

Geographic range size, life history and rates of diversification in Australian mammals

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Abstract

What causes species richness to vary among different groups of organisms? Two hypotheses are that large geographical ranges and fast life history either reduce extinction rates or raise speciation rates, elevating a clade's rate of diversification. Here we present a comparative analysis of these hypotheses using data on the phylogenetic relationships, geographical ranges and life history of the terrestrial mammal fauna of Australia. By comparing species richness patterns to null models, we show that species are distributed nonrandomly among genera. Using sister-clade comparisons to control for clade age, we then find that faster diversification is significantly associated with larger geographical ranges and larger litters, but there is no evidence for an effect of body size or age at first breeding on diversification rates. We believe the most likely explanation for these patterns is that larger litters and geographical ranges increase diversification rates because they buffer species from extinction. We also discuss the possibility that positive effects of litter size and range size on diversification rates result from elevated speciation rates.

Introduction

Even closely related lineages often vary widely in species richness. Within the mammals, for example, the order Rodentia (rodents) contains around 1700 species, while the order Dermoptera (flying lemurs) has only two species (Macdonald, 1995). What are the causes of this variation? Broadly, there are three ways that species richness variation among lineages can arise. The first is simply by chance: unpredictable sequences of historical events may have left different lineages with the different numbers of species that we see today (Raup *et al.*, 1973). The second is age: some lineages are older than others, so have had more time to accumulate species (Cracraft, 1984; Ricklefs & Schluter, 1993; Barraclough *et al.*, 1998). The third is that species could differ in biological traits that influence the rate of species diversification.

Because the net rate of diversification is the difference between the rate of addition of species to a clade by speciation and the rate of loss of species from a clade by extinction, any trait which elevates speciation rate or lowers extinction rate can increase the rate of diversification. A variety of biological traits have been suggested to influence diversification rates, including traits associated with life history, sexual selection, body size and ecology (Dial & Marzluff, 1988; Marzluff & Dial, 1991; Farrell & Mitter, 1993; Barraclough *et al.*, 1995, 1998, 1999; Mitra *et al.*, 1996; Gaston & Blackburn, 1997; Gittleman & Purvis, 1998; Moller & Cuervo, 1998; Owens *et al.*, 1999).

In this paper, we focus on the influence of geographical range size and life history traits on rates of diversification. Owens *et al.* (1999) found that diversification rates among bird families were positively correlated with the total geographical area occupied by each family, which they attributed to increased opportunities for allopatric speciation provided by the greater area. However, little is known about the association between diversification rate and the mean sizes of geographical

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ranges of individual species within a clade. On the one hand, a species with a large geographical range should be buffered from relatively localized environmental disturbances. This may lower the rate of extinction, so clades in which the mean size of individual species' ranges is larger may have a higher diversification rate (Rosenzweig, 1995). On the other hand, if speciation occurs largely by allopatric subdivision of species' ranges (Brown & Lomolino, 1998; Barraclough & Vogler, 2000), then a higher speciation rate will increase the rate of range division, which may reduce the mean size of ranges within a clade. In this case, the diversification rate could be negatively associated with mean range size. So the association between mean range size and diversification rate could be either positive or negative; these conflicting predictions have not been resolved. To our knowledge, only one previous study has examined the association between diversification rate and mean range size of species within clades, and found no evidence for a significant association, positive or negative (Gaston & Blackburn, 1997). That study used birds as a model taxon, which, because of their high dispersal abilities, may not be representative of the majority of taxa.

Another suggestion has been that 'fast' life history promotes faster diversification (Marzluff & Dial, 1991; Rohde, 1992). Together, small body size, high reproductive output and short generation times generate fast population growth, allowing populations to recover quickly from low numbers and maintain high population densities (Damuth, 1981; Pimm *et al.*, 1988). This should help buffer species from extinction caused by disturbances or stochastic population fluctuations. It has also been suggested that the probability of speciation will be higher in species with shorter generations, as it allows a greater number of selection-driven changes to accumulate in a given period of time (Marzluff & Dial, 1991; Rohde, 1992; Rosenheim & Tabashnik, 1993).

In order to test associations between geographical range size, life history and rates of diversification, we compiled a database on the terrestrial mammal fauna of Australia. A long history of biogeographical isolation and very high level of endemism, as well as available data on species-level phylogenetic relationships for the whole assemblage, make this group a good model for testing macroevolutionary hypotheses using phylogenetic comparative methods. We first show that patterns of species richness in this assemblage are inconsistent with null models in which species are randomly distributed among genera, so it is unlikely that chance is the major determinant of species richness patterns. We use these null models to identify taxa which are more species-rich than expected by chance. We then use sister-clade contrasts, which control for differences in the age of clades, to demonstrate that rates of diversification are positively associated with the mean size of geographical ranges and with reproductive output, but are not associated with body size or generation time.

Methods

This study includes all nonvolant, terrestrial, indigenous Australian mammal species. This assemblage consists of 210 species distributed among 76 genera (Strahan, 1995), including those species which have become extinct in the 200 years since European settlement. We began by examining whether patterns of species richness were consistent with the random distribution of species among genera, by comparing the observed distribution to suitable null models. There are a range of possible null models which can be applied to species distribution patterns (Dial & Marzluff, 1989). Here we follow Owens *et al.* (1999) and use both Poisson and Geometric distributions as our null models. A Poisson distribution is expected under a model where species are randomly allocated to genera (Owens *et al.*, 1999), while a Geometric distribution is expected under a process of random cladogenesis in which each lineage has an equal probability of giving rise to two daughter lineages at any given time (Nee *et al.*, 1992). The fit of the observed distribution to each null distribution was tested using a χ^2 goodness-of-fit test, with species richness grouped into three classes (1–2, 3–4 and >4). This was performed to ensure that frequencies in all cells were large enough to meet the assumptions of the test, as relatively few genera have more than four species (see Fig. 1a). We then identified those genera which have significantly more species than expected under the null models, by examining whether the number of species for each genus was larger than the 95th percentile value of the null distributions.

We used Strahan's (1995) reference, 'The Mammals of Australia' to compile a database of body sizes (mean female mass), reproductive rates (mean litter size) and generation times (mean female age at first breeding), for as many species as possible. Litter size was used as a measure of reproductive rate because the number of litters per year is not known reliably for many species. Where several published values were obtained for the same species, the arithmetic mean value was used. Geographic range size was measured from distribution maps published in Strahan (1995), using a Planix 56 digital planimeter (Tamaya Technics Inc., Tokyo, Japan) to digitize distribution boundaries which were then scaled to square kilometres. For 65 species for which the distribution is known to have declined in the past 200 years, Strahan (1995) provides estimates of the extent of distribution at the time of European settlement, based on indigenous knowledge and historical records. Where given, these reconstructed distributions were used to measure range size. We used clade averages (mean values of all species in a clade) for each of the four variables in the analyses.

We analysed sister-clade contrasts to test for correlates of diversification rates in a way which controls for differences in the ages of clades (Barraclough *et al.*, 1998). To identify pairs of sister clades, we used a

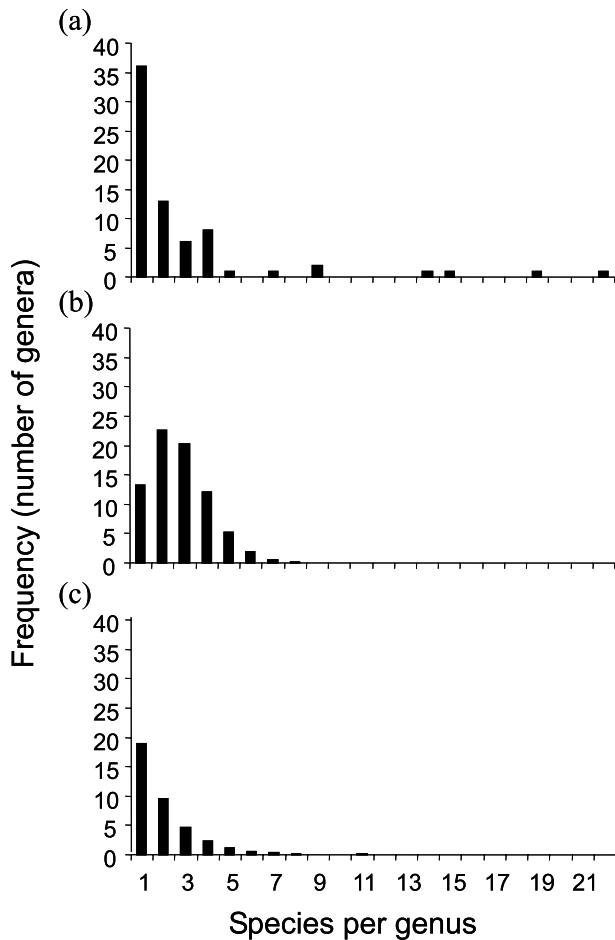


Fig. 1 Frequency distributions of 210 species of Australian mammals among 76 genera: (a) the observed distribution, (b) the random distribution expected under a Poisson model, (c) the random distribution expected under a Geometric model.

composite phylogeny of Australian mammals compiled from published phylogenies (see Cardillo & Bromham, 2001). From this phylogeny we selected the maximum number of phylogenetically independent (nonoverlapping) pairs of sister genera, with several genera grouped together in some cases to provide a monophyletic clade (Table 1). For each pair of sister clades, contrasts in species richness were calculated as: $1 - (\text{lower value} / \text{higher value})$. Calculating contrasts in this way results in a set of contrasts bounded between zero and one, in which larger differences in species richness between sister clades are represented by larger contrast values. Calculating contrasts as ratios rather than differences ensures that the sizes of contrasts are unaffected by the magnitude of species richness values. For each test, contrasts were labelled positive or negative, depending on the direction of the association with the predictor variable. Under the null hypotheses of no associations between diversification rate and each predictor variable,

Table 1 Pairs of sister clades used in the analysis.

Clade 1	Species	Clade 2	Species
<i>Perameles</i>	4	<i>Isodon</i>	3
<i>Macrotis</i>	2	<i>Chaeropus</i>	1
<i>Caloprymus</i> / <i>Aepyprymnus</i> / <i>Bettongia</i>	6	<i>Potorous</i>	3
<i>Macropus</i> / <i>Wallabia</i>	14	<i>Onychogalea</i>	3
<i>Petrogale</i>	15	<i>Dendrolagus</i>	2
<i>Cercartetus</i>	4	<i>Burramys</i>	1
<i>Wyulda</i> / <i>Trichosurus</i>	3	<i>Spilocuscus</i> / <i>Phalanger</i>	2
<i>Vombatus</i> / <i>Lasiorninus</i>	3	<i>Phascogale</i>	1
<i>Antechinus</i>	8	<i>Phascogale</i>	2
<i>Dasyurus</i> / <i>Parantechinus</i> / <i>Pseudantechinus</i>	8	<i>Dasyurus</i> / <i>Sarcophilus</i>	5
<i>Sminthopsis</i>	18	<i>Ningau</i>	3
<i>Rattus</i>	7	<i>Pogonomys</i>	1
<i>Conilurus</i> / <i>Leporillus</i> / <i>Mesembriomys</i>	6	<i>Melomys</i>	3
<i>Zyzomys</i>	5	<i>Uromys</i>	2
<i>Pseudomys</i> / <i>Mastacomys</i>	23	<i>Notomys</i>	9

the number of positive and negative contrasts, and their combined magnitudes, should be approximately equal. We used nonparametric Wilcoxon signed-ranks tests to test for significant departures from this expectation. For geographical range size, a two-tailed test was used as both larger and smaller range sizes have been predicted to be associated with faster diversification. For all other variables, one-tailed tests were used.

Results

The distribution of the 210 species of Australian terrestrial mammals among the 76 genera is significantly different from both Poisson ($\chi^2_2 = 24.12$, $P < 0.0001$) and Geometric ($\chi^2_2 = 32.27$, $P < 0.0001$) null distributions. The observed distribution has more species-poor and more species-rich genera than expected under both null models (Fig. 1). For example, there are 36 genera containing only one species compared with 13.2 and 19 expected under Poisson and Geometric models, respectively. There are four genera containing more than 10 species, although none are expected under the Poisson model and less than one expected under the Geometric model. Seven genera contain significantly ($P < 0.05$) more species than expected under both null models (Table 2): the kangaroos (*Macropus*), rock wallabies (*Petrogale*), antechinuses (*Antechinus*), dunnarts (*Sminthopsis*), rats (*Rattus*), hopping mice (*Notomys*) and 'false mice' (*Pseudomys*).

We identified 15 phylogenetically independent pairs of sister clades from the Australian mammal phylogeny (Table 1), although not all pairs had sufficient data for all four variables (geographical range size, body size, litter size and age at first breeding). Results of the four tests are shown in Table 3. Geographic range size showed a

Table 2 Genera containing significantly more species than expected by chance under both Poisson and Geometric null models, as described in the text. *P* is the proportion of genera under the null distribution which contain more species than the observed values, and corresponds to the probability that each genus contains that many species by chance.

Genus	Number of species	<i>P</i> (Poisson)	<i>P</i> (Geometric)
<i>Pseudomys</i>	22	<0.0001	<0.0001
<i>Sminthopsis</i>	18	<0.0001	<0.0001
<i>Petrogale</i>	15	<0.0001	<0.0001
<i>Macropus</i>	14	<0.0001	<0.0001
<i>Notomys</i>	9	0.0005	0.002
<i>Antechinus</i>	8	0.002	0.004
<i>Rattus</i>	7	0.009	0.008

Table 3 Results of Wilcoxon signed-ranks tests on sister-clade contrasts for the effects of geographical range size and life history on rates of diversification. Positive contrasts are those in which the association with species richness is positive. *P*-values shown are based on a two-tailed test for geographical range size, one-tailed tests for female mass, litter size and age at first breeding.

Variable	Contrasts	Positive contrasts	<i>P</i> -value
Geographic range size	15	12	0.04
Female mass	14	7	0.44
Litter size	9	7	0.02
Age at first breeding	9	5	0.38

positive association ($P = 0.04$, two-tailed test) with diversification rate: clades with larger mean ranges tended to contain more species than their sister clades with smaller ranges. Litter size also showed a positive association with diversification rate ($P = 0.02$, one-tailed test): clades with larger mean litters tended to have more species than their sisters with smaller litters. Neither body size nor age at first breeding showed a significant association with diversification rate.

Discussion

In this study we have used the Australian terrestrial mammal fauna to test several hypotheses for the variation in numbers of species among higher taxa. In Australian mammals variation in species richness is greater than expected under two null models, suggesting that species richness patterns are the result of more than just a random process of cladogenesis. There are a number of possible null models for the phylogenetic distribution of species richness, and our conclusion that species are nonrandomly distributed depends on the assumptions of the particular models we have chosen. However, our result is consistent with previous work: nonrandom distributions of species among higher taxa appear to be the rule within a wide range of animal

assemblages, when tested against a variety of null models (Dial & Marzluff, 1989; Owens *et al.*, 1999).

Using contrasts between sister-clades to control for differences in clade age, we have shown that at least part of the variation in species richness in Australian mammals is associated with two traits, geographical range size and litter size. These two traits are not correlated with each other among species (regression through the origin on phylogenetically independent contrasts: $r^2 = 0.003$, $P = 0.71$), so it is likely that they are each associated independently with diversification rate. The sister-clade relationships that we assumed for this analysis were based on a composite phylogeny from the most recent and comprehensive phylogenies available. However, the patterns we have found may need to be re-examined if future work produces conflicting estimates of Australian mammal phylogeny. Another assumption of our analysis is taxonomic equivalence: whether a 'species' in one clade represents the same level of evolutionary divergence as a 'species' in a different clade. This would be a particular problem if the way in which taxonomists define species boundaries was systematically related to the variables we have tested. This seems unlikely for reproductive rate or generation time because species are rarely delineated on the basis of life history traits (with the possible exception of body size, which was not a significant correlate of diversification rate in this study). On the other hand, it is possible that geographical range size has some influence on species definitions: widely separated populations of a species spread over a large geographical area may be more likely to be considered separate species than less widely separated populations. Although this effect might bias towards a negative relationship between range size and diversification rate, it is difficult to see how it could bias towards the positive relationship that we have found.

The positive association between mean geographical range size and rate of diversification suggests that larger ranges are associated with either lower extinction rates or higher speciation rates, or both. Larger ranges may reduce the risk of extinction of a species by allowing the species to attain a higher total population size (Gaston & He, 2002), and by giving the species access to more refuges from disturbances. Therefore, a local area from which a subpopulation goes extinct is more likely to be repopulated from elsewhere in the species' range, reducing the extinction risk of the species as a whole. This is supported by evidence that contemporary extinction risk in mammals is strongly influenced by geographical range size (Purvis *et al.*, 2000a). Nevertheless, it is also possible that the positive association between range size and diversification rate results from a higher speciation rate, depending on the predominant mechanism of speciation. In particular, this could result from a combination of two processes: (1) If larger ranges are more likely to be intersected by geographical barriers, so that species with larger ranges are subject to higher rates of

allopatric speciation (Rosenzweig, 1995), (2) If geographical ranges of newly formed daughter species expand early in the species' history, to approximate the size of the range of the parent species (Jablonski, 1987; Webb & Gaston, 2000). If both of the above processes occur commonly, a clade in which species have larger ranges would have a higher speciation rate without an ongoing reduction in the mean size of ranges through allopatric subdivision. The result would be a positive association between diversification rate and mean geographical range size. However, this idea assumes that parent and daughter species are not kept separated by competitive exclusion, or by the continued existence of the geographical barrier which led to the speciation event in the first place. Until more evidence comes to light to support a particular model of range division and expansion in mammals, a lowered extinction rate seems a more plausible explanation for the observed positive association between range size and diversification rate.

The only previous study to have tested for a link between mean range size and diversification rates using phylogenetic methods used New World birds as a model assemblage, and found no significant association (Gaston & Blackburn, 1997). Why should there be a range size effect in Australian mammals but not New World birds? One possibility is that the factors which determine extinction rates may differ between the two assemblages. The majority of New World bird species inhabit the tropical regions of South and Central America and have relatively small breeding ranges (Blackburn & Gaston, 1996a,b). Small ranges may be more viable in this relatively productive, stable region than in the low-productivity, highly unpredictable environments which characterize most of the Australian continent. Therefore, range size may be a less-important determinant of extinction rates in the New World than in Australia. It is also possible that greater dispersal abilities provided by flight allow birds to more easily avoid environmental disturbances, again making small geographical ranges a less critical influence on extinction rates. Comparing the effect of geographical range size on diversification rate between taxa which differ in their dispersal abilities would be one way of testing this hypothesis.

Our study also provides evidence that higher diversification rates are associated with larger litters. The most likely explanation for this is that species with larger litters have a reduced risk of extinction. Larger litters contribute to a higher intrinsic rate of population increase, which may allow populations reduced by disturbances to recover rapidly, as well as the rapid establishment of populations by colonists of new areas. This link is supported by evidence that larger litters are also significantly associated with reduced contemporary extinction risk in Australian mammals (Cardillo, in press). However, it is also possible that the positive association between litter size and diversification rate results from an elevated speciation rate. Marzluff & Dial

(1991) argued that a higher reproductive output increases the successful colonization of new areas, promoting range expansion and subsequent diversification as populations adapt to new resources. Larger litters might also increase the available genetic variation in each generation, which could enhance the rate of speciation if genetic variation is limiting for adaptation, or if genetic variation drives the divergence of isolated populations. This suggestion is consistent with observed associations between clutch size and rate of molecular evolution in snakes (Bromham, 2002) and between rate of molecular evolution and rate of species diversification in passerine birds and angiosperms (Barracough *et al.*, 1998; Barracough & Savolainen, 2001).

Two other aspects of life history examined in this study, age at first breeding and body size, showed no association with diversification rate. These results are largely consistent with the findings of previous studies. Although Marzluff & Dial (1991) found a significant association between age at first breeding and diversification rate in mammals generally, they found no such association in rodents or marsupials, the two orders which make up the Australian terrestrial mammal fauna. Similarly, Owens *et al.* (1999) found no association between age at first breeding and diversification rate in birds. Of the studies which have used phylogenetic methods to examine the link between body size and diversification rate in various taxa, only one (Gittleman & Purvis, 1998) found a significant association, and then only within two subclades of the Carnivora. A detailed phylogenetic analysis of the link between body size and diversification rate across 38 phylogenies from a wide range of taxa (Orme *et al.*, 2002) concluded that there is little evidence for an effect of body size on diversification rates. Rather than diversification rate being elevated by a fast life history 'package', it seems that particular aspects of life history, such as litter size, are important, while others, such as body size, have little or no effect.

The lack of an association between body size and diversification rates in Australian mammals is surprising in the light of the megafaunal extinction event of the late Pleistocene. As on many other continents, most of Australia's large mammal species (>10 kg) disappear from the fossil record from 100 000 to 20 000 years ago: examples include the 2000-kg *Diprotodon*, and *Procoptodon*, a 200-kg macropod (Flannery, 1990). Although this might be expected to have biased the present-day distribution of species richness in favour of clades with smaller-bodied species, this was not evident from our study. In fact, our result is consistent with a recent discovery by Johnson (2002) that it was not body size which determined the likelihood of mammal extinction during the late Pleistocene, but reproductive rate. Using reproductive rates of extinct species reconstructed from their body sizes, Johnson showed that species with low annual reproductive output were less likely to have survived, regardless of their body size. Hence, both our

analysis of body size – diversification patterns, and Johnson's analysis of the mechanisms of Pleistocene mammal extinctions, agree that Pleistocene mammal extinctions may actually have been less size-biased than is apparent from the fossil record.

The results of this study, together with those of Johnson (2002), also have implications for the question of whether extinction rates over long timescales (and hence macro-evolutionary patterns) and present-day extinction risk status in contemporary assemblages have common biological drivers (Purvis *et al.*, 2000b). Some traits appear to influence extinction on different timescales: litter size and geographical range size show positive associations with diversification rates as shown here, as well as negative associations with contemporary extinction risk (Purvis *et al.*, 2000a; Cardillo, in press). However, the lack of an association between body size and diversification rates in this and other studies (Orme *et al.*, 2002) contrasts with findings that smaller-bodied mammal species seem to be less vulnerable to contemporary extinction threats than larger species (Purvis *et al.*, 2000a; Cardillo & Bromham, 2001). Contemporary declines and extinctions result from rapid processes associated with recent human modification of landscapes, such as rapid habitat loss or degradation, or the introduction of exotic predators and competitors. The association between body size and extinction threat can vary depending on the type of threat most commonly encountered. For example, Owens & Bennett (2000) showed that human persecution and predation has a greater effect on larger-bodied bird species, while habitat loss has a greater effect on smaller species. The great change in extinction threats brought about by recent human activity, compared with the slower processes which elevate extinction rates over evolutionary timescales, might mean that larger-bodied species are comparatively more vulnerable now than they have been in the past.

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