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Extrinsic versus intrinsic factors in the decline and extinction of Australian marsupials

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Recent attempts to explain the susceptibility of vertebrates to declines worldwide have largely focused on intrinsic factors such as body size, reproductive potential, ecological specialization, geographical range and phylogenetic longevity. Here, we use a database of 145 Australian marsupial species to test the effects of both intrinsic and extrinsic factors in a multivariate comparative approach. We model five intrinsic (body size, habitat specialization, diet, reproductive rate and range size) and four extrinsic (climate and range overlap with introduced foxes, sheep and rabbits) factors. We use quantitative measures of geographical range contraction as indices of decline. We also develop a new modelling approach of phylogenetically independent contrasts combined with imputation of missing values to deal simultaneously with phylogenetic structuring and missing data. One extrinsic variable—geographical range overlap with sheep—was the only consistent predictor of declines. Habitat specialization was independently but less consistently associated with declines. This suggests that extrinsic factors largely determine interspecific variation in extinction risk among Australian marsupials, and that the intrinsic factors that are consistently associated with extinction risk in other vertebrates are less important in this group. We conclude that recent anthropogenic changes have been profound enough to affect species on a continent-wide scale, regardless of their intrinsic biology.

Keywords: endangered species; extinction; phylogenetic comparative methods; introduced species; mammals; multiple imputation

1. INTRODUCTION

In his influential assessment of extinctions in modern species, Diamond (1989) reported that four extrinsic processes were the main culprits: the evil quartet of habitat loss, over-exploitation, introduced species and chains of extinction. However, recent analysis of extinction risk in vertebrates has shifted the focus away from extrinsic mechanisms of decline, and on to how intrinsic factors are related to threatened species status. These studies have identified body size, life history, geographical range size, trophic level, habitat use, ecological and social specialization, and phylogenetic-lineage age as risk factors (Bennett & Owens 1997, 2002; Gaston & Blackburn 1997; Purvis *et al.* 2000; Harcourt *et al.* 2002; Johnson *et al.* 2002; Cardillo 2003). It is often not clear why certain traits affect species' sensitivity to the particular extrinsic disturbances responsible for declines. Extrinsic and intrinsic factors have rarely been modelled together (but see Blackburn & Gaston (2002) and Owens & Bennett (2000) for birds).

In Australia, explanations for the pattern of mammal extinctions have been based on associations between threat status and intrinsic factors, particularly diet (herbivory), habitat (arid climate zone, non-forest habitat) and a nonlinear relationship with body size (Burbidge & McKenzie 1989; Morton 1990; Smith & Quin 1996). These attributes are themselves correlated, and until

recently (Cardillo & Bromham 2001; Johnson *et al.* 2002; Cardillo 2003) no attempt was made to partition out independent effects. It has generally been assumed that there are common extrinsic causes of most declines of Australian marsupials, because declines closely followed European settlement and the spread of introduced grazers and predators (red foxes) in different parts of the continent. However, this assumption has never been quantitatively tested. A widely accepted interpretation has been that 'critical weight range' (CWR) species (those weighing 35–5500 g; Burbidge & McKenzie 1989) declined the most, because mammals of this size are particularly vulnerable to predation by foxes, especially when ground-level shelter and food are depleted by sheep and rabbits (Burbidge & McKenzie 1989; Morton 1990). Morton (1990) attributed the susceptibility to extinction of CWR arid-zone mammals to their low mobility, reliance on fertile sites also preferred by stock and high energy requirements. More recent studies have concluded that the fact that CWR mammals were the preferred prey size of foxes may often be sufficient explanation for their decline (Short & Smith 1994; Smith & Quin 1996; Short 1998). However, the premise behind all of these scenarios has recently been challenged by Cardillo & Bromham (2001), who showed that the CWR is an artefact of the distribution of Australian mammal body sizes, such that risk is randomly distributed with respect to body size, except in small species, which are more likely to persist.

The overall aim of this study is to understand the ecological basis of interspecific variation in decline and extinction in Australian marsupials. Cardillo & Bromham

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(2001) and Johnson *et al.* (2002) both found that some lineages are more extinction-prone than others, but the reasons for this remain unclear. We quantify and directly test the hypothesis that range declines are explained by variation in a combination of extrinsic factors (overlap with fox, rabbit and sheep distributions, rainfall) and intrinsic factors (reproductive rate, body weight, habitat specialization, past geographical range, diet). We also introduce a new technique, based on multiple imputation, for dealing with missing data in comparative analyses.

2. MATERIAL AND METHODS

(a) *Data and definitions*

We investigated five intrinsic factors (body size, reproductive rate, habitat specialization, diet and former geographical range size) and four extrinsic factors (annual rainfall and the extents of range overlaps with the current geographical distributions of the European red fox, rabbit and sheep). We did not include phylogenetic-lineage age (Johnson *et al.* 2002) because this measure cannot be included in phylogenetic comparative analyses based on species-level data. The dataset consisted of all 145 Australian marsupial species of known geographical range and body size, with only a handful of very poorly known species being omitted. Detailed definitions and datasets for reproductive rate (number of offspring produced per female per year), climate (annual mean rainfall in the centre of the geographical range) and body size are given in Fisher *et al.* (2001). Type of diet was ranked as follows: 4, greater than 50% invertebrates or vertebrates; 3, nectar or fruit with invertebrates; 2, seeds, grass, roots, leaves, fruit and invertebrates; 1, greater than 50% grass or browse. Habitat specialization was defined as the number of vegetation structural types used, as reported in Strahan (1995) and Maxwell *et al.* (1996) (categories based on Specht (1970)). Former geographical range sizes were calculated by overlaying a grid of *ca.* 50 km × 50 km squares onto digitized range maps from Strahan (1995) and counting overlapping grid squares. The same approach was used to compare former ranges of marsupials before European occupation with the current distributions of sheep, rabbits and foxes taken from distribution maps in Smith & Quin (1996). All maps were based on equal-area projections. Body size, range size and reproductive rate were \log_{10} -transformed, and range overlaps were arcsine-transformed.

We used two different indices of range decline as the dependent variable. The first index, hereafter referred to as 'persistence', was calculated using the Anscombe transformation,

$$\arcsin\left(\sqrt{\frac{E + 3/8}{P + 3/4}}\right),$$

where E is the current range size and P is the original range size (measured in number of grid squares; 2500 km² units) (Anscombe 1948). An Anscombe transformation was used because it performs better than the traditional arcsine transformation for proportion data if values of zero and one are common. The grid-square method given above was also used to calculate the former and current ranges given in Strahan (1995), which consist of coarse-grained maps showing geographical ranges (but not patchiness of occupation) compiled from museum records and historical accounts. The second index of decline, hereafter referred to as 'decline score', was one criterion used to assign IUCN categories of threat to marsupials (Maxwell *et al.* 1996), and is a rank of decline accounting for distribution patchiness. The persistence measure differs in direction from the decline

score, because if current range size is large in relation to former range size, persistence will be high (less decline), whereas the decline score is largest for extinct species. We did not use IUCN categories of extinction risk as an index of range decline for two reasons; first, because they include non-declining species with naturally small ranges, and, second, because some intrinsic factors used in our models were used to assign IUCN threat status (e.g. low reproductive rate and small geographical range; Maxwell *et al.* 1996; Bennett & Owens 1997). In analysing past declines rather than current categories of extinction risk or current population sizes, we take the 'declining population paradigm' approach of Caughley (1994).

Our use of two different indices of decline reduced the possibility that artefacts of the scoring method influenced our results. The persistence measure derived from maps (Strahan 1995) did not take account of distribution patchiness caused by habitat variation, thus it was imprecise for species with very small ranges. The decline score did account for distribution and habitat discontinuities at all scales, and may have been more contemporary because it was based on the opinions of current researchers (Maxwell *et al.* 1996). However, methods of assigning decline scores were inconsistent. For example, recent declines of some forest species such as tree kangaroos, but not historical declines of grassland dwellers, were partly inferred from habitat-clearing rates rather than distribution surveys.

(b) *Statistical analysis*

To minimize the risk that our results are an artefact of the comparative method employed, we performed analyses both on raw species values and on phylogenetically independent contrasts (Felsenstein 1985). Contrasts were calculated using the composite marsupial phylogeny given in Fisher *et al.* (2001), using branch lengths with node height proportional to clade size. We tested for correlations between the absolute values of contrasts and their standard deviations, to check whether type I error rate needed to be controlled by adjusting branch lengths (Diaz-Uriarte & Garland 1998). Body weight and diet need no branch-length transformation, as the correlations between the absolute values of the contrasts and their standard deviations were not significant. Variables other than body weight and diet were transformed with the Ornstein–Uhlenbeck (OU) procedure (Felsenstein 1988; Blomberg *et al.* 2003). We used the implementation described in Blomberg *et al.* (2003), with an OU parameter equal to 0.667, which produced a tree with extended terminal and compressed internal branches. We used the 'ape' package for *R* to calculate contrasts (Ihaka & Gentleman 1996; Paradis *et al.* 2002). Multiple regressions of independent contrasts were then performed through the origin.

Geographical range size may not be inherited strictly phylogenetically, meaning that the underlying model of evolution implied by calculating contrasts may not be correct. However, we used calculated phylogenetically independent contrasts of range size for simplicity, because studies of mammalian range size under alternative models of evolution have come to equivalent conclusions (Letcher & Harvey 1994).

Out of the 145 species, 43 were missing data on reproductive rate and/or habitat specialization, out of which 10 were extinct species. Potential biases from these missing data could have been a serious problem because it was important to include species that are now extinct, or that declined very severely during the nineteenth century (when most extinctions occurred), in our analyses. Rather than discarding a third of the data, and thereby running the risk of biasing our analyses through non-

random taxon selection (Ackerly 2000), we used multiple imputation (MI) of missing data to create five replicate datasets (Rubin 1977, 1987). The goal of MI is to provide unbiased estimates of parameters from data, together with standard errors that take account of the imputation procedure, via the following steps (Allison 2000): (i) impute missing values according to an appropriate model, incorporating variation; (ii) repeat M times, producing M 'complete' datasets; (iii) analyse each dataset using standard statistical techniques; (iv) calculate parameter estimates by averaging the estimates from the M datasets to produce point estimates; (v) calculate standard errors for parameter point estimates by initially averaging squared standard errors of the M estimates, then calculating the variance of the parameter estimates across datasets; and finally (vi) combine the two quantities according to the following formula (Rubin 1987; Barnard & Rubin 1999):

$$s_b = \sqrt{\frac{1}{M} \sum_k s_k^2 + \left(1 + \frac{1}{M}\right) \left(\frac{1}{M-1}\right) \sum_k (b_k - \bar{b})^2},$$

where s_b is the final standard error of the point estimate, M is the number of imputed datasets, s_k is the standard error for the k th dataset, b_k is the parameter estimate (e.g. a regression coefficient) for the k th dataset and \bar{b} is the mean of the parameter estimates over the M datasets.

To impute individual data points, we employed predictive mean matching (Little 1988), a semi-parametric stochastic regression method where a multiple regression model is first used to find a complete 'donor' case whose predicted regression score is closest to the case with the missing value. The missing value is then replaced by the one from the donor case. Stochastic variation is introduced into the process because the values for the beta coefficients in the regression model are chosen at random from their joint posterior distribution, which is simulated using a Markov chain Monte Carlo procedure (e.g. van Buuren & Oudshoorn 2000). Calculations were carried out in the 'mice' package for *R* (Ihaka & Gentleman 1996; van Buuren & Oudshoorn 2000).

We imputed the raw dataset five times, to construct five new complete datasets. We then computed phylogenetically independent contrasts for each of the five datasets. We next conducted a stepwise multiple regression on each imputed dataset, to obtain a 'consensus' model. A variable was included in the consensus model if it was included in the majority of the five models arrived at by the stepwise procedure. We performed the same process for the five sets of independent contrasts. We then analysed the resulting consensus models to obtain pooled parameter estimates and standard errors separately for both the raw species data and the independent contrasts, using the pooling procedure for MI, outlined above.

MI was first developed for use with survey datasets in the social sciences (e.g. Rubin 1987), but we suggest that it may also prove useful for multivariate comparative datasets where missing data is an obvious problem (see Ackerly 2000). One limitation to its use in cross-species analysis is that there are currently no imputation methods that incorporate phylogenetic information. While phylogenetic methods would be preferable, ordinary predictive mean matching should produce similar results if the donor case is usually a close relative of the species with the missing data.

The main assumption in MI is that values in the dataset are missing at random (MAR). This does not mean that missing values must be a random subsample of the entire dataset (i.e.

missing completely at random), but simply that the probability of being missing can depend on the observed data, but not on those data that are missing (Schafer & Olsen 1998). Unfortunately, it is not possible to test this assumption without additional data, and it is not possible to relax the MAR assumption without replacing it with other equally non-testable assumptions. However, methods that assume MAR are expected to perform better than *ad hoc* procedures such as the deletion of incomplete cases, or single imputation involving replacing the missing value with the group mean (Schafer & Olsen 1998). It is also important to remember that the problem of non-random missing data is a general problem in comparative analyses, not just in those using MI. As Ackerly (2000) has recently shown, non-random missing data can lead to serious problems in the interpretation of comparative analyses that use case-wise deletion to cope with missing values. Such biases are, however, typically ignored in multivariate comparative models. An exception is Purvis *et al.* (2000), who, using a heuristic stepwise model selection procedure, reintroduced previously deleted variables into the model in cases where dropping a variable led to an increased sample size (owing to fewer missing values in the reduced dataset). MI provides an alternative simple and efficient approach to the problem of missing data that is well grounded in statistical theory (Rubin 1987).

Because this is, to our knowledge, the first use of MI in conjunction with phylogenetic methods, we repeated our analyses without MI, by building standard stepwise multiple regressions using independent contrasts and case-wise deletion of missing values (after appropriate branch-length transformations as above).

3. RESULTS

(a) *Analyses based on raw species data*

We calculated that 40% (persistence) or 51% (decline score) of Australian marsupial species have declined. Our two measures of range decline were incompletely correlated ($r = 0.84$, $p < 0.0001$), indicating that the two measures disagreed about the extent of decline for many species. Nevertheless, analysis of raw species data showed that several intrinsic and extrinsic factors were significantly correlated with decline. Body weight was the most important predictor of decline for both the persistence and the decline-score measures (tables 1 and 2), and in both cases, this relationship was nonlinear (humped). The extent of range overlap with sheep was strongly significant for both measures. Decline was also associated with lower rainfall for both measures of decline, and with habitat specialization and a more vegetarian diet (marginally non-significantly for the decline-score measure). Range overlaps with rabbits and foxes were not independently correlated with decline, although range overlaps between the three introduced species were correlated with each other, especially in the case of sheep and foxes (sheep versus foxes: $r = 0.85$, $p < 0.0001$; foxes versus rabbits: $r = 0.56$, $p < 0.0001$; rabbits versus sheep: $r = 0.60$, $p < 0.0001$). According to the persistence measure, species that had larger original geographical ranges have declined more (table 1). Reproductive rate was not associated with any variation in either persistence or decline score. Approximately 40% of the variation was explained in both models.

Table 1. Results of stepwise multiple regression model of range persistence, using raw species data.

(Degrees of freedom for each parameter do not equal the model denominator degrees of freedom because the multiple imputation procedure adjusts the degrees of freedom to account for missing data (Barnard & Rubin 1999). Range persistence calculated from Strahan (1995); 95% CI is the 95% confidence interval of the coefficient estimate. Mean multiple $r^2 = 0.44$, mean $F_{7,134} = 15.2$, $p < 0.0001$.)

variable	coefficient	95% CI	<i>t</i>	d.f.	<i>p</i>
variables in final model					
intercept	3.15	2.61 to 3.69	11.5	132	< 0.0001
weight ²	0.19	0.12 to 0.27	5.3	117	< 0.0001
habitat number	0.03	0.001 to 0.054	3.2	98	0.0002
rain	0.0002	7.5×10^{-6} to 0.0003	2.1	120	0.004
diet	-0.11	-0.21 to -0.023	-2.5	95	0.015
past range	-0.15	-0.28 to 0.001	-2.2	122	0.003
sheep	-0.29	-0.45 to -0.14	-3.7	126	0.0003
weight	-1.24	-1.61 to -0.87	-6.6	122	< 0.0001
variables not in final model					
rabbit	0.12	-0.17 to 0.40	0.8	129	0.42
fox	0.10	-0.17 to 0.37	0.7	131	0.47
reproductive rate	-0.002	-0.003 to 0.02	-0.2	52	0.86

Table 2. Results of stepwise multiple regression model of range-decline score, using raw species data.

(Degrees of freedom for each parameter do not equal the model denominator degrees of freedom because the multiple imputation procedure adjusts the degrees of freedom to account for missing data (Barnard & Rubin 1999). Range-decline scores are from Maxwell *et al.* (1996); 95% CI is the 95% confidence interval of the coefficient estimate. Mean multiple $r^2 = 0.40$, mean $F_{6,135} = 14.9$, $p < 0.0001$.)

variable	coefficient	95% CI	<i>t</i>	d.f.	<i>p</i>
variables in final model					
weight	9.26	6.60 to 111.93	6.9	130	< 0.0001
sheep	1.83	0.74 to 2.91	3.34	133	0.0001
diet	0.61	-0.05 to 1.26	1.8	107	0.07
rain	-0.002	-0.003 to -0.0009	-4.15	133	< 0.0001
habitat number	-0.14	-0.27 to -0.02	-2.25	100	0.003
weight ²	-1.52	-2.04 to -0.99	-5.74	127	< 0.0001
intercept	-8.93	-12.44 to -5.44	-5.04	132	< 0.0001
variables not in final model					
past range	0.49	-0.52 to 1.50	0.96	124	0.34
reproductive rate	0.02	-0.17 to 0.20	0.18	41	0.86
fox	-0.42	-2.38 to 1.55	-0.42	131	0.68
rabbit	-0.55	-2.63 to 1.53	-0.52	130	0.60

(b) Analyses based on contrasts

Our two measures of range decline were also correlated in the phylogenetic comparative analysis ($r = 0.31$, $p = 0.0002$). Despite body weight being the most powerful predictor of marsupial declines in the raw species data, neither body size nor rainfall were correlated with decline after we accounted for non-independence caused by shared ancestry. The only contrast variable significantly associated with both measures of decline was range overlap with sheep (tables 3 and 4). One intrinsic variable, habitat specialization, was also included in the stepwise regression models of both measures of decline and was significant for persistence but not for decline score. No other variables were consistently important. Species that had larger original geographical ranges were more likely to have declined according to the persistence measure but not the decline score (tables 3 and 4). Only 7–13% of the

variation was explained in both models. Range overlaps between the three introduced species were also correlated with each other when contrasts were considered, especially in the case of sheep and foxes (sheep versus foxes: $r = 0.9$, $p < 0.0001$; foxes versus rabbits: $r = 0.71$, $p < 0.0001$; rabbits versus sheep: $r = 0.74$, $p < 0.0001$).

When we calculated contrasts without imputing missing data, the range overlap with sheep was still the only consistently important variable ($p = 0.007$ and coefficient value of -0.25 for persistence, and $p = 0.04$ and coefficient value of 1.4 for decline score). Past geographical range and habitat specialization were also still independently significantly correlated with persistence, but not with decline score ($p = 0.01$ and coefficient value of -0.15, and $p = 0.04$ and coefficient value of 0.02, respectively). In contrast to the MI method, when we analysed the data with the traditional case-wise deletion

Table 3. Results of stepwise multiple regression model of range persistence, using contrast data.

(Degrees of freedom for each parameter do not equal the model denominator degrees of freedom because the multiple imputation procedure adjusts the degrees of freedom to account for missing data (Barnard & Rubin 1999). Range persistence calculated from Strahan (1995); 95% CI is the 95% confidence interval of the coefficient estimate. Mean multiple $r^2 = 0.13$, mean $F_{3,138} = 6.69$, $p = 0.0003$.)

variable	coefficient	95% CI	<i>t</i>	d.f.	<i>p</i>
variables in final model					
habitat number	0.03	0.01 to 0.05	3.24	104	0.002
past range	−0.15	−0.27 to −0.04	−2.30	132	0.010
sheep	−0.29	−0.44 to −0.13	−3.58	134	0.0005
variables not in final model					
rabbit	0.11	−0.20 to 0.42	0.70	127	0.49
diet	0.03	−0.02 to 0.08	1.16	127	0.25
fox	0.03	−0.28 to 0.34	0.19	131	0.85
reproductive rate	0.02	−0.009 to 0.04	1.22	106	0.23
weight	0.02	−0.03 to 0.07	0.73	129	0.47
weight ²	0.004	−0.008 to 0.01	0.63	130	0.53
rain	0.00002	−0.0001 to 0.0002	0.27	130	0.79

Table 4. Results of stepwise multiple regression model of range-decline score, using contrast data.

(Degrees of freedom for each parameter do not equal the model denominator degrees of freedom because the multiple imputation procedure adjusts the degrees of freedom to account for missing data (Barnard & Rubin 1999). Range-decline scores are from Maxwell *et al.* (1996); 95% CI is the 95% confidence interval of the coefficient estimate. Mean multiple $r^2 = 0.07$, mean $F_{2,139} = 5.39$, $p = 0.0056$.)

variable	coefficient	95% CI	<i>t</i>	d.f.	<i>p</i>
variables in final model					
sheep	1.79	0.61 to 2.96	3.01	136	0.003
habitat number	−0.14	−0.28 to 0.006	−1.90	84	0.06
variables not in final model					
past range	0.49	−0.66 to 1.64	0.84	125	0.40
fox	0.04	−2.28 to 2.36	0.04	130	0.97
rain	−0.0006	−0.002 to 0.0007	−0.90	130	0.37
weight	−0.03	−0.41 to 0.36	−0.13	129	0.90
weight ²	−0.04	−0.13 to 0.04	−1.01	129	0.31
reproductive rate	−0.07	−0.26 to 0.12	−0.69	67	0.49
diet	−0.23	−0.59 to 0.14	−1.24	125	0.22
rabbit	−0.43	−2.79 to 1.93	−0.36	128	0.72

method, annual reproductive rate was correlated with persistence ($p = 0.01$, coefficient value of 0.04). Annual reproductive rate was not correlated with decline score.

4. DISCUSSION

Our results indicate that variation in an extrinsic variable—range overlap with an introduced species (the sheep)—is a more consistent predictor of decline and extinction of Australian marsupials than any of the intrinsic variables included in this study. This result is in contrast to recent findings that body size, diet, geographical range size, ecological specialization and reproductive rate are significantly and independently related to extinction risk for other terrestrial vertebrates (Bennett & Owens 1997, 2002; Purvis *et al.* 2000; Owens & Bennett 2000; Harcourt *et al.* 2002). Duncan & Lockwood (2001) attributed their failure to find correlations between declines of freshwater fishes and intrinsic biology to the severity of habitat degradation affecting waterways worldwide. In the

case of marsupials, the mechanism by which sheep affect persistence is also likely to be habitat degradation associated with pastoral expansion, rather than direct competition for food, as herbivory was not independently related to extinction risk in this study or in Johnson *et al.* (2002). We suggest that the impacts of pastoralism and the associated changes in Australian marsupial habitats are so profound that they have affected species on a continent-wide scale, regardless of their reproductive potentials, body sizes and trophic levels, across habitats with varying rainfall. This is consistent with the patterns of range contraction in Australian mammals, which followed the spread of land-use changes and introduced species: many mammals are now restricted to the edges of their former distributions (Channell & Lomolino 2000). Studies of decline trajectories have shown that expansion of alien-mammal distributions and accompanying land-use change closely preceded contraction of many marsupial ranges (Caughley & Gunn 1995; Short 1998). Three-quarters of the species in our dataset with greater than 90% range

decline are now restricted to the western edge of Western Australia, or to offshore islands with minimal human impact. All of these species' ranges contracted to the west, as extrinsic threats moved east to west over several decades. Marsupials in New South Wales (the point of invasion of all the threats, in the southeast) declined earliest (Dickman *et al.* 1993). Rabbits invaded while sheep numbers were near an all-time peak in the 1890s, then foxes invaded, coinciding with the period of greatest mammal losses (Short 1998).

Ecological specialization is thought to increase susceptibility to decline and extinction because more specialized species cope less well with environmental change (e.g. Harcourt *et al.* 2002). In support of this idea, Owens & Bennett (2000) found that ecological specialization was associated with extinction risk in birds that were declining owing to habitat loss, but not in species threatened by predation or hunting. Although no intrinsic variables were consistently significant, habitat specialization was included in all of our models (tables 1–4). Taxa that used fewer habitat types tended to decline more. This was not because species using fewer habitats were geographically restricted to regions containing rare habitats: there was no association between small former range size and decline. A plausible explanation is that marsupials with more specialized habitat requirements are less likely to succeed if they are forced out of their preferred habitats when they are degraded.

Apart from habitat specialization, the main intrinsic ecological and life-history characteristics of declining vertebrates worldwide are: large body size, low reproductive rate, high trophic level and small geographical range size. Body size is implicated because larger species have slower reproduction, lower population densities and are vulnerable to hunting (Diamond 1989; Bennett & Owens 1997; Purvis *et al.* 2000). Low reproductive rate often correlates with decline and extinction because of the inability of slow-breeding animals to recover from local population crashes, which accumulate into large-scale range declines, and because of these species' inability to survive high rates of predation (Bennett & Owens 1997, 2002; Purvis *et al.* 2000). This particularly applies to those species affected by introduced predators that cannot make up for losses to predation through recruitment (Sinclair *et al.* 1998; Owens & Bennett 2000). Nevertheless, we found no correlations between reproductive rate and decline in our analyses. This result contrasts with the conclusion of Cardillo (2003), that mammalian taxa with small litters relative to body size are more threatened, at least in mesic Australian habitats. It is difficult to identify the precise cause of this difference in results, because there are so many methodological differences between the two studies. Plausible explanations include differences in taxonomic scope (Cardillo (2003) included rodents in his dataset, and we used marsupials only), the way in which variables were scored (e.g. litter size versus reproductive rate), the index of decline (IUCN threat status versus geographical range contraction) and the method of handling missing data in multiple regressions (case-wise deletion of all data for species with any values missing versus MI). When we repeated our analyses without MI, we found a positive relationship between persistence and reproductive rate. This was the only qualitative difference between the

results of the two methods, indicating that discarding taxa in which information on reproductive rate was missing from the whole dataset (the standard stepwise multiple regression procedure) would have biased our final results.

Johnson *et al.* (2002) demonstrated that older lineages of marsupials are more vulnerable to extinction. They suggested two possible reasons. One explanation is that taxa become more sensitive to environmental change with time, perhaps because they evolve lower fecundity. Our results do not support this mechanism, but they do support Johnson *et al.*'s alternative explanation that older clades are more vulnerable because they are more specialized.

Although herbivory has been implicated as a risk factor because of the potential competition with stock for food (e.g. Burbidge & McKenzie 1989), we found no independent relationship between diet and decline for contrast data (tables 3 and 4). Carnivory rather than herbivory has been linked to extinction risk in other mammals (e.g. Purvis *et al.* 2000), because carnivores are vulnerable to prey extinctions. This mechanism is unlikely to apply to carnivorous Australian marsupials, as they nearly all rely on insect prey.

Small geographical range size is thought to increase extinction risk because of its relationship with low population size and the associated danger from demographic and environmental stochasticity (Gaston 1994). Unlike other recent studies of birds and mammals (e.g. Channell & Lomolino 2000; Purvis *et al.* 2000; Blackburn & Gaston 2002; Harcourt *et al.* 2002), our study found that small geographical range size did not promote marsupial declines. In fact, geographically restricted species have been somewhat protected from declines (tables 1 and 3). This is consistent with the finding of Johnson *et al.* (2002) that forest-dwelling marsupial taxa are less extinction prone. Forests are geographically restricted in Australia in comparison with the extensive (and degraded) inland plains.

Past explanations for Australian mammal extinctions have been based on the relationship between body size ('CWR status') and decline (Burbidge & McKenzie 1989; Morton 1990; Short & Smith 1994). Analyses that have not incorporated phylogenetic information have invariably found a humped relationship between threat status and body weight (e.g. Short & Smith 1994; Johnson *et al.* 2002). We found no such relationship using contrast data. Our results agree with those of Cardillo & Bromham (2001), who found no relationship between phylogenetic contrasts in body size and extinction risk for Australian mammals in general, although threat status varied between marsupial families. Johnson *et al.* (2002) concluded that marsupial genera vary significantly in their risk of extinction, and that intermediate mean body masses are over-represented in genera containing more threatened species. Nonetheless, our finding, that range overlap with sheep is the strongest and most consistent predictor of decline, supports previous hypotheses that cite habitat degradation by sheep as a major ultimate threat (Burbidge & McKenzie 1989; Morton 1990; Short & Smith 1994; Smith & Quin 1996). We emphasize that this does not mean that other extrinsic factors are not important. Taxa that overlapped substantially with sheep were also likely to encounter high densities of foxes, which

invaded at roughly the same time (Short 1998) (overlap with foxes versus overlap with sheep: $r = 0.85$). Additionally, most of the variation remains unexplained in our multivariate models. This is probably because: (i) the precise combinations of extrinsic threats vary idiosyncratically across species, with no other single factor predominating; and (ii) indices of threatening processes and range decline are necessarily indirect and coarse-grained, adding noise to the model. In particular, a more exact index of the environmental impact of sheep than range overlap might explain more variation.

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