), while all living marsupials of mainland Australia that are above the CWR are herbivores,

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Table 1. Significance of regressions of persistence of marsupial taxa on body mass for all taxa, and within subdivisions of the full taxon set, from analyses on raw data

Model	Effect size and significance of mass terms†			
	logMass	logMass^2	$F_{(\text{dgrees of freedom})}$	R^2
All taxa	**–0.07***	**0.17*******	**17.63*******$_{(2,161)}$	0.17
Ground-living	**–0.07***	**0.22*******	**20.80*******$_{(2,133)}$	0.23
Arboreal	–0.08	0.03	1.50$_{(2,28)}$	0.03
Low-rainfall	**–0.28*******	**0.25*******	**23.68*******$_{(2,64)}$	**0.43**
High-rainfall	–0.00	0.09*	2.78$_{(2,94)}$	0.06
Ground-living and low-rainfall	**–0.29*******	**0.29*******	**27.49*******$_{(2,54)}$	**0.50**

Bold type indicates significant effects; significance values: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; ****$P < 0.0001$. †Effect size is the unit change in persistence associated with a unit change in the mass variable; significance judged by a *t*-test.

Table 2. Significance of regressions of persistence of marsupial taxa on body mass for all taxa, and within various subdivisions of the full taxon set, from analyses on phylogenetically independent contrasts (notes as for Table 1)

Model	Effect size and significance of mass terms†			
	logMass	logMass^2	$F_{(\text{degrees of freedom})}$	R^2
All taxa	**–0.86***	**0.15****	**3.55****$_{(2,161)}$	0.03
Ground-living	**–0.89***	**0.14***	**3.24***$_{(2,129)}$	**0.03**
Arboreal	–0.42	0.09	0.64$_{(2,28)}$	0.00
Low-rainfall taxa	**–1.03****	**0.21****	**5.12****$_{(2,64)}$	**0.14**
High-rainfall taxa	–0.57	0.09	2.00$_{(2,91)}$	0.04
Ground-living and low-rainfall	**–1.38****	**0.27****	**7.76****$_{(2,54)}$	**0.22**

some of which have benefited from habitat change in pastoral lands.

Why are arboreal species less extinction-prone?

Our results demonstrate that ground-dwelling species are more likely to suffer declines and extinctions than similar sized arboreal species. This is unlikely to be due to the influence of life history traits as many arboreal species have lower reproductive rates and a slower life history than similar sized ground-dwelling species. Instead, the primary factor is likely to be ground-dwelling predators (Johnson 2006). Further evidence for the decline of terrestrial species comes from a recent analysis of the diet of sooty owls (Bilney *et al.* 2006). Prior to European settlement, sooty owls consumed a large array of terrestrial mammal species, but only three terrestrial mammal species were detected in their current diet, a reduction of at least eight species. Bilney *et al.* (2006) suggest that predation by foxes and cats has reduced the amount of terrestrial prey available for owls.

In our analysis the relationship between arboreality and persistence did not hold when we corrected for phylogeny. The reason for this might be that in marsupials, genera and in some cases families tend to be either entirely ground-living or arboreal. This means that there are few phylogenetic contrasts in ground-living *versus* arboreality. Analysis using independent contrasts therefore has low power to find evidence that ground-living is significant in shaping relationships of persistence to body mass. This is not evidence that ground-living has no effect, only that any effect that it does have cannot easily be separated from the phylogeny.

Why are species with low-rainfall distributions more at risk?

Declines for marsupials in the CWR are also more evident in species which occur in areas with low annual rainfall. Our results support a recent study by McKenzie *et al.* (2007), who also determined that mammal losses have been greatest in arid regions and lowest in high rainfall areas. They suggest that arid-zone species may be more at risk because of a variety of factors, including increased pressure from land use change, introduced herbivores and the impacts of fire (McKenzie *et al.* 2007). We would emphasize that medium-sized species in open habitats are likely to be more exposed to predators.

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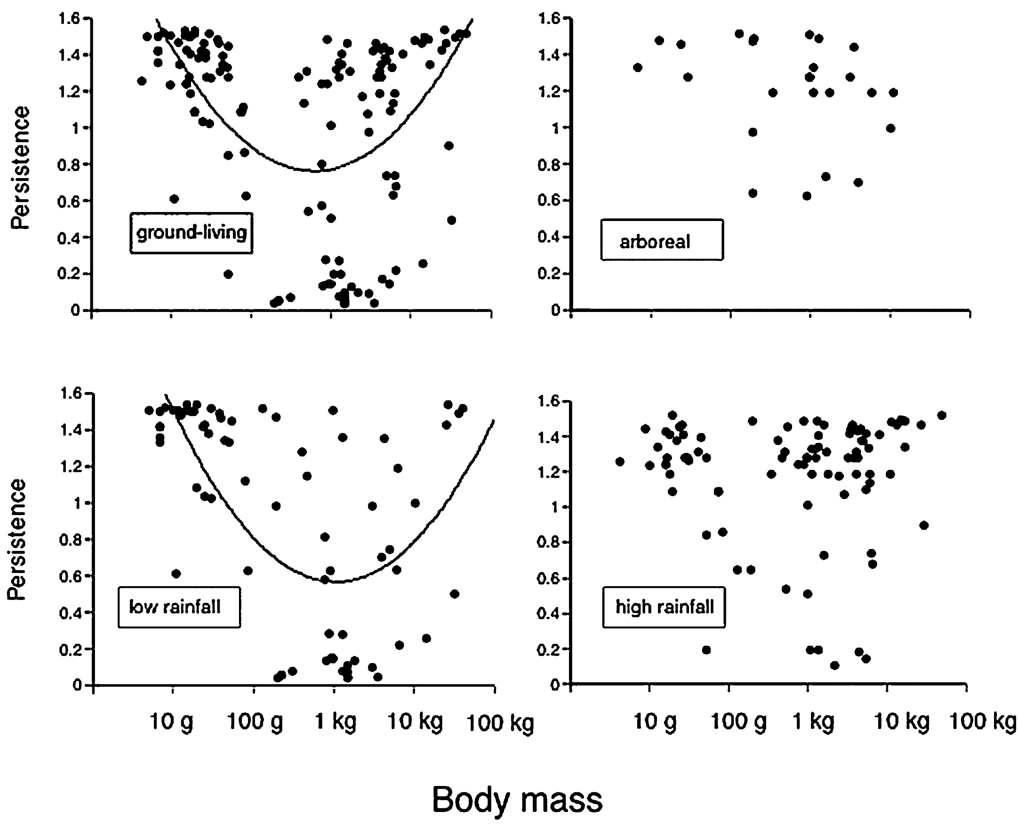

Fig. 2. Relationships of persistence to body mass in Australian marsupials, contrasted for ground-living *versus* arboreal taxa, and taxa from low *versus* high-rainfall regions (see Table 1 for significance tests).

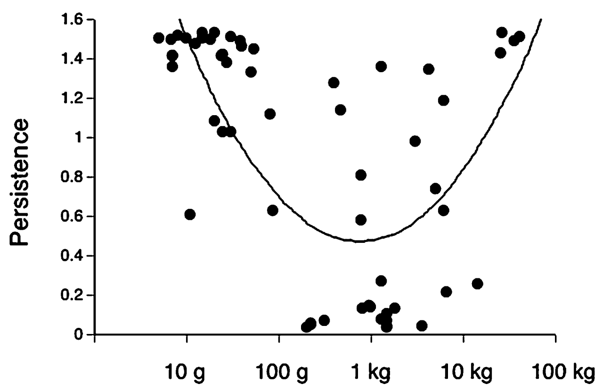

Fig. 3. Relationship of persistence to body mass in ground-living marsupials from low-rainfall regions (see Table 1 for significance tests).

The fact that proportionally fewer arboreal species occur in low-rainfall areas also contributes to the relationship of rainfall to persistence. Of the 32 arboreal species included, 69% fell in the high rainfall category. This concentration of arboreal species in high-rainfall areas tended to increase the effect of rainfall on persistence when arboreal and ground-dwelling taxa were lumped together. This should mean that ground-dwelling species in high rainfall areas may be at higher risk than previously thought. The fact that declines have been noted in a variety of terrestrial mammals in Kakadu National Park supports this (Woinarski *et al.* 2001).

In conclusion, our results suggest that the CWR is a useful descriptor of the pattern of past decline of Australian marsupial species, especially for ground-living species from semi-arid and arid habitats. The CWR may therefore be a useful predictor of risk of decline in the future.

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