

This paper has been retracted

Hanna & Cardillo (2014) Predation selectively culls medium-sized species from island mammal faunas. *Biology Letters* 10: 20131066, published 2 April 2014

Following publication, I was made aware of some errors and omissions in the island mammal database that formed the basis for this paper. All known errors were corrected and the database constructed from scratch. On reanalysis, the basic finding of size-selectivity in island mammal extinctions was upheld, but the new results better supported a positive size x extinction association, rather than a hump-shaped one (i.e. Figure 1c rather than Figure 1b).

Unfortunately, the editors of *Biology Letters* did not allow me the opportunity to correct the record and present the new database and new results in the form of a correction article. Instead, they decided to issue a retraction (*Biol. Lett.* 10, 20131066, published online 2 April 2014. doi:10.1098/rsbl.2013.1066).

As of December 2016, I am preparing the new data and results for publication elsewhere. As soon as this is accepted for publication, this note will be updated with the new publication details. Until then, **please do not use the dataset provided as supplementary information with this paper**. Feel free to cite the paper for the methods or approach, but please do not cite it for the results or conclusions.

Marcel Cardillo

Predation selectively culls medium-sized species from island mammal faunas

Emily Hanna and Marcel Cardillo

Biol. Lett. 2014 **10**, 20131066, published 2 April 2014

Supplementary data

["Data Supplement"](#)

<http://rsbl.royalsocietypublishing.org/content/suppl/2014/03/31/rsbl.2013.1066.DC1.html>

References

[This article cites 18 articles, 5 of which can be accessed free](#)

<http://rsbl.royalsocietypublishing.org/content/10/4/20131066.full.html#ref-list-1>

Subject collections

Articles on similar topics can be found in the following collections

[ecology](#) (735 articles)

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

Research



Cite this article: Hanna E, Cardillo M. 2014 Predation selectively culls medium-sized species from island mammal faunas. *Biol. Lett.* **10**: 20131066.
<http://dx.doi.org/10.1098/rsbl.2013.1066>

Received: 16 December 2013

Accepted: 11 March 2014

Subject Areas:

ecology

Keywords:

extinction risk, mammals, predation, body size

Author for correspondence:

Marcel Cardillo

e-mail: marcel.cardillo@anu.edu.au

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2013.1066> or via <http://rsbl.royalsocietypublishing.org>.

Conservation biology

Predation selectively culls medium-sized species from island mammal faunas

Emily Hanna and Marcel Cardillo

Macroevolution and Macroecology Group, Research School of Biology, Australian National University, Building 116, Daley Road, Canberra, Australian Capital Territory 0200, Australia

Globally, elevated extinction risk in mammals is strongly associated with large body size. However, in regions where introduced predators exert strong top-down pressure on mammal populations, the selectivity of extinctions may be skewed towards species of intermediate body size, leading to a hump-shaped relationship between size and extinction risk. The existence of this kind of extinction pattern, and its link to predation, has been contentious and difficult to demonstrate. Here, we test the hypothesis of a hump-shaped body size–extinction relationship, using a database of 927 island mammal populations. We show that the size-selectivity of extinctions on many islands has exceeded that expected under null models. On islands with introduced predators, extinctions are biased towards intermediate body sizes, but this bias does not occur on islands without predators. Hence, on islands with a large-bodied mammal fauna, predators are selectively culling species from the lower end of the size distribution, and on islands with a small-bodied fauna they are culling species from the upper end. These findings suggest that it will be difficult to use predictable generalizations about extinction patterns, such as a positive body size–extinction risk association, to anticipate future species declines and plan conservation strategies accordingly.

1. Introduction

The biological selectivity of species decline and extinction offers clues to the relative importance of different threatening processes. Recognizing predictable patterns of extinction, or particular traits that make species especially vulnerable to different threats, presents the possibility of identifying species at potential future risk and planning conservation strategies pre-emptively [1]. In mammals, one of the strongest patterns of biological selectivity involves body size: in most comparative analyses of mammal extinction risk, larger size is associated with higher risk [2–5]. An obvious explanation for this association is the negative scaling of life-history speed with size, leading to lower rates of population growth and recovery [6], and lower population densities [6,7], in larger species. Furthermore, there appear to be synergistic effects whereby larger species are more sensitive to a given threatening factor than small species [3].

In this context, any exceptions to the expected positive size–risk association are worthy of investigation, for two main reasons. First, such exceptions would undermine the generality of the positive size–risk association and hence its usefulness for pre-emptive conservation planning. Second, such exceptions may point to agents of species decline that exert an unusually strong pressure on mammal populations in the lower or intermediate parts of the body size distribution. It has been suggested that Australian mammals represent a major exception to the positive size–risk relationship. Most extinctions and severe declines in Australian mammals have been within an intermediate body mass range of 35–5500 g, known as the ‘critical weight range’ [8]. This corresponds broadly to the preferred prey-size range of feral cats and red foxes, which are probably responsible for catastrophic declines and extinctions among Australian mammals [8]. An energetic explanation has also been

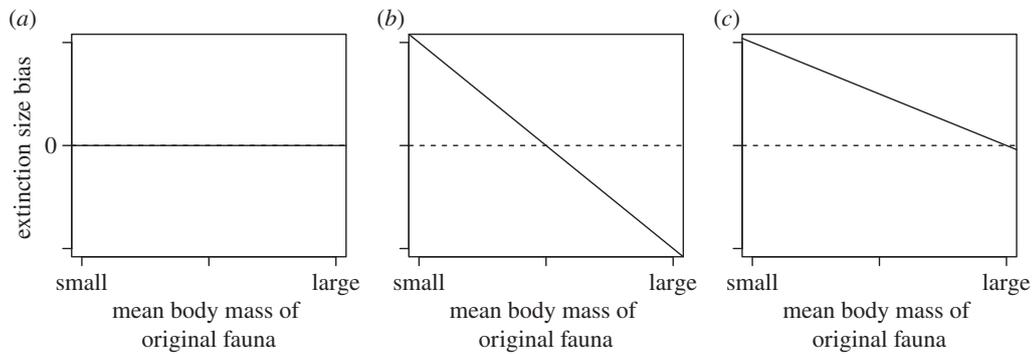


Figure 1. Expected patterns of extinction size bias in plots of mean body mass of the original mammal fauna of islands against the standardized effect size of extinction size bias. (a) Extinctions consistent with null model; (b) extinctions biased towards intermediate sizes; (c) positive size–extinction association.

offered, which argues that medium-sized species have the combined disadvantage of higher energy needs than small species and lower mobility than large species [8–10].

However, the existence of a hump-shaped association between size and extinction risk in Australian mammals has been contentious. Cardillo & Bromham [11] showed that the numbers of extinct and threatened species of 35–5500 g are no greater than expected under null models and supported instead a positive size–risk association. Other studies have supported the existence of a hump-shaped pattern within restricted geographical and ecological subsets of Australian mammals [12–14]. Whether introduced predators drive such patterns, however, is difficult to determine. While local eradication of cats and foxes have been linked to increases in populations of medium-sized mammals, the role of predators in driving a hump-shaped size–risk association across whole assemblages has only been inferred from the overlap (or lack thereof) between the distributions of mammal species and introduced predators across broad geographical regions [12,13].

We use a large database of island mammal populations to test the hypothesis that introduced predators bias extinctions towards intermediate body sizes. Islands provide an excellent system for testing this hypothesis, because they represent, in effect, a large set of independent replicate experiments in the exposure of an indigenous mammal fauna to exotic predators. If predators exert sufficient pressure on mammal populations to generate a hump-shaped size–risk pattern, then on islands with predators we should expect the size distribution of extinct species to cluster around an intermediate body size within the typical prey-size range of the predators. On islands lacking predators, a plausible alternative pattern is that extinctions cluster around body sizes towards the upper end of the body size distribution, as expected under the typical positive association between size and risk. On all islands, the null expectation is that the body size distributions of extinct species are indistinguishable from those of the same number of species sampled randomly from the original fauna of each island.

2. Material and methods

(a) Database

Our database includes records of the presence and extinction of 927 populations of 106 native non-volant mammal species, on 321 Australian islands, together with data on the presence of introduced exotic species, species-average body masses and

island geographical data. A population is defined as a given species on a given island. Where island-specific body mass data were available, these were used in preference to species values [15]. The introduced predators we consider are cats, foxes and dingoes. It is difficult to distinguish the ecological role of dingoes, established in Australia for several thousand years, from feral domestic dogs, so we consider both as ‘dingoes’. Full details of database construction are provided in [16], and the database itself is provided in the electronic supplementary material, table S1.

(b) Testing size-selectivity and size-bias of island extinctions

For each island with at least one extinct and one extant native mammal species, we calculated a test statistic d_e that quantifies the degree of dispersion of extinct species body masses (w) around a given body mass value (m)

$$d_e = \sum_{i=1}^n \left| \log \left(\frac{w_i}{m} \right) \right|,$$

where n is the total number of extinct species. For each island, we found the value of m that minimized d_e , using the ‘optimize’ function in R to search m values across the interval 10–20 000 g. We generated a null model for m by repeating this procedure for 1000 sets of n species sampled from the original mammal fauna of the island (i.e. extant + extinct indigenous species). Extinctions were considered size-selective if the observed m deviated significantly from the null distribution under a two-tailed test with $\alpha = 0.05$.

We then examined the direction of the extinction size bias with respect to the body size distribution of the original fauna on each island. We calculated a standardized effect size for the extinction size bias as (observed m – median null m)/s.d. of null m . Plotting the size-bias effect size against the mean body size of island faunas reveals patterns of size-selective extinction (figure 1). If extinctions are biased towards intermediate sizes, there should be a negative relationship in which the slope crosses zero on the y -axis (figure 1*b*).

3. Results

Of the 321 islands in the database, 59 have suffered mammal extinctions, of which 43 have at least one extant indigenous species. Of these 43 islands, we found evidence for size-selective extinction (observed $m \neq$ null) on 20 islands (electronic supplementary material, table S2). The direction of size-bias in extinctions was divided almost equally, with observed $m >$ null on 10 islands and observed $m <$ null on 11 islands. The plot of extinction size-bias effect size against

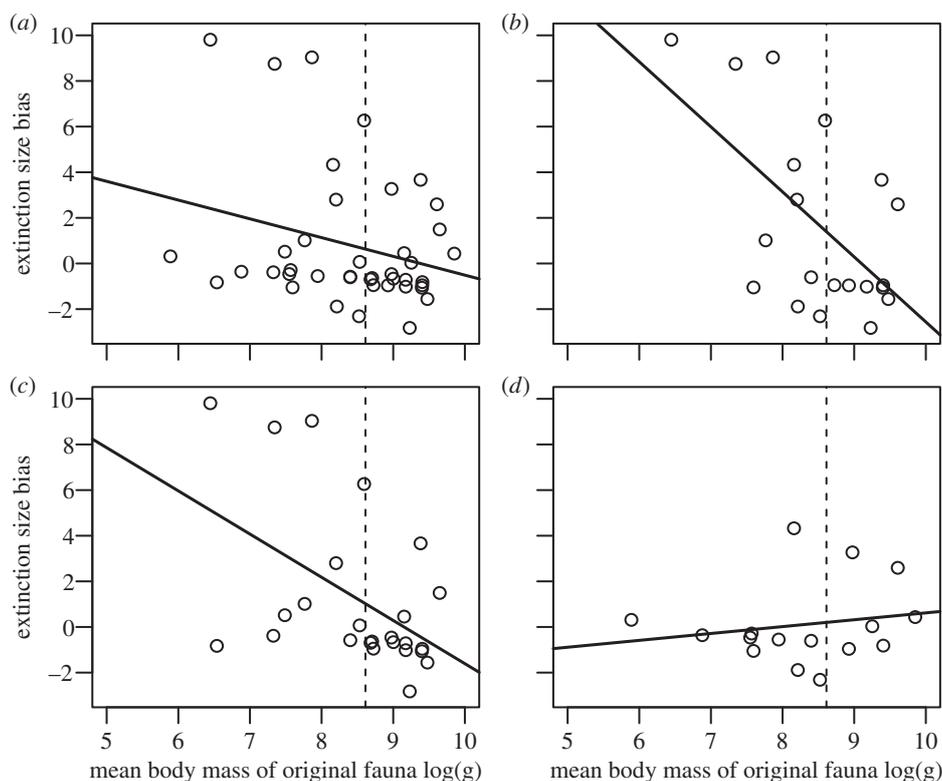


Figure 2. Observed plots of mean body mass against extinction size bias. The vertical dashed line indicates the upper limit of the ‘critical weight range’ (35–5500 g). Plots are shown for (a) all islands with more than 0 extinctions and more than 0 species extant; (b) islands on which extinctions have been significantly size-biased; (c) islands with at least one of the three large introduced predators (cats, foxes and dingoes) and (d) islands without any large introduced predators.

the mean mass of original island faunas has a negative slope, although the association is not significant across all islands (figure 2a; slope = -7.85 , $p = 0.14$, d.f. = 41). Across islands with size-selective extinctions, however, there is a significant negative association (figure 2b; slope = -2.85 , $p = 0.006$, d.f. = 18). Across islands with at least one introduced large predator (cats, foxes or dingoes), the association is significantly negative (figure 2c; slope = -1.89 , $p = 0.01$, d.f. = 24), but non-significant across islands without any of these predators (figure 2d; slope = 0.3 , $p = 0.51$, d.f. = 14). In all models, body mass was log-transformed, and we removed one island with a studentized residual more than 60. As this island had a mean body mass of original fauna at the lower end of the x -axis (103.5 g), removal of this outlier had a conservative effect on the models. We tested for spatial autocorrelation in the residuals of the model presented in figure 2a, but found no significant spatial effect on size-bias residuals (Moran’s $I = -0.038$, $p = 0.68$), justifying the use of non-spatial regressions.

4. Discussion

The immediate causes of extinction are no great mystery—usually, one or more of the ‘evil quartet’ (hunting, habitat loss, introduced species or coextinctions; [17]). It is less obvious why different species respond differently to similar threat types. Large-scale comparative analyses have begun to answer this question by showing that numerous biological traits mediate the influence of external threats on species’ extinction risk. Evidence for some particularly consistent and common relationships, including a positive association between body mass and extinction risk, presents the possibility

of assigning data-deficient species to provisional threat categories or planning pre-emptive conservation measures [1]. While the largest mammal species have notable disadvantages in the face of human impacts, our results show that medium-sized species are likely to be even more vulnerable than large species where exotic predators are the primary threat, although this will depend on the size of the key predators in any given system. This casts doubt on the universality of a positive association between size and extinction risk.

The major novelty of our analysis is twofold. First, data on mammal extinctions for a large number of islands, with and without introduced predators, provide a degree of replication not found in previous continental-scale analyses [11,12,14]. Second, our tests for extinction size bias are performed with reference to the body size distribution of each island’s original fauna, which provides an appropriate null model. Although we found a clear difference in extinction size bias between islands with and without predators, it is possible that the presence of predators covaries with some environmental feature of islands that drives the size bias. However, this seems unlikely. We tested the size-bias effect size against three island environmental features (area, distance from mainland and mean annual rainfall), but none showed significant univariate associations, or improved the fit of the models presented in the Results. Our results also reject the energetic hypothesis for higher extinction risk in medium-sized species [8–10], because under this hypothesis the hump-shaped pattern should also be seen on islands without predators. The presence of at least one species of large introduced predator therefore appears to be the best explanation for the pattern of extinction size bias towards intermediate body sizes.

While the findings of our study support previous claims that medium-sized mammal species in Australia have been

unusually vulnerable to predator-driven extinction [8,12], the suggested 'critical weight range' of 35–5500 g appears to have little biological reality. If this range did reflect the zone of elevated extinction vulnerability, we would expect the extinction size bias to be close to zero for islands with a mean faunal body mass within this range. Instead, these islands tend to have an extinction size bias that is highly positive (figure 1c), suggesting extinctions are more frequent for species above 5500 g. This pattern is actually more consistent with evidence for an upper prey size for foxes of around

10 kg [18]. Dingoes also take prey larger than 5500 g [19], but only three islands have dingoes as the sole large predator species, making it difficult to distinguish their role from that of foxes.

Acknowledgements. We thank Xia Hua for advice on the analysis.

Data accessibility. The data and full analysis results are provided in the electronic supplementary material.

Funding statement. E.H. was supported by an Australian Postgraduate Scholarship.

References

1. Lee TM, Jetz W. 2011 Unravelling the structure of species extinction risk for predictive conservation science. *Proc. R. Soc. B.* **278**, 1329–1338. (doi:10.1098/rspb.2010.1877)
2. Cardillo M. 2003 Biological determinants of extinction risk: why are smaller species less vulnerable? *Anim. Conserv.* **6**, 63–69. (doi:10.1017/S1367943003003093)
3. Cardillo M, Mace GM, Jones KE, Bielby J, Bininda-Emonds ORP, Sechrest W, Orme CDL, Purvis A. 2005 Multiple causes of high extinction risk in large mammal species. *Science* **309**, 1239–1241. (doi:10.1126/science.1116030)
4. Davidson AD, Hamilton MJ, Boyer AG, Brown JH, Ceballos G. 2009 Multiple ecological pathways to extinction in mammals. *Proc. Natl Acad. Sci. USA* **106**, 10 702–10 705. (doi:10.1073/pnas.0901956106)
5. Purvis A, Gittleman JL, Cowlshaw G, Mace GM. 2000 Predicting extinction risk in declining species. *Proc. R. Soc. Lond. B* **267**, 1947–1952. (doi:10.1098/rspb.2000.1234)
6. Fenchel T. 1974 Intrinsic rate of natural increase: the relationship with body size. *Oecologia* **14**, 317–326. (doi:10.1007/BF00384576)
7. Damuth J. 1981 Population density and body size in mammals. *Nature* **290**, 699–700. (doi:10.1038/290699a0)
8. Burbidge AA, McKenzie NL. 1989 Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. *Biol. Conserv.* **50**, 143–198. (doi:10.1016/0006-3207(89)90009-8)
9. Morton SR. 1990 The impact of European settlement on the vertebrate animals of arid Australia: a conceptual model. In *Proc. Ecological Society of Australia* **16**, 201–213.
10. Short J, Smith A. 1994 Mammal decline and recovery in Australia. *J. Mammal.* **75**, 288–297. (doi:10.2307/1382547)
11. Cardillo M, Bromham L. 2001 Body size and risk of extinction in Australian mammals. *Conserv. Biol.* **15**, 1435–1440. (doi:10.1046/j.1523-1739.2001.00286.x)
12. Johnson CN, Isaac JL. 2009 Body mass and extinction risk in Australian marsupials: the 'critical weight range' revisited. *Austral. Ecol.* **34**, 35–40. (doi:10.1111/j.1442-9993.2008.01878.x)
13. Fisher DO *et al.* 2013 The current decline of tropical marsupials in Australia: is history repeating? *Glob. Ecol. Biogeogr.* **23**, 181–190. (doi:10.1111/geb.12088)
14. Chisholm RA, Taylor R. 2010 Body size and extinction risk in Australian mammals: an information-theoretic approach. *Austral. Ecol.* **35**, 616–623. (doi:10.1111/j.1442-9993.2009.02065.x)
15. Van Dyck S, Strahan R. 2008 *The mammals of Australia*. Sydney, Australia: New Holland Publishers.
16. Hanna E, Cardillo M. 2014 Island mammal extinctions are determined by interactive effects of life history, island biogeography and mesopredator suppression. *Glob. Ecol. Biogeogr.* **23**, 395–404. (doi:10.1111/geb.12103)
17. Diamond JM, Ashmole NP, Purves PE. 1989 The present, past and future of human-caused extinctions (and Discussion). *Phil. Trans. R. Soc. Lond. B* **325**, 469–477. (doi:10.1098/rstb.1989.0100)
18. Kinnear JE, Sumner NR, Onus ML. 2002 The red fox in Australia: an exotic predator turned biocontrol agent. *Biol. Conserv.* **108**, 335–359. (doi:10.1016/S0006-3207(02)00116-7)
19. Brook L, Kutt A. 2011 The diet of the dingo (*Canis lupus dingo*) in north-eastern Australia with comments on its conservation implications. *Rangeland J.* **33**, 79–85. (doi:10.1071/RJ10052)