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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 findings and conclusions of this paper remained robust, but there were a few small changes in the results. I am currently preparing a correction article to present the corrected and updated database and the new results. Please contact me (marcel.cardillo@anu.edu.au) if you would like a copy of the new database.

Please do not use or cite the database provided as supplementary data with this paper on the GEB website.

Marcel Cardillo

RESEARCH
PAPER



Island mammal extinctions are determined by interactive effects of life history, island biogeography and mesopredator suppression

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ABSTRACT

Aim Understanding extinction on islands is critical for biodiversity conservation. Introduced predators are a major cause of island extinctions, but there have been few large-scale studies of the complexity of the effects of predators on island faunas, or how predation interacts with other factors. Using a large database of island mammal populations, we describe and explain patterns of island mammal extinctions as a function of introduced predators, life history and geography.

Location Three hundred and twenty-three Australian islands.

Methods We built a database of 934 island mammal populations, extinct and extant, including life history and ecology, island geography and the presence of introduced predators. To test predictors of extinction probability, we used generalized linear mixed models to control partially for phylogenetic non-independence, and decision trees to more fully explore interactive effects.

Results The decision trees identified large mammals (> 2.7 kg) as having higher extinction probabilities than small species (< 2.7 kg). In large species, extinction patterns are consistent with island biogeography theory, with distance from the mainland being the primary predictor of extinction. For small species, the presence of introduced black rats is the primary predictor of extinction. As predicted by mesopredator suppression theory, extinction probabilities are lower on islands with both black rats and a larger introduced predator (cats, foxes or dingoes), compared with islands with rats but no larger predator. Similarly, extinction probabilities are lower on islands with both a mid-sized (cats or foxes) and a larger (dingoes) predator, compared with islands with cats or foxes only.

Main conclusions Island mammal extinctions result from complex interactions of introduced predators, island geography and prey biology. One conservation implication of our results is that eradication of introduced apex predators (cats, foxes or dingoes) from islands could precipitate the expansion of black rat populations, potentially leading to extinction of native mammal species whose remaining populations are confined to islands.

Keywords

Apex predator, extinction, introduced species, island biogeography, islands, mesopredator release.

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INTRODUCTION

Islands play a critically important role in conservation, both because they host many endemic species (Alcover *et al.*, 1998)

and because they may serve as the last refuge for populations of species that are otherwise extinct. It is likely that the single most important agent of species extinction on islands is introduced predators and other exotic species (Blackburn *et al.*, 2004), with

strong evidence that the presence of introduced predators on islands is associated with the decline and extinction of mammals, birds and amphibians (Blackburn *et al.*, 2004; Walsh *et al.*, 2012). Describing and understanding patterns of island extinctions, and the role of introduced predators in driving extinction patterns, is therefore of key importance in the conservation of global island biodiversity.

There have been few broad-scale analyses describing the complexity of island extinction patterns across a large number of island populations (but see Blackburn *et al.*, 2004; Walsh *et al.*, 2012). In island datasets where introduced predators are present on some islands but not others, the simplest prediction of extinction patterns would be a positive association between the presence of introduced predators and the extinction of island populations. However, there are several reasons why real patterns may be more complex than this. First, it has been predicted that where several predators occupying multiple trophic levels are present in an ecosystem, apex (top-order) predators can mitigate extinctions of prey species by suppressing populations of smaller mesopredators (Courchamp *et al.*, 1999). Conversely, the reduction or extirpation of a population of apex predators can lead to a trophic cascade, whereby the population of a mesopredator can rapidly increase, elevating predation pressure on prey populations. This phenomenon is known as mesopredator release (Soule *et al.*, 1988; Courchamp *et al.*, 1999; Crooks & Soule, 1999). In predator–prey interactions among carnivores (intraguild predation), it is more common for a larger carnivore to kill individuals of a smaller species, although smaller carnivores are also known to kill juveniles of a larger species (Palomares & Caro, 1999). There is now considerable evidence for mesopredator release and intraguild predation in a variety of ecosystems (Palomares & Caro, 1999; Johnson *et al.*, 2007; Johnson & VanDerWal, 2009; Letnic *et al.*, 2009a,b; Ritchie & Johnson, 2009; Wallach *et al.*, 2009). However, these processes have been studied mostly at the population level, and their contribution to broad-scale patterns of extinction and biodiversity remains poorly known.

A second possible source of complexity in island extinction patterns is that life-history attributes of prey species may influence patterns of extinction (Walsh *et al.*, 2012). Over the past decade, comparative studies have shown that life-history traits such as body size or age at weaning, and ecological traits such as habitat preference, are associated with differences in extinction risk among mammal species (Cardillo *et al.*, 2008; Davies *et al.*, 2008). Life-history traits may interact with external drivers of extinction: for example, larger mammal species appear more sensitive to a range of threatening processes, such as hunting, than small species (Cardillo *et al.*, 2005).

Finally, population dynamics on islands may be influenced by island geography. Under island biogeography theory (MacArthur & Wilson, 1967), extinction rates are expected to be elevated on islands that are smaller (as population sizes are limited) or more isolated from other landmasses (as populations are less frequently replenished by immigrants).

The relative importance of predation, life history and island biogeography, as well as the way they combine and interact to

influence extinction probabilities on islands, remains poorly understood. In this study, we attempt to disentangle these three processes by analysing extinction patterns in a large database of mammal populations on 323 Australian islands. Australian islands offer a good case study for analysing island mammal extinctions for several reasons. First, Australia has suffered a large proportion (> 25%) of the world's mammal extinctions in recent times (McKenzie *et al.*, 2007; IUCN, 2011). Second, introduced predators are recognized as probably the single most important agent of species decline in Australian mammals (Johnson, 2006). Third, at least eight mammal species originally widespread on the Australian mainland are now confined to relict island populations (Burbidge *et al.*, 2008), lending a particular urgency to attempts to explain patterns of island mammal extinctions. The existence of hundreds of islands with different geographic features, some predator-free and others with one or more introduced predator species, provides an opportunity for a powerful natural experiment aimed at understanding the ecological processes leading to extinction. If island extinctions are predictable from simple linear processes, they should be amenable to simple conservation planning rules. If, on the other hand, extinctions are the result of a more complex interplay of factors, it would necessitate a more targeted, case-by-case approach to planning the conservation of biodiversity on islands.

METHODS

Database construction

The baseline data on island geographic features, and the presence and extinction of native mammal species, was from the Australian islands database of Abbott & Burbidge (1995). Abbott & Burbidge's (1995) database includes data from field surveys of islands up to April 1992. For the purposes of our analysis, therefore, a mammal population believed to have gone extinct from an island prior to April 1992 is considered to be an extinction, and a population believed to have been present on an island in April 1992 is considered currently present, unless this was contradicted by more recent information. We consider each mammal species on each island to be a single population. We scored each population as currently present (1) or formerly present but now extinct (0). Records used in the Abbott & Burbidge (1995) database began in the early 1800s (and include some subfossil data), with the first dated extinction occurring in approximately 1855 (*Macropus eugenii* from Thistle island, South Australia). We omitted inconclusive records of native mammal presence.

We updated the Abbott & Burbidge (1995) database with more recent data by searching journal articles (published after 1991) and government reports. To confirm that updated records were attached to the correct islands in the Abbott & Burbidge (1995) database, we matched islands by name, state, island group name, island size and latitude/longitude, between the database and each new data source. Our final database consisted

of 934 mammal populations of 107 species from 323 islands (see Appendix S1 in Supporting Information).

The most common introduced predators on Australian islands fall into three broad size groups: small (black rat *Rattus rattus*), medium-sized (red fox *Vulpes vulpes* and domestic cat *Felis catus*) and large (dingo *Canis lupus dingo*, feral domestic dogs *Canis lupus familiaris*, and their hybrids from interbreeding). Feral domestic dogs and dingoes were grouped together. Ecologically, feral dogs and dingoes fulfil similar roles, and interbreed, meaning that a distinction between wild domestic dogs and dingoes is often not possible (Ritchie *et al.*, 2012); hereafter we refer to both as 'dingoes'. The presence of the introduced species (black rats, red foxes, domestic cats and dingoes) on each island was from the Abbott & Burbidge (1995) database, with additional data from government reports (Burbidge, 2004; Tasmanian Department of Primary Industries, Parks, Water and Environment, 2008; Australian Department of Sustainability, Environment, Water, Population and Communities, 2010). Introduced species were recorded as present, extinct (i.e. formerly present but now absent) or never present, on each island. In some cases, data were available on the timing of introductions and native mammal extinctions, allowing us to code introduced species as present or absent with respect to each native mammal population. For example, if the extinction of a particular native population occurred before the introduction of an exotic predator to the same island, we coded the predator as 'absent' with respect to that native population.

In some cases, records of presence or extinction of native species on islands are likely to have been influenced by direct human intervention. Records of extinct Australian native species that were known to have been introduced, or reintroduced following extinction, were removed from the database, as these extinctions may have resulted from factors associated with the introduction process, rather than the ecological factors we were interested in testing. Where a native mammal was removed from the island intentionally (such as the grey kangaroo on Granite Island, South Australia), the record was removed and not considered to be an extinction or a presence.

We recorded adult body mass of each native mammal species from the PanTHERIA database (Jones *et al.*, 2009). Previous studies have shown that the vertical level at which a species nests can influence vulnerability to extinction (Johnson & Isaac, 2009), so we recorded nesting level for 99 species, from Van Dyck & Strahan (2008), coded as follows: 1, below ground, including burrows, soil cracks, caves or rock fissures; 2, both below ground and at ground level; 3, ground level; 4, both ground level and trees; and 5, tree hollows, tree canopy or tree branches.

Extinction models

We analysed patterns of mammal extinction at the island level ($n = 323$) and the population level ($n = 934$). As the response variable for island-level analyses, we quantified the extinction probability for each island as the percentage of native species recorded on the island at any time that are no longer present on

the island (e.g. on Maria Island there are 14 species present and one species formerly present but now absent, so extinction probability is 6.7%). We regarded the definition of 'apex' and 'meso' predators as relative rather than absolute, as we wished to examine whether (1) the largest introduced predator (dingo) acts to suppress populations of each of the smaller introduced predators (black rat, cat, fox), and (2) the mid-sized introduced predators (cat and red fox) act to suppress populations of black rats. We therefore performed separate analyses in which we considered each of the cat, fox or dingo to be the 'apex' predator, and each of the black rat, cat or fox as the 'meso' predator. For each apex/mesopredator combination, we began with a visual examination of mean extinction probabilities on islands with different combinations of predator types. We plotted extinction probabilities for four sets of islands: (1) both apex predator and mesopredator present; (2) neither apex predator nor mesopredator present; (3) apex predator but not mesopredator present; (4) mesopredator but not apex predator present. We compared mean extinction probabilities across the four sets of islands using ANOVA.

We then tested the effect of introduced predators, prey species biology and island geography as predictors of extinction probabilities across populations. We used two analytical approaches with complementary strengths (Bielby *et al.*, 2010): generalized linear mixed models (GLMMs) and decision trees. GLMMs allow for the partial control of phylogenetic non-independence among populations by including taxonomic level (species, genus, family, order) as nested random grouping factors in models. Decision trees are well suited to dissecting complex interactions among multiple predictor variables and are considered by some authors to offer greater predictive accuracy than linear models (De'ath & Fabricius, 2000; Davidson *et al.*, 2009; Bielby *et al.*, 2010). Decision trees are increasingly applied to analyses of the multiple factors driving extinction risk, and to improve accuracy of predictions of species decline and extinction (Davidson *et al.*, 2009; Bielby *et al.*, 2010). However, decision trees cannot account for phylogenetic non-independence, so we feel it is important to use this method in combination with a method such as GLMM that at least partially accounts for phylogeny.

Relationships between population extinction (coded as a binary variable where 0 = extinct and 1 = present) and life history and extrinsic variables were analysed using GLMMs in the R library nlme (Lindstrom & Bates, 1990). Island area and species body mass were log-transformed before modelling to normalize the error distribution. The structure of the dataset (with multiple island populations for most species) precluded the use of phylogenetically independent contrasts to control for phylogenetic non-independence. Although there have been recent advances in controlling for phylogenetic non-independence when datasets include multiple populations per species (Stone *et al.*, 2011; Revell & Reynolds, 2012), these methods require population-specific information on life-history traits which is not currently available. We therefore partially controlled for phylogenetic non-independence by including taxonomic levels (species, genus and family) as nested random

Table 1 Comparisons of generalized linear mixed models of the effects of life history, island geography and introduced predators, on extinction probability of island mammal populations. The top five models are shown, in order of increasing Akaike information criterion (AIC) value. Models have dingoes as the apex predator, and the following as the mesopredator: (a) black rats; (b) cats; (c) foxes.

Predictors	Degrees of freedom	AIC	Δ AIC
(a)			
Black rat + log(prebody mass) + dingo	826	247.7	0
Black rat + log(prebody mass)	827	250.2	2.5
Black rat \times dingo	825	254.8	7.1
Black rat + dingo	826	258.8	11.1
Black rat \times log(prebody mass)	826	260.2	12.6
(b)			
Cat + log(prebody mass) + dingo	826	259.5	0
Cat + log(prebody mass)	827	260.1	0.6
Cat \times log(prebody mass)	826	271	11.5
Cat + dingo	826	272.4	12.9
Cat	827	272.6	13.1
(c)			
Fox + log(prebody mass)	827	259.8	0
Fox + log(prebody mass) + dingo	825	265.8	5.9
Fox \times log(prebody mass)	826	269.9	10.1
Fox	827	272.7	12.9
Fox + prey nesting level	826	273.6	13.8

grouping factors in the models. We fitted a set of a priori models (Table 1) and compared them using the difference between the Akaike information criterion (AIC) for each model and that of the best-fitting model (Δ AIC).

Conditional inference decision trees were created using the R package *PARTY* (Hothorn *et al.*, 2009) to examine interactions among predictor variables. *PARTY* uses a statistical approach to get the most homogeneous subgroups (in terms of the response variable) at each level of the conditional inference decision tree through recursive binary partitioning of the dataset. The statistical tests applied ensure that variable selection is unbiased (unlike in traditional classification and regression trees which are biased towards those variables with the most levels; Breiman *et al.*, 1984) and that overfitting does not occur, as the tree is finished as soon as no further significant relationship between the response and predictors can be found (Hothorn *et al.*, 2006, 2009). No further pruning of the resultant trees is required, with *PARTY* delivering optimal trees with statistically significant pathways and terminal nodes.

RESULTS

Comparisons of extinction probabilities among island sets

Examination of mean extinction probabilities across sets of islands with different combinations of introduced predators

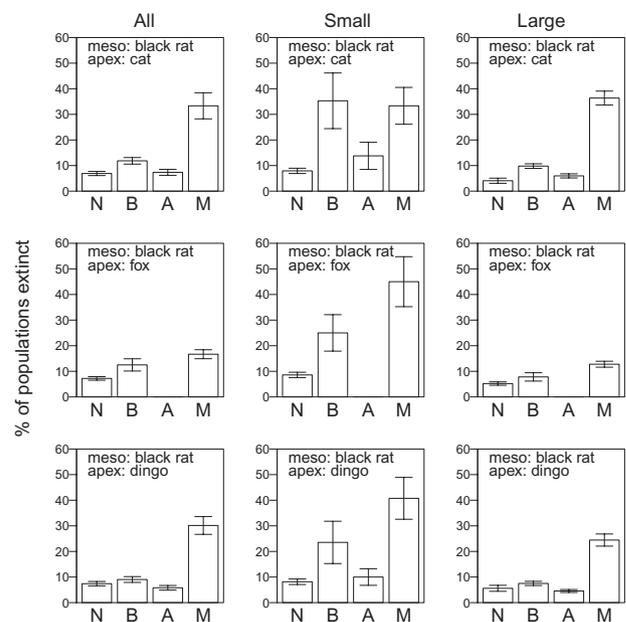


Figure 1 Mean (± 1 SE) extinction proportions (percentage of island populations that have gone extinct) across sets of islands with black rats as the mesopredator, and cats, foxes or dingoes as the apex predator. Bars represent mammal species on different island subsets, as follows: N, neither apex predator nor mesopredator present; B, both the apex predator and mesopredator present; A, apex predator only present; M, mesopredator only present. Results are shown for all islands, small islands only (< 4094 km²) and large islands only (> 4094 km²).

(Figs 1 & 2) supports mesopredator suppression, with foxes and cats acting as both apex predators (suppressing black rats) and as mesopredators (being suppressed by dingoes). When black rats are considered the mesopredator and cats, foxes or dingoes considered the apex predator (Fig. 1), extinction is significantly higher on islands where the mesopredator is present but the apex predator is absent, compared with islands where neither, both or the apex predator only are present (ANOVA, $P < 0.001$, d.f. = 3 and 931 for cats, foxes and dingoes as the apex predator). The same pattern is evident when cats or foxes are considered the mesopredator and dingoes the apex predator (Fig. 2; ANOVA, $P < 0.001$, d.f. = 3 and 931 for both cats and foxes as the mesopredator).

Although these patterns are strongly suggestive of a mesopredator suppression effect, a similar pattern could result if larger predators are less likely than smaller predators to be found on smaller islands, where extinction of native prey species could be higher due to island biogeography effects. However, examining the patterns separately for large and small islands, using median island size as the cut-off, shows that all patterns remain the same for large islands (ANOVA, $P < 0.001$, d.f. = 3 and 458 for all mesopredator and apex predator combinations; Figs 1 & 2). On small islands, mesopredator-only islands have the highest mean extinction probability in most cases (ANOVA, $P < 0.001$, d.f. = 3 and 460 when black rats are the mesopredator and either foxes or dingoes are the apex predator; $P < 0.001$ when cats are

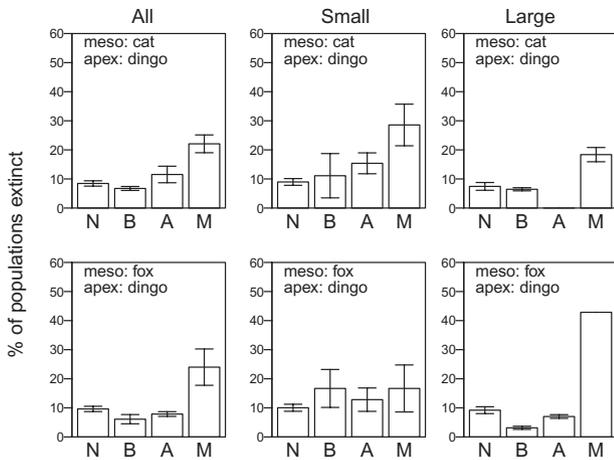


Figure 2 Mean (± 1 SE) extinction proportions (percentage of island populations that have gone extinct) across sets of islands with cats or foxes as the mesopredator and dingoes as the apex predator. Bars represent mammal species on different island subsets, as follows: N, neither apex predator nor mesopredator present; B, both the apex predator and mesopredator present; A, apex predator only present; M, mesopredator only present. Results are shown for all islands, small islands only (< 4094 km²) and large islands only (> 4094 km²).

the mesopredator and dingoes the apex predator), but the differences between these and other island sets is obscured by a general elevation in extinction on small islands (Figs 1 & 2).

Generalized linear mixed models

GLMMs show that island extinctions are influenced by all three of the hypothesized mechanisms described in the Introduction: introduced predators, life history and island biogeography. The full set of model comparisons is given in Appendix S2, and the top five models for each mesopredator (cats, foxes, dingoes) are shown in Table 1. Comparisons of univariate models show that black rats have a greater influence on extinction than other introduced predators, with a strongly positive association between the presence of black rats and extinction of native mammal populations (GLMM, $P < 0.001$). The presence of dingoes, on the other hand, shows a weak negative association with extinction (GLMM, $P = 0.098$). The fit of the univariate models is not improved by the addition of island area, distance from mainland or prey nesting level, either as additive or interactive terms (Table 1, Appendix S2). The addition of prey body mass, however, improves model fit, with additive body mass terms giving a better fit than interactive terms. Fit of the black rat + log(prebody mass) and the cat + log(prebody mass) models are further improved by the addition of dingoes (Table 1a, b). In both models, there are negative relationships between dingo presence and mammal extinction (Table 2).

Decision trees

We fitted three alternative models using black rats as the mesopredator, with dingoes, cats or foxes as the apex predator.

Table 2 Best-fitting models when the apex predator is assumed to be the dingo and the mesopredator is assumed to be (a) black rat, (b) cat, and (c) red fox.

Predictor	Slope	Standard error	<i>t</i>	<i>P</i>
(a)				
Black rat	0.052	0.012	4.3	0
Log(prebody mass)	0.031	0.009	3.4	0.001
Dingo	-0.036	0.010	-3.4	0.001
(b)				
Cat	0.034	0.013	2.6	0.01
Log(prebody mass)	0.033	0.009	3.6	0.001
Dingo	-0.039	0.013	-3.1	0.002
(c)				
Fox	-0.001	0.014	-0.1	0.936
Log(prebody mass)	0.034	0.009	3.6	0.001

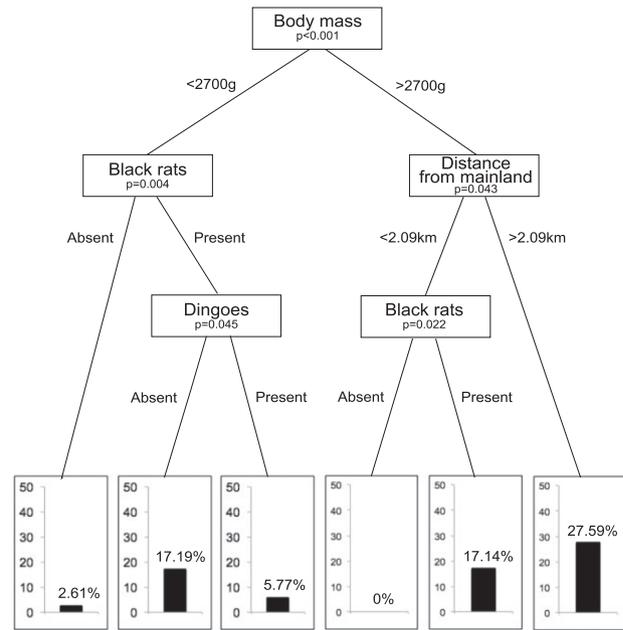


Figure 3 Decision tree showing interactive effects of life history, island geography and predation on island mammal extinctions, with dingoes as the apex predator and black rats as the mesopredator. Percentages are percentage of species with these criteria that have gone extinct.

We then fitted two additional models, with foxes or cats as the mesopredator and dingoes as the apex predator. All life-history and geographic variables (see Methods) were included in each model. With rats as the mesopredator, results were similar whether dingoes (Fig. 3) or foxes (Fig. 4) were included as the apex predator in the model. The first split identifies large body mass as the primary determinant of extinction risk, with a cut-off of 2.7 kg. For species heavier than 2.7 kg, extinction probability is higher on islands more distant from the mainland (> 2.1 km), consistent with the expectations of island biogeography theory. For large species on less isolated islands, the pres-

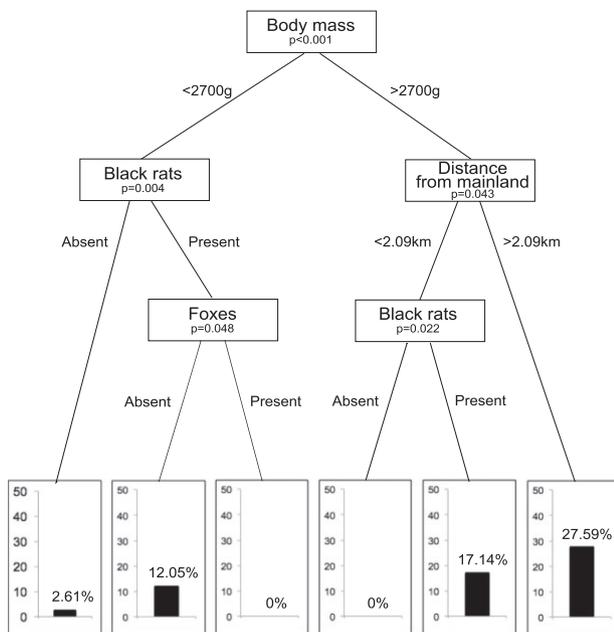


Figure 4 Decision tree showing interactive effects of life history, island geography and predation on island mammal extinctions, with the red fox as the apex predator and black rat as the mesopredator. Percentages are percentage of species with these criteria that have gone extinct.

ence of black rats elevates extinction risk. For species below 2.7 kg, the presence of black rats is the primary predictor of extinction risk. When black rats are present, the presence of dingoes or foxes as an apex predator is associated with a significant reduction in extinction probabilities. When cats are the apex predator, this final split is not present (Appendix S3, Fig. S3). However, the mitigating influence of cats on extinction in the presence of black rats can be seen in a decision tree that only includes cats and black rats (permutation test, $P = 0.003$; see Appendix S3, Fig. S4). With foxes or cats as the mesopredator and dingoes as the apex predator, the decision trees indicated a first split between large and small species, and a subsequent split between more and less isolated islands; the model with foxes also included a further split involving foxes (see Appendix S3, Figs S1 & S2).

In summary, probability of extinction is highest for (1) large species on islands distant from the mainland, (2) large species on islands close to the mainland with black rats, and (3) small species on islands with black rats but no apex predator.

DISCUSSION

As previous analyses of vertebrate extinctions on islands have demonstrated (Blackburn *et al.*, 2004; Walsh *et al.*, 2012), our results show that introduced predators are an important driver of island mammal extinctions. However, extinction probability is not a simple positive function of the presence of introduced predators on islands. Rather, the effects of introduced species act in concert with biological and geographic factors to determine

extinction probabilities, in ways that are, in some cases, counterintuitive and difficult to predict.

A key predictor of island mammal extinction is large body size. This finding is consistent with previous comparative analyses that have shown larger mammal species tend to have a higher extinction-risk classification on the IUCN Red List (e.g. Cardillo *et al.*, 2005). Intriguingly, the primary split in our decision-tree analysis divides small and large mammal species at a cut-off body mass value of 2.7 kg. This value is remarkably similar to the 3 kg threshold identified in a previous study as the body mass above which mammal species become sharply more susceptible to factors that elevate extinction risk (Cardillo *et al.*, 2005), and is also similar to a split of 5.5 kg in an analysis of mammal extinction risk globally (Davidson *et al.*, 2009). Although there are a number of reasons to expect a continuous increase in proneness to extinction with increasing body size (e.g. population density and reproductive output decline with body size: Bielby *et al.*, 2007), the reasons for a sharp increase in proneness to extinction above 2.7–5.5 kg remain unclear. Nonetheless, the repeated occurrence of a similar body-mass threshold in several independent analyses suggests an underlying biological cause that warrants further investigation.

For mammal species above 2.7 kg, about the size of a brushtail possum (*Trichosurus vulpecula*), geography is a key determinant of extinction, with extinction probability higher on islands more distant from the mainland. This is consistent with island biogeography theory, which predicts that extinction rates increase with isolation of islands as a result of lower immigration rates from source populations (Brown & Kodric-Brown, 1977; Brown & Lomolino, 1998). However, the role played by immigration in maintaining equilibrium species richness in island mammal assemblages is not clear. If rates of dispersal to islands are very low, island assemblages may not be in equilibrium at all, but are likely to represent ‘relaxation faunas’ that are the outcome of extinctions from sets of species isolated following sea-level rise at the end of the Pleistocene (Harcourt & Schwartz, 2001). On the other hand, some authors have demonstrated a decline in the diversity of non-volant mammals with increasing isolation in some island systems, and have concluded that overwater dispersal does play a significant role in structuring island mammal faunas (Heaney, 1986; Lomolino, 1994; Hoekstra & Fagan, 1998).

Alternatively, the link between island isolation and extinction probability may result from processes other than immigration. It has been suggested that the longer populations are isolated from predators, the more likely it is that predator recognition and costly antipredator behaviour, such as watchfulness or group vigilance, will be lost, making more isolated populations more susceptible when they are re-exposed to predators (Kavaliers, 1990; Blumstein & Daniel, 2005). Evidence from a recent comparative analysis (Blumstein & Daniel, 2005) suggests that loss of antipredator behaviour can occur within the relatively short time period that many of the islands in our dataset have been isolated from the mainland (i.e. since the Last Glacial Maximum, c. 23,000 years ago). It is possible that antipredator behaviour has been lost to a greater degree in populations on

islands that are more isolated, and thus likely to have been separated from mainland populations for a greater length of time. Our results offer mixed support for this explanation. On the one hand, the decision trees (Figs 3 & 4) do not show that populations on more distant islands are more susceptible to the presence of predators. On the other hand, the GLMM model that includes foxes, distance to mainland and their interaction, gives a significant interaction term ($P = 0.039$), suggesting that populations on more isolated islands are indeed more susceptible to the presence of foxes. In other models, however, there are no significant interactions between mainland distance and other introduced predators.

Another possibility is that island isolation covaries with another geographic or climatic variable that influences extinction probabilities, such as island area or rainfall. For the islands in our dataset, however, there is no correlation between island area and distance from the mainland (Pearson's product-moment correlation, $r = -0.04$, $P = 0.75$, d.f. = 307). On the other hand, there is a tendency for more distant islands to have lower mean annual rainfall (Pearson's product-moment correlation, $r = -0.09$, $P = 0.02$, d.f. = 307). Furthermore, extinction probability is inversely associated with mean annual rainfall across populations within our island dataset (GLMM, $P = 0.0001$). However, both rainfall and distance from mainland are independently associated with higher extinction risk when both predictors are included in a GLMM ($P = 0.0001$ and $P = 0.002$, respectively). Therefore, while rainfall patterns may contribute to variation in extinction probability across islands, they cannot completely account for the effect of isolation.

For mammal species below 2.7 kg predation becomes the key driver of extinction, with a clear positive association between the presence of black rats and extinction probability. The black rat's dispersal abilities, high reproductive rates and ecological flexibility have made it one of the most pervasive introduced species on islands world-wide (Van Dyck & Strahan, 2008; Harris, 2009; Banks & Hughes, 2012). Black rats have been strongly implicated in declines and extinctions of island bird populations (e.g. Atkinson, 1985; Blackburn *et al.*, 2004; Jones *et al.*, 2008), with black rats known to predate on adults, chicks and eggs (Jones *et al.*, 2008). The impact of black rats on mammals is also persuasive, though less well documented than for birds. Harris (2009) found that the black rat is implicated in small mammal extinctions on islands world-wide. After black rat eradication on Boodie and Middle islands, Western Australia, the number of burrowing bettongs (*Bettongia lesuer*) and golden bandicoots (*Isodon auratus*), respectively, rose considerably (Morris, 2002). Black rats are able to capture prey up to their own body size (approximately 300 g), which may include juveniles of species that reach larger sizes as adults, and may also have an impact on populations of mammals through competition or disease transmission (Harris, 2009; Banks & Hughes, 2012). Stokes *et al.* (2009) showed that removal of black rats does not change the body condition of adults of the Australian native rat, *Rattus fuscipes*, but does increase juvenile recruitment, implying either direct competition or predation by black rats on juvenile native rats.

We found that the adverse effect of black rats on island mammal populations is strongly mitigated by the presence of a larger predator, with cats, foxes and dingoes all providing such a mitigating effect. The role of dingoes in the suppression of introduced mesopredators has been well documented (Johnson *et al.*, 2007; Johnson & VanDerWal, 2009; Letnic *et al.*, 2009a,b, 2012; Ritchie & Johnson, 2009). Some authors have suggested that dingoes be reintroduced or allowed to re-establish in areas from which they have been eradicated to provide top-down control of mesopredators (Johnson *et al.*, 2007; Dickman *et al.*, 2009; Ritchie & Johnson, 2009; Wallach *et al.*, 2010; Ritchie *et al.*, 2012), a controversial suggestion given the long-standing efforts by the pastoral industry to control dingoes in areas grazed by livestock. Previous work has focused primarily on the role of dingoes in the suppression of cats and foxes, which are widely considered to be among the primary agents of decline and extinction of native mammals in Australia (Johnson, 2006). Two of the findings from our study point to mesopredator suppression effects that have not previously received much attention: (1) that dingoes suppressing black rats has a stronger effect on the rate of extinction of native mammals than dingoes suppressing cats and foxes; and (2) that cats and foxes themselves play a role as apex predators in suppressing black rat populations. Indeed, our GLMM results indicate a weakly negative association between extinction probability and the presence of dingoes or foxes. This suggests that any direct pressure of dingoes or foxes on native mammal populations is likely to be smaller than the mitigating influence of dingoes or foxes on black rat populations. It is possible that the three larger predators control rats through direct predation: dietary studies have shown that black rats are predated upon by dingoes (Brook & Kutt, 2011), cats and foxes (Clarke & Cameron, 1998; Molsher *et al.*, 2000). In addition, competition and non-lethal behavioural interactions may also serve to suppress the breeding and population growth of black rats on islands where larger predators are present (Ritchie *et al.*, 2012).

CONCLUSIONS

The complexity of processes that seem to drive extinction patterns on islands has implications for the conservation and management of island mammal populations. In Australia and other parts of the world where exotic species introductions have had a major impact on native faunas, the prevailing management paradigm emphasizes the eradication of exotic species whenever and wherever possible. However, as evidence accumulates for the effects of mesopredator release and trophic cascades, the wisdom of this approach has begun to be questioned (e.g. Johnson *et al.*, 2007; Letnic *et al.*, 2012). Our comparative results suggest that mesopredator release can have particularly severe effects on island mammal populations. Given that black rats are a major threat to native mammals, the eradication of cats, foxes or dingoes from islands could result in considerable loss of island mammal biodiversity through the release of rat populations. Paradoxically, with the last remaining populations of some mammal species confined to relict island populations, it is

conceivable that eradication of cats, foxes or dingoes could lead to the complete extinction of some species. A more appropriate management programme should aim to balance the eradication of smaller and larger predators (Courchamp *et al.*, 2011).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Database of Australian island mammal populations.

Appendix S2. Comparisons of generalized linear mixed models of the effects of life history, island geography, and introduced predators, on extinction probability of island mammal populations.

Appendix S3. Decision trees for models with foxes and cats as mesopredators, and cats as apex predator.

BIOSKETCHES

Emily Hanna and **Marcel Cardillo** have research interests in macroevolution, macroecology, community ecology and conservation. Current projects include community assembly and extinction in island mammal populations, and the diversification and ecology of the plant family Proteaceae.

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