

Phylogeny and the selectivity of extinction in Australian marsupials

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Abstract

Recent studies have suggested that contemporary losses of species are unevenly distributed over phylogenies. Here, we show that species of Australian marsupials are at higher risk if they belong to genera that are species-poor, old or phylogenetically distinct. Extinction risk in this group is also related to habitat and body size, being higher for species from non-forested habitats and of intermediate body size. We tested the extent to which the phylogenetic selectivity of extinction was explained by this ecological pattern. We found that while genus size and distinctiveness explain no variation in extinction risk that is not accounted for by habitat and body size, there is a significant residual association of genus age with extinction risk. This suggests that while species in small and distinctive genera are at high risk because they are overrepresented in non-forested habitats and intermediate body size classes, species in old genera are at higher risk over the range of body sizes and habitats and may be intrinsically vulnerable to extinction.

INTRODUCTION

As a result of human activities, species are now going extinct at a rate that is without precedent since the end-Cretaceous mass extinction event (Pimm *et al.*, 1995). The full biological significance of this is not yet clear, in part because species are not being lost at random with respect to their phylogeny. In birds and mammals, extinction rates tend to be highest in genera, families and orders that already have few species (Hughes, 1999; Russell *et al.*, 1999; Purvis *et al.*, 2000; Euler, 2001). Also, older lineages of birds tend to contain more threatened species (McDowell, 1969; Gaston & Blackburn, 1997), and some data on plants suggest higher rates of threat among primitive families (Hodgson 1986, but see Schwartz, 1993). Some of the best-known threatened taxa, such as tuataras (*Sphenodon*) and giant pandas (*Ailuropoda melanoleuca*), are noteworthy for their phylogenetic distinctiveness (May, 1990).

The disproportionate loss of species from small, old or distinct lineages will result in a much greater depletion of biological diversity and evolutionary history than if extinctions were randomly distributed over phylogenies. Because they have few close relatives, these species possess many traits that are not represented elsewhere in their phylogenies, and their extinction results in the

complete loss of those traits (Vane-Wright, Humphries & Williams, 1991; Faith, 1994; Crozier, 1997; Nee & May, 1997; Purvis *et al.*, 2000).

In this study we investigated the pattern of recent extinctions and current threat over the marsupial phylogeny. We had two concerns. This first was to characterize this pattern in terms of the three attributes of lineages identified above – species richness, age and distinctiveness – and to identify which was most strongly associated with current extinction rates once the others were taken into account. We expected that there would be correlations among these variables (distinct lineages might also be old and have few species, for example) so that an association of extinction risk with one variable would also produce correlations with others. For the purpose of identifying indicators of extinction risk, it is important to take these correlations into account.

Second, we wanted to distinguish between two possible classes of mechanism that could produce higher extinction risk for species with few close relatives: (1) such species might be intrinsically sensitive to threatening processes, and thus be especially likely to decline in response to a given set of stresses; (2) they might not be intrinsically extinction-prone but might be vulnerable because they occur in situations that have been highly exposed to threats. Among Australian marsupials, herbivorous species from inland (non-forested) habitats and of intermediate body size have suffered most

extinctions and continue to be most threatened (Burbidge & McKenzie, 1989; Morton, 1990; Woinarski & Braithwaite, 1990). This pattern reflects the impact of a particular set of threatening processes in inland Australia, the most important of which have been modification of habitat for and by sheep, invasion by rabbits and foxes, and, perhaps, changes to fire regimes resulting from cessation of the traditional burning practices of Aboriginal Australians. These threatening processes may have had their greatest impact on medium-sized herbivores because (1) they depend on vegetation cover that was removed by sheep, rabbits and wildfire; (2) they come into direct competition with rabbits for food; (3) they are preyed on by foxes. The selective removal of species with few close relatives might be explained if such species are overrepresented in intermediate body-size classes and non-forested habitats. We tested this by re-examining associations of extinction risk with phylogenetic variables after removing the effects of diet, body size and habitat.

METHODS

Data

Our phylogeny covered the whole of the Australian/New Guinean marsupial radiation (see Appendix). However, inclusion of New Guinea species in our analysis was limited by lack of information on their conservation status. Flannery (1995a,b,c) and Flannery, Martin & Szalay (1996) assigned species from the New Guinea region to the categories 'Endangered', 'Vulnerable' or 'Secure', but for 19 (25.7%) of 74 species they could not make an assessment, and for those species that were classified it is not clear how these categories relate to the IUCN classification that we used for Australian species (see below). Moreover, our characterization of threatening processes applies to the Australian but not the New Guinean fauna (where it is mainly larger arboreal species that are threatened, by human predation). For these reasons we restricted our analysis to genera that occur only in Australia, or that have species in both Australia and New Guinea but are predominantly Australian. For these genera we calculated the proportion of species threatened (hereafter referred to as the 'extinction risk' for that genus), where a 'threatened' species was one listed as extinct, critically endangered, endangered or vulnerable in the IUCN Action Plan for Australian Marsupials and Monotremes (Maxwell, Burbidge & Morris, 1996), or, for New Guinea species, as 'Endangered' and 'Vulnerable' by Flannery (1995a,b,c) or Flannery *et al.* (1996). Only three of 152 species of Australian marsupials are given the uncertain status 'data deficient' by Maxwell *et al.* (1996). These were excluded from analysis. This resulted in the removal of one monotypic genus (*Antechinomys*), leaving 51 genera.

Each genus was scored for three taxonomic/phylogenetic variables: (1) *size* – the total number of species in the genus (including species outside Australia); (2) *age*

– the time since divergence from its closest living relative, in millions of years; (3) *phylogenetic distinctiveness* – the number of nodes separating the genus from the root of the phylogeny (a small value indicating a high degree of distinctiveness). Estimates for ages of genera were taken from Kirsch *et al.*'s (1997) phylogeny. For genera not included in Kirsch, Lapointe & Springer's study ($n = 14$) we had no direct estimate of age, but all such genera were bracketed by a younger and older node of known age, and we assumed an age midway between these upper and lower limits. We also assigned a value to each genus for the following ecological variables: (1) proportion in forest – the proportion of species in the genus that had more than half their original geographic range in forested habitats, with such habitats identified as vegetation types 1, 2, 6–12, 21–24, and 26–33 on the map provided by Bridgewater (1987); (2) body mass – the mean mass (g) of all species in the genus (Strahan, 1995); (3) diet category – herbivore, omnivore or carnivore/insectivore (Strahan, 1995).

Our taxonomy followed Maxwell *et al.* (1996), subject to modifications of generic arrangements required by recent data on phylogenetic relationships (see Appendix). A total of 51 genera was included in the analysis.

Data analysis

Exploratory analyses of relationships among variables used local regression smoothers (i.e., loess smoothers, Cleveland & Devlin, 1988) to examine non-linear relationships. Spearman's rank correlation was used to examine relationships among variables, with tests of significance based on a normalized z -statistic. Generalized linear models (McCullagh & Nelder, 1989), using a logit link function and assuming a binomial distribution of variance, were used to examine relationships of extinction risk to phylogenetic and ecological variables. Owing to non-linearities revealed in exploratory analysis we used generalized additive models (Hastie & Tibshirani, 1990) in model selection. These models allow non-parametric smooth terms to be included to account for non-linear relationships between the logit-transformed response and the covariates. Model selection was based on Akaike's Information Criterion (AIC) (Akaike, 1973), where the model selected for inference was the one that minimized the AIC. This method selects a 'best approximating' model from a candidate set of considered models. Likelihood ratio tests were also used in support of AIC results. The variables genus size, genus age and body mass were transformed to base 2 logarithms.

We carried out our analysis at the genus level because this provided a large number of units that represent a wide range in all the variables we considered. Genera were treated as independent; we did not control for association of variables in the phylogeny because some of our predictors of extinction risk (age and phylogenetic distinctiveness) were themselves properties of the phylogeny. However, genera may not be truly independent,

especially in the case where groups of two or more genera arise from the same node in the phylogeny. Such genera will have identical values for age and distinctiveness, and it is possible that shared extinction-biasing traits inherited from their common ancestor could result in them having similar levels of threat. To test for variability in extinction risk among genera in such groups we examined the effect of the groupings on extinction risk by comparing a full model with each genus as a group (that fits the data perfectly) to a model where extinction risk depends on the sub-grouping (i.e., a group term which assigns sister genera to the same group). The comparison was significant ($\chi^2_{14} = 33.68$, $P = 0.002$), indicating that there is strong variability in extinction risk within sub-groups of sister genera, and suggesting that including them as independent units in the analysis was reasonable.

RESULTS

Phylogenetic selectivity of extinction

Interrelationships among our phylogenetic predictor variables are shown in Figure 1. The significant rank-order correlations among these variables were between genus age and phylogenetic distinctiveness ($z = -3.24$, $P < 0.01$) and between genus size and genus age ($z = -2.10$, $P < 0.05$).

There were highly significant non-linear relationships of extinction risk to genus size ($\chi^2 = 24.4$, d.f. = 3, $P < 0.0001$) and genus age ($\chi^2 = 12.5$, d.f. = 3, $P < 0.01$) and a linear relationship of extinction risk to phylogenetic distinctiveness ($\chi^2 = 8.4$, d.f. = 1, $P < 0.005$) (Fig. 2). Extinction risk tended to be highest for relatively small, old and distinct genera. Genus size ex-

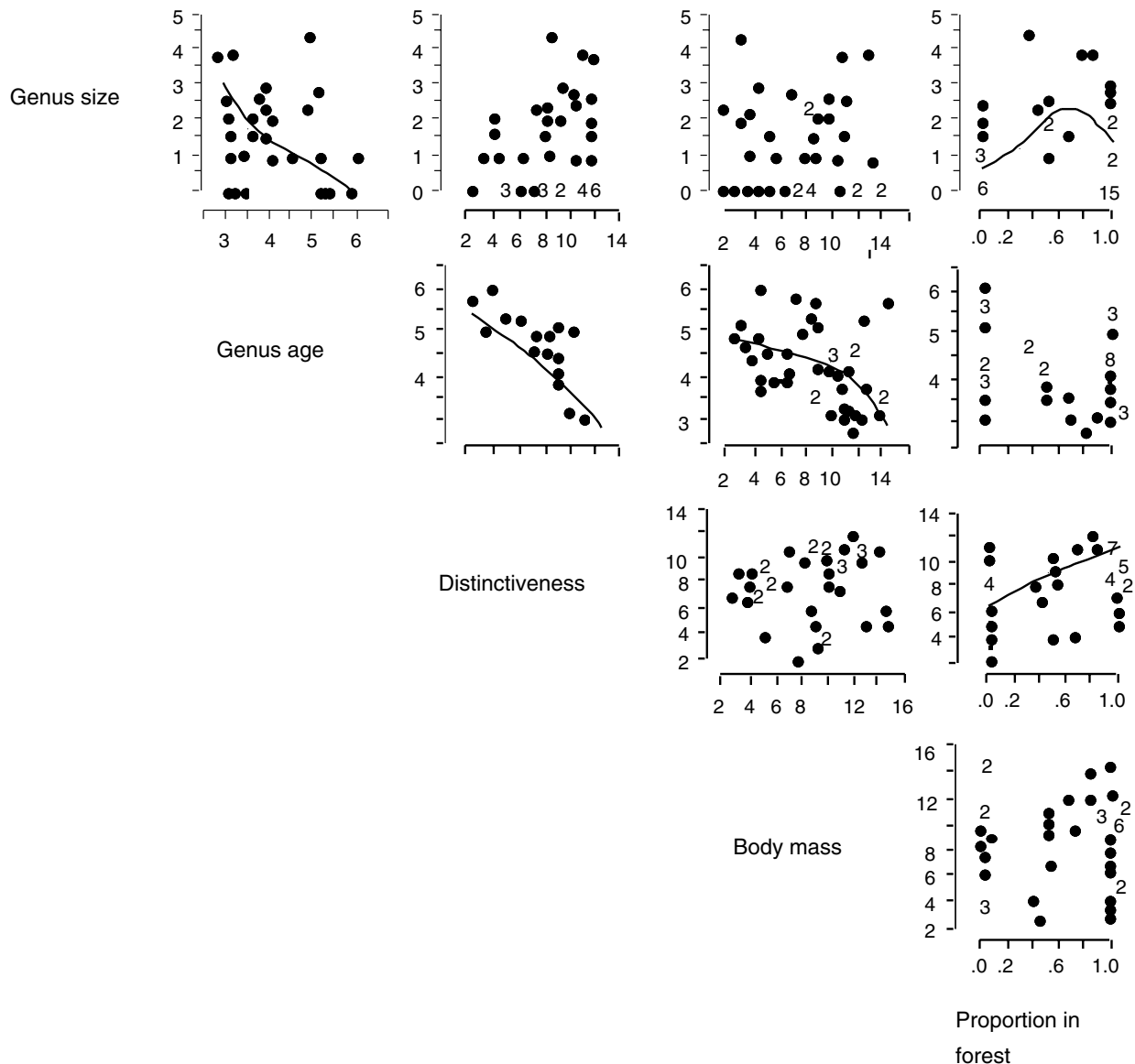


Fig. 1. Scatterplots illustrating interrelationships among predictor variables. Where correlations are significant, fitted lines are shown. Numbers represent multiple points with the same values.

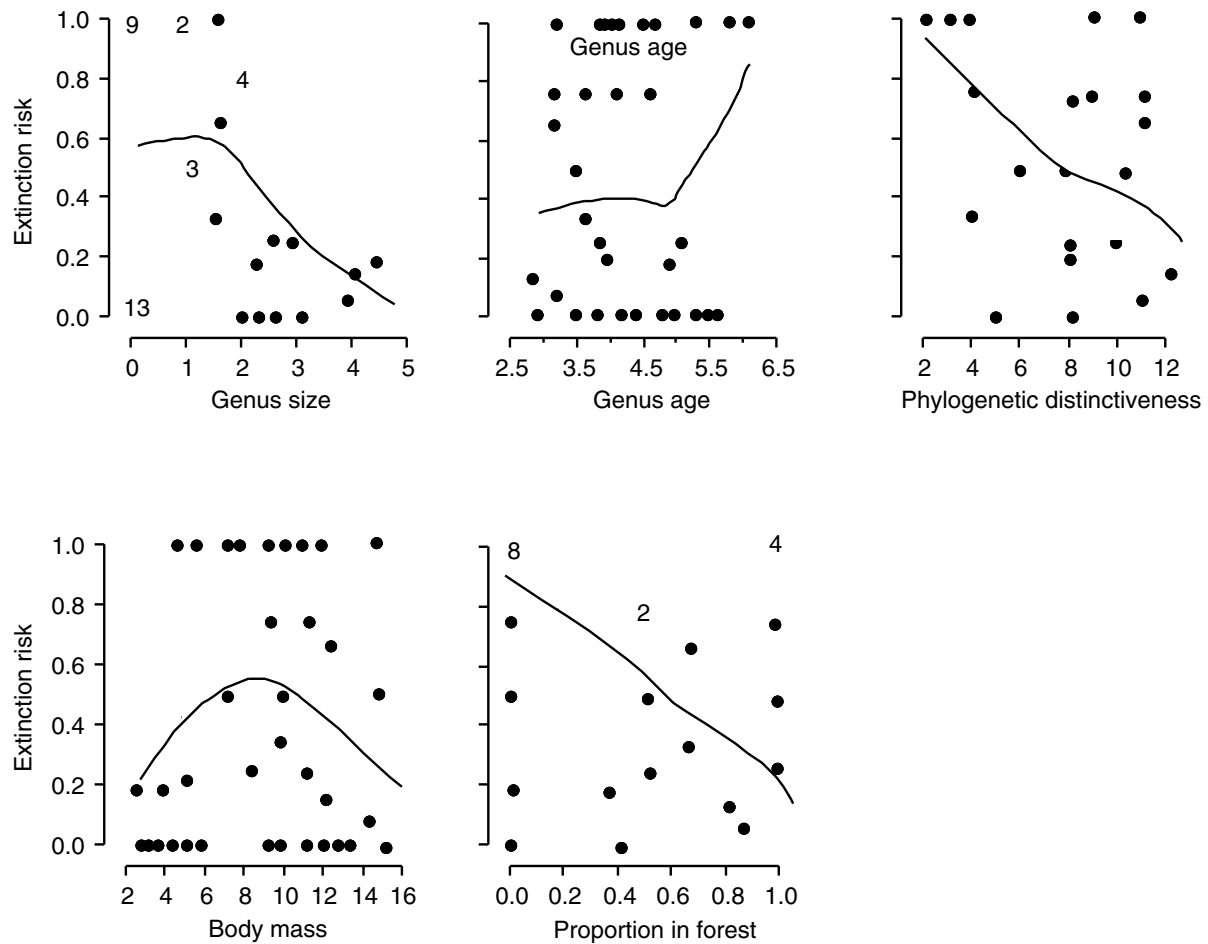


Fig. 2. Significant relationships between predictor variables and extinction risk.

plained more variation in extinction risk (28.3%) than did age (14.6%) or phylogenetic distinctiveness (9.8%).

To build a model explaining variation in extinction risk, taking into account the effects of all three phylogenetic variables, we began with a global generalized additive model that included smooth terms (d.f. = 3) for each of genus size, genus age, and phylogenetic distinctiveness (AIC = 74.1, d.f. = 10). The candidate set of models examined was nested within the global model to determine whether individual terms could be simplified to smooth terms with fewer degrees of freedom, simplified to linear terms, or dropped completely. The reduced model excluded phylogenetic distinctiveness (AIC = 70.4, d.f. = 7, variance explained = 31.5%). However, a model with a smooth term for genus size and a linear term for genus age was almost equally supported (AIC = 70.8, d.f. = 5), and genus age could be dropped from this model (AIC = 69.4, d.f. = 4, variance explained = 28.33%). Thus there was strong evidence only for a relationship of genus size to extinction risk ($\chi^2 = 24.4$, d.f. = 3, $P < 0.0001$).

Interaction of ecological and phylogenetic variables

There was strong evidence for a non-linear relationship between body mass and extinction risk ($\chi^2 = 19.6$, d.f.

= 3, $P < 0.001$) and a linear relationship between proportion in forest and extinction risk ($\chi^2 = 11.4$, d.f. = 1, $P < 0.001$; Fig. 2). Body mass and proportion in forest explained 22.8% and 13.2% respectively of the variation in extinction risk. There were several significant correlations among our phylogenetic and ecological predictor variables (Fig. 1). Genus age was negatively correlated with body mass ($z = -3.11$, $P < 0.01$); phylogenetic distinctiveness was correlated with proportion of species in forest ($z = 2.92$, $P < 0.05$) and (marginally) with body mass ($z = 1.98$, $P = 0.05$). Genus size was positively correlated with proportion in forest if completely forest-dwelling genera were excluded from analysis ($P < 0.01$).

We selected a model of extinction risk incorporating phylogenetic and ecological variables, as follows. From the global generalized additive model (AIC = 67.9, d.f. = 17), which included smooth terms (d.f. = 3) for each of genus size, genus age, phylogenetic distinctiveness and body mass, a smooth term (d.f. = 2) for proportion in forest, and the factor diet (d.f. = 2) the term for diet was dropped (AIC = 64.2, d.f. = 15), the terms for genus size and age were simplified to linear terms and phylogenetic distinctiveness was dropped (AIC = 55.9, d.f. = 8), proportion in forest was simplified to a linear term (AIC = 54.2, d.f. = 7), and genus size was dropped (AIC

= 53.2, d.f. = 6). The final model explained 52.0% of the variation among genera in extinction risk, and included significant terms for genus age ($\chi^2 = 3.9$, d.f. = 1, $P < 0.05$), body mass ($\chi^2 = 33.3$, d.f. = 3, $P < 0.0001$) and proportion in forest ($\chi^2 = 21.4$, d.f. = 1, $P < 0.0001$). Extinction risk increased with genus age, declined with proportion in forest, and was highest at intermediate body masses (Fig. 3).

DISCUSSION

The current wave of extinction is removing species selectively from the marsupial phylogeny: there are higher rates of recent extinction and current threat in relatively small, old and phylogenetically distinct genera. That is, the probability of extinction is highest for species that have few close relatives, a pattern that has also emerged in studies of other groups (see Introduction). We found correlations between genus size and genus age, and between genus age and phylogenetic distinctiveness – small genera tended to be old, and old genera tended to be phylogenetically distinct. Genus size was most significantly related to extinction risk, and genus age and phylogenetic distinctiveness did not contribute significantly to models relating phylogeny to extinction risk when interrelationships among variables were taken into account. That is, the size of genus to which species belonged was the clearest marker of their proneness to extinction.

Our analysis of the ecological pattern of extinction risk provided quantitative support for previous conclusions that in Australia medium-sized marsupials from non-forested habitats are subject to the highest risks of extinction, although we extended previous reviews by showing that diet was not related to extinction risk independently of the effects of body size and habitat. Cardillo & Bromham (2001) have recently re-evaluated the relationship between body size and extinction risk for Australian mammals, and found no significant decline in extinction risk at larger body sizes. Our results agree with theirs to the extent that we found the decline in risk at larger sizes to be substantially weaker than the increase at small size, although in our analysis it was significant. Inclusion of variables for body size and habitat in the extinction model reduced the evidence for direct relationships of phylogenetic variables to extinction risk, suggesting that to a large degree the relationship of phylogeny to extinction was due to covariation of phylogenetic and ecological variables. For example, most genera of medium-sized marsupials that occur predominantly in non-forested habitats also have few species; this association appears sufficient to explain the selective removal from the marsupial phylogeny of species from small genera. We did find, however, that the ages of genera remained significantly and positively associated with extinction risk for their member species. That is, there is evidence for an effect of genus age on extinction risk that appears independent of the ecological measures we looked at, suggesting that species in older genera may be intrinsically more susceptible to threats than are species in young genera.

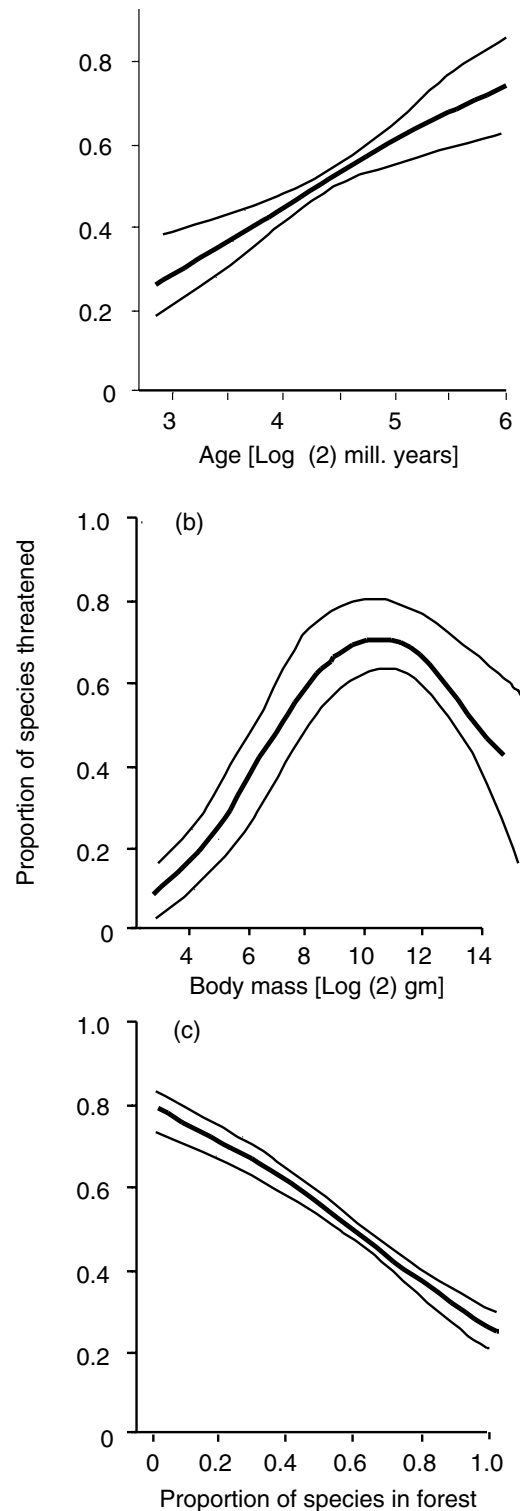


Fig. 3. Effects on extinction risk in marsupial genera of (a) genus age, (b) mean body mass and (c) proportion of species in forested habitats, when the effects of other variables are held constant.

Why might old (or, for that matter, small and distinct) lineages be more prone to extinction? There are at least three possible scenarios. First, a correlation between the age of a taxon and its vulnerability to extinction could arise in a non-causal way when age is estimated from a

molecular phylogeny. Variations in extinction rate among lineages are presumably due to the distribution of extinction-biasing traits, such as low fecundity or ecological specialization, that produce intrinsic sensitivity to environmental disturbances in some groups. Such traits are likely to be shared among close relatives (Bennett & Owens, 1997), and lineages that have always possessed them will have experienced a high rate of extinction throughout their history. Such lineages are likely as a result to be species-poor and surviving members will be found on long branches in a phylogeny constructed from relationships among living species. In this case, the estimated ages of lineages will not truly reflect their times of origin, but rather will depend on extinction rates, with no tendency for the extinction risk of species to increase with the time since origination of the lineages to which they belong.

Second, it might be that these groups have become increasingly extinction-prone as they have aged. This could happen if, for example, lineages tend to evolve towards greater ecological specialization or lower fecundity, thus becoming more sensitive to environmental change. Such a mechanism has been proposed to explain taxon cycles on island archipelagoes (Ricklefs & Cox, 1978; Ricklefs & Bermingham, 1999), and it might apply at larger scales to continental faunas; it is hinted at, for example, in Webb & Gaston's (2000) observation that range size tends to decline with age in bird species. Third, old lineages may happen to have features that make them more vulnerable to human-caused environmental change, but not to natural extinction; in this case, their vulnerability is more recent – so should contribute little to their current species-paucity and distinctiveness.

Distinguishing between these mechanisms will be difficult without detailed data on history of extinctions from the fossil record. The fact that in our analysis genus size predicted extinction risk argues against the suggestion that taxa differ in their sensitivity to human-caused but not natural extinction. Further, our finding that age was the only phylogenetic variable that remained significantly related to extinction when ecological correlates of extinction risk were taken into account is consistent with a direct relationship between age and intrinsic vulnerability to extinction.

Whatever the underlying causes of the pattern, however, it is clear that the marsupial phylogeny is losing its evolutionary history and genetic diversity at a rate considerably greater than implied by its already high loss of species. Further, there are grounds for being especially concerned by threats to species in relatively old genera (Erwin, 1991; Brooks, Mayden & MacLennan, 1992): such genera not only tend to be small and distinctive, but may be intrinsically more vulnerable to extinction than younger genera.

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APPENDIX: THE MARSUPIAL PHYLOGENY

The phylogeny we worked with (Fig. 1) is based on Kirsch, Lapointe & Springer's (1997) synthesis of DNA hybridization studies of marsupials. Kirsch *et al.* resolved the relationships and ages at divergence of most (41) extant genera of Australian and New Guinean marsupials. Other reconstructions of the marsupial phylogeny are available, and there are disagreements particularly over the relationships of higher taxa (Colgan, 1999). However, we relied on the structure proposed by Kirsch *et al.* because it is the most comprehensive reconstruction of the marsupial phylogeny yet published, and because it provides estimates of divergence dates for many lineages. The additional studies noted below were used to place taxa not included in Kirsch *et al.*'s study, and to incorporate revisions where more recent gene-sequence data provide strong support for change. The resulting composite phylogeny includes all recently extant genera of marsupials from Australia, New Guinea and the islands of the South West Pacific, except for the monotypic bandicoot genus *Rhynchomeles*.

Springer *et al.* (1998), using mitochondrial and nuclear gene sequences, concluded that *Notoryctes* is the sister taxon of the Dasyuromorphia, not Diprotodontia plus Microbiotheriidae as suggested by Kirsch *et al.* (1997). The position of *Chaeropus* and the relationships of other bandicoot genera follow the analysis of 12S rRNA by Westerman *et al.* (1999). The position of *Hypsiprymnodon* is based on the mtDNA sequence data of Burk, Westerman & Springer (1998). No molecular data are available to resolve the relationship of *Lagostrophus* to other macropods and we follow

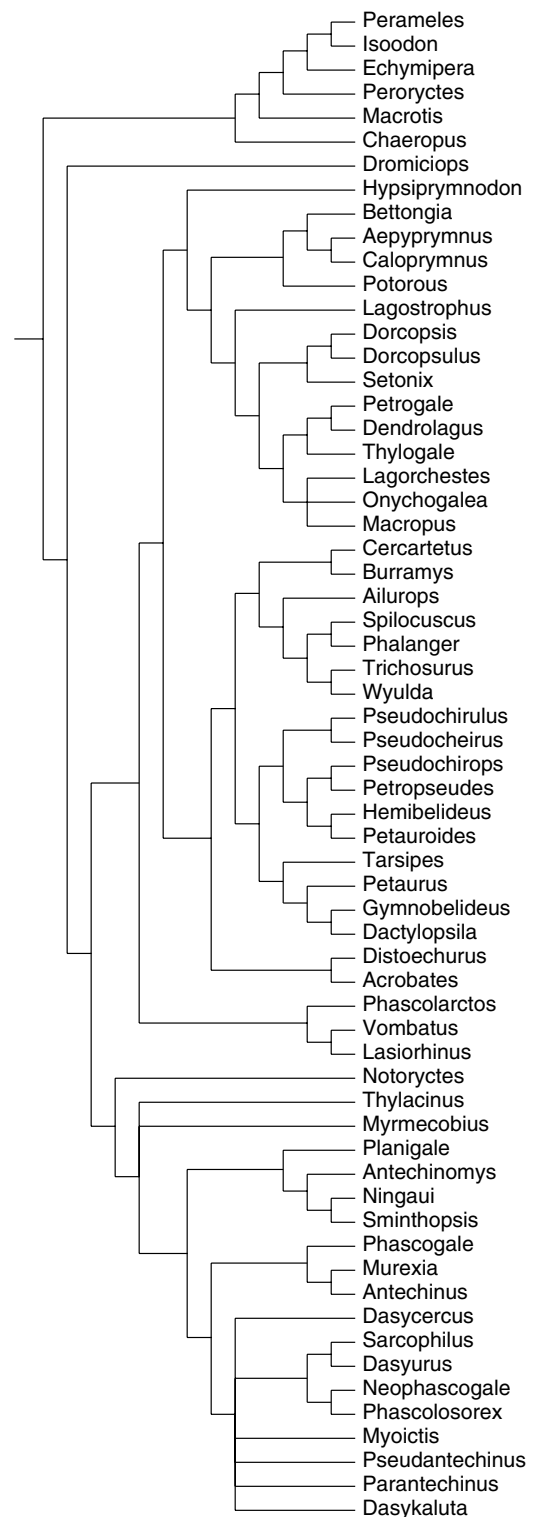


Fig. 1. Composite phylogeny of Australian and New Guinean genera of marsupials.

Flannery (1989) who, on morphological grounds, placed *Lagostrophus* in the Sthenurinae, sister to all Macropodinae. Flannery (1989) also concluded that the extinct genus *Caloprymnus* is sister to *Aepyprymnus*. Kirsch *et al.*'s (1997) study did not include *Lagorchestes* or *Onychogalea*, and Burk *et al.*'s (1998) study of

mtDNA was unable to resolve the relationships of these genera within the sub-family macropodinae, but Flannery (1989) suggests a close interrelationship among *Macropus*, *Onychogalea* and *Lagorchestes*. The relationships of *Burramys*, *Acrobates* and *Tarsipes* follow Edwards and Westerman's (1995) DNA hybridization study. Placement of *Petropseudes*, *Ailurops* and *Wyulda* follow Flannery (1995). Krajewski, Butler & Westerman (1997b), using mitochondrial and nuclear gene sequences, show that *Thylacinus* is a member of the Dasyuromorphia. *Myrmecobius* is conventionally classified as a separate family (Myrmecobiidae) within the Dasyuromorphia, but relationships to the other families of Dasyuromorphs (Dasyuridae and Thylacinidae) have not yet been clarified. This uncertainty is recognized by a basal trichotomy in the Dasyuromorphia. Relationships among Dasyurines cannot be resolved fully from Kirsch *et al.*'s (1997) study because of their non-inclusion of the genera *Parantechinus*, *Pseudantechinus*, *Myoictis*, *Neophascogale*, *Phascosorex* and *Sarcophilus*, which are all suggested by Krajewski *et al.*'s (1994) study of mitochondrial DNA to be part of a monophyletic Dasyurinae. A study combining mitochondrial and nuclear sequences (Krajewski *et al.*, 1997c) was unable to resolve the relationships of Dasyurines, other than to confirm the monophyly of *Dasyurus*, place *Sarcophilus* as the sister group to *Dasyurus*, and conclude that *Phascosorex* and *Neophascogale* are sister taxa. Kirsch *et al.* (1997) did not include *Antechinomys* or *Ningaui*, but the location of these genera within a monophyletic Sminthopsinae is confirmed by Krajewski *et al.* (1994), and the relationships of the genera *Ningaui*, *Planigale*, *Antechinomys* and *Sminthopsis* have been resolved by Krajewski *et al.* (1997a; Blacket *et al.*, 1999).

According to Kirsch *et al.*'s (1997) phylogeny, *Echymipera* is paraphyletic, including *Microperoryctes*; here, '*Echymipera*' is taken to include both taxa. Likewise, *Wallabia* is included within *Macropus*, and *Strigocuscus* is included within *Phalanger*. Mitochondrial and nuclear gene sequences strongly suggest that the New Guinea 'Antechinus' are more closely related to *Murexia* than to Australian *Antechinus* (Armstrong, Krajewski & Westerman, 1998). Here, *Antechinus* includes only Australian species.

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