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A comparison of current and reconstructed historic geographic range sizes as predictors of extinction risk in Australian mammals

Emily Hanna *, Marcel Cardillo

Centre for Macroevolution & Macroecology, Research School of Biology, Australian National University, Canberra 0200, Australia

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ABSTRACT

Comparative studies of extinction risk in vertebrate taxa often find that a small geographic range size is the strongest predictor of a high rate of species decline. This suggests that narrowly distributed species are more vulnerable to human impacts, which may have implications for the predictive use of comparative extinction-risk models in conservation planning. However, this association is potentially circular because many species that have suffered substantial declines now have small geographic ranges, making it difficult to separate the role of range size as a predictor of extinction risk from its role as a response to human impact. Here we use data for Australian mammals to compare models of extinction risk that include current geographic range size with models that include historic range sizes reconstructed for the period before European settlement. We find that current range size is a strong predictor of a species' IUCN Red List classification. However, when historic range sizes are used, range size is non-significant and life-history traits assume primary importance in the model. Models that include current range size also tend to underestimate levels of latent extinction risk (the discrepancy between a species' current extinction risk and that predicted from its biological traits), giving misleading predictions of the species and regions with greatest potential for future species declines. The results suggest that there is circularity in the use of current range size to predict rates of species decline, and that species with inherently small distributions are not necessarily the most vulnerable to human impact.

1. Introduction

Nearly a quarter of the world's mammal species are threatened with extinction (IUCN, 2009), with the distribution of threatened species being non-random with respect to geography and phylogeny (Davies et al., 2008; McKinney, 1997; Purvis et al., 2005; Russell et al., 1998). Species declines are driven by external threatening processes such as habitat loss or introduced predators (Davies et al., 2008), and this is reflected in geographic variation in the distribution of threatened species. At the same time, certain phylogenetic groups are more likely to contain threatened species than others, even within the same geographic regions, suggesting that extinction risk is also affected by heritable biological traits. For example, top carnivores may be more vulnerable because their populations tend to be smaller and they are sensitive to declines in prey populations (Carbone and Gittleman, 2002), while mammals with long gestation periods may be more susceptible to decline because they have slow population growth (Gittleman, 1993). The extinction risk of a species can therefore be regarded as the result of exposure to external threatening processes, mitigated or exacerbated by intrinsic biological traits (Cardillo et al., 2005; Fisher et al., 2003).

Although intensive field-based studies of single species remain the cornerstone of conservation biology, multispecies comparative studies can uncover the general patterns of extinction risk that can help explain why some kinds of species seem to be more extinction-prone than others (Cardillo and Meijaard, 2011; Fisher et al., 2003). Comparative models of extinction risk involving hundreds of species have been used to obtain a clearer picture of the broad patterns of extinction risk, and to draw conclusions about the external and intrinsic drivers of species declines in a range of taxa (e.g. Cardillo et al., 2005; Davies et al., 2008; Jones et al., 2003; Owens and Bennett, 2000). Further, comparative models have been used to project species declines into the future in an attempt to predict the species and geographic regions likely to warrant future conservation attention (Cardillo, 2006; Cardillo et al., 2006, 2004).

In comparative studies of extinction risk in mammals, the one factor most consistently and strongly associated with high extinction risk has been a small geographic range size. Small range size has been linked to higher rates of species decline across mammals generally (Cardillo et al., 2008), as well as within particular mammal subgroups including carnivores and primates (Purvis et al., 2000) and megachiropteran bats (Jones et al., 2003). Small range size has also been associated with high risk in non-mammal taxa,

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* Corresponding author. Tel.: +61 02 6125 9138; fax: +61 02 6125 5573.
E-mail addresses: emily.hanna@anu.edu.au (E. Hanna), marcel.cardillo@anu.edu.au (M. Cardillo).

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including birds (Lee and Jetz, 2011) and amphibians (Murray and Hose, 2005). Many of these studies have used analysis methods that attempt to avoid potential circularity by considering only threatened species listed under criterion A of the IUCN Red List (IUCN, 2001), which is based on rates of decline rather than absolute range or population size (e.g. Cardillo et al., 2003, 2008, 2005, 2004; Jones et al., 2003; Price and Gittleman, 2007; Purvis et al., 2000). Nonetheless, concerns about circularity remain. Most of the geographic range estimates available for mammal species represent current distributions that, for species that have undergone severe declines, are often substantially smaller today than in the past (IUCN et al., 2008; Sechrest, 2005). Hence, it is difficult to disentangle the role of range size as a biological predictor of extinction from its role as a response to species decline.

Historic geographic ranges reconstructed for a period before the onset of severe human impact may be a better reflection of species' "natural" distributions, that are the product of climatic tolerances, habitat requirements and interactions with other species (Brown and Lomolino, 1998; Gaston, 2009; Munguia et al., 2008). It could be argued, therefore, that using historic rather than current ranges in comparative analyses should provide a more accurate picture of the role of range size as a predictor of extinction risk across species. For Australian mammals, a recently constructed database of species' pre-European distributions, based on historic records, indigenous knowledge and subfossil data (Burbidge et al., 2008) permits such an analysis. Many Australian mammal species have suffered severe declines and now occupy ranges that are a tiny fraction of their ranges only a century ago, making this a good case study for the comparison of current and historic range sizes.

As well as the uncertain role of range size, a further issue with comparative studies of extinction risk is the incompleteness of large comparative datasets, which usually contain numerous missing values. One previous study dealt with this by using multiple imputation methods to generate a complete "pseudo-dataset" (Fisher et al., 2003). More commonly, studies apply a heuristic approach to searching model space first used by Purvis et al., (2000). However, this strategy can follow alternative model-fitting pathways that may arrive at a large number of very different final models. Searching for a single best-fitting model implies a level of confidence in that single result which is often not deserved, as alternative models may fit the data nearly as well (Johnson and Omland, 2004; Whittingham et al., 2006). This is a potentially serious issue if comparative extinction risk models are used for predictive purposes.

In this study, we present a comparative analysis of extinction risk for Australian mammals that attempts to address the two issues described above. To address the geographic range issue, we compare models that use current range size as a predictor variable with those that use reconstructed historic range sizes from the database of Burbidge et al. (2008). To address the missing data issue, we use an approach to fitting comparative models based on model ranking and averaging (Johnson and Omland, 2004). We apply the heuristic search strategy of Purvis et al. (2000), but rather than retaining a single "best" model, we combine the results of multiple models. The resulting consensus model provides statistically more robust parameter estimates for subsequent predictive use as well as indicating which variables carry the most weight in their relationship with extinction risk.

In addition to comparing the results of comparative extinction risk models, we use the models to calculate latent extinction risk, the discrepancy between a species' current extinction risk and its risk predicted from biological traits (Cardillo et al., 2006). A positive latent risk value suggests that a species is currently less threatened than its biology would indicate, and could rapidly become more threatened if external threat levels increase. We examine the geographic distribution of average latent risk to identify the regions of greatest potential future mammal declines, and we examine the influence of using historic versus current range size on these predictions.

2. Material and methods

2.1. Datasets

As a measure of extinction risk for use with phylogenetically independent contrasts, we converted the species' Red List extinction risk ratings (IUCN, 2009) into a numerical index (least concern = 0, near threatened = 1, vulnerable = 2, endangered = 3, critically endangered = 4, extinct in the wild/extinct = 5), following Purvis et al. (2000). Given that 85% of Australia's terrestrial mammals are endemic (State of the Environment 2011 Committee, 2011), and the range outside Australia tends to be small for non-endemic species, it is likely that global extinction risk classifications are, on the whole, an accurate reflection of extinction risk within Australia. Species listed as threatened for reasons other than population or geographic range decline rates (criterion A of the Red List: IUCN, 2001), such as small geographic range (criterion B of the Red List) or small population size (criteria C and D of the Red List) were excluded from model-fitting (Purvis et al., 2000) to minimize this source of circularity and for consistency with previous comparative studies using the Red List. Species listed as data deficient were also removed. The resultant database consisted of 172 (out of an initial 235) marsupial, rodent and monotreme species.

As putative predictors of extinction risk, we used a set of biological variables from the PanTHERIA database (Jones et al., 2009), with some missing values filled by searching the recent literature (see Appendix for the full list). We added data on nesting level, as follows: 1 = below ground, i.e. burrows, soil cracks, caves and/or rock fissures; 2 = both below ground and on ground level nests; 3 = ground level; 4 = both ground level and tree hollows; and 5 = tree hollows, tree canopy and/or tree branches. We assigned each species to at least one of the following broad habitat classifications: desert (including sand and gibber plains); rocky, including scree; heathland; scrubland/shrubland, including mallee; grassland, including sedgeland; woodland, including mulga; forest – sparse understory; forest, general; forest – dense understory; rainforest; swamp/mangrove; and permanent water bodies.

Both past and current range sizes were recorded for each species. Range sizes were based on the species' historical (pre-European settlement) and current presence in each of the 85 bioregions of the Interim Biogeographic Regionalisation for Australia (IBRA) (Burbidge et al., 2008: see Fig. 1), with range being an estimate of the "extent of occurrence" (IUCN, 2001) rather than area of occupancy (Burbidge et al. 2008; IUCN, 2001). Burbidge et al. (2008) estimated historical distributions using a combination of evidence from oral history and indigenous knowledge, museum specimens, published data, and subfossil data; vagrant records were not included. Burbidge et al. (2008) give an estimate of the current status of each species within each bioregion, as follows: E = extinct, SD = severe decline (>90%), D = decline (50–90%), P = persists (still occupies >50% of historical range within bioregion). To estimate historic range size for each species we simply summed the areas of bioregions formerly inhabited by the species. The current range size for each species was calculated by summing the areas of bioregions historically inhabited after adjusting for range decline. Thus, the area of each bioregion historically inhabited by a species was multiplied by zero where the species' status = E, by 0.1 where the status = SD, by 0.5 where the status = D, and by one where the status = P. This provides a crude estimate of range sizes, but we chose to calculate current ranges in this