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Rarity of a top predator triggers continent-wide collapse of mammal prey: dingoes and marsupials in Australia

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Top predators in terrestrial ecosystems may limit populations of smaller predators that could otherwise become over abundant and cause declines and extinctions of some prey. It is therefore possible that top predators indirectly protect many species of prey from excessive predation. This effect has been demonstrated in some small-scale studies, but it is not known how general or important it is in maintaining prey biodiversity. During the last 150 years, Australia has suffered the world's highest rate of mammal decline and extinction, and most evidence points to introduced mid-sized predators (the red fox and the feral cat) as the cause. Here, we test the idea that the decline of Australia's largest native predator, the dingo, played a role in these extinctions. Dingoes were persecuted from the beginning of European settlement in Australia and have been eliminated or made rare over large parts of the continent. We show a strong positive relationship between the survival of marsupials and the geographical overlap with high-density dingo populations. Our results suggest that the rarity of dingoes was a critical factor which allowed smaller predators to overwhelm marsupial prey, triggering extinction over much of the continent. This is evidence of a crucial role of top predators in maintaining prey biodiversity at large scales in terrestrial ecosystems and suggests that many remaining Australian mammals would benefit from the positive management of dingoes.

Keywords: mesopredator release; trophic cascade; extinction; predation; *Canis lupus dingo*

1. INTRODUCTION

Research over the last decade has shown that large top predators, such as wolves and big cats, may have very significant effects in structuring terrestrial communities and maintaining species diversity in lower trophic levels. The best-known mechanism by which this happens is through predator control of populations of generalist herbivores. With removal of large predators, these herbivores may become over abundant and displace some species while destroying habitat for many others (Berger *et al.* 2001; Terborgh *et al.* 2001). For example, eradication of wolves, *Canis lupus*, and grizzly bears, *Ursus arctos*, in Grand Teton National Park resulted in a fivefold increase in moose density, with consequent over browsing of riparian vegetation and disappearance of migratory birds dependent on such vegetation (Berger *et al.* 2001).

Another mechanism by which top predators might contribute to maintenance of species diversity is through control of mid-sized predators, or mesopredators. Some mesopredators are generalists with high capacity for population increase. In the absence of top-down control, they may increase in abundance, leading to intensification of predation pressure on smaller prey species. This process of 'mesopredator release' can, in theory, result in extinction of some prey species (Courchamp *et al.* 1999). Large terrestrial predators are being made rare worldwide as a result of persecution by humans and habitat fragmentation. This means that mesopredator release has the potential to cause general declines in biodiversity. Some studies have demonstrated declines in prey as a result of mesopredator release in small habitat patches without large predators (Palomares *et al.* 1995; Crooks & Soulé 1999). However, we still have little information on the effects of this process on biodiversity at large scales (Terborgh *et al.* 1999).

Eighteen species of Australian mammal have become extinct since European settlement, representing almost half of all mammal extinctions worldwide in the last 200 years, and many more have declined severely (Maxwell et al. 1996). What caused these declines and extinctions is not always clear, but most evidence points to introduced foxes, *Vulpes vulpes*, and cats, *Felis catus*, as the main cause (Short *et al.* 1992; Gibson *et al.* 1994; Dickman 1996*a*,*b*; Smith & Quin 1996; Short 1998; Burbidge & Manly 2002; Johnson 2006). Extinctions followed the arrival and spread of these predators both on the mainland and offshore islands (Short 1998; Burbidge & Manly 2002; Johnson 2006). Conversely, islands that are free of foxes and/or cats support many mammal species which are extinct on the mainland, and control of introduced predators on the mainland allows surviving populations to recover (Short *et al.* 1992; Kinnear *et al.* 1998). Cats occur throughout mainland Australia and foxes are widespread in all areas except the northern tropics. Overkill by medium-sized predators is therefore a ubiquitous threat for small ground-dwelling mammals in Australia.

Australia's largest extant predator is the dingo *C. lupus dingo*. There is observational evidence that where dingoes

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are locally abundant, foxes and cats are rare (Newsome 2001; Glen & Dickman 2005). Dingoes kill these smaller predators, and foxes evidently fear and avoid dingoes (O'Neill 2002; Mitchell & Banks 2005). Dingoes may therefore limit populations of foxes and cats. European settlers persecuted dingoes, especially in areas taken up for sheep grazing. This continues and has resulted in dingoes being rare or absent from about half of the continent (Fleming *et al.* 2001). It is therefore possible that suppression of dingoes could have contributed to high rates of extinction of native mammals by allowing the intensity of predation from foxes and cats to increase.

If this idea is correct, marsupial species that occur in parts of Australia where dingoes remain abundant should have declined less than the species from regions where dingoes are rare. We tested this prediction in a continental-scale analysis of the extinction pattern in ground-dwelling Australian marsupials. For each such species, we measured the extent of range decline since European settlement and tested whether this was affected by the proportion of the original range that overlaps with dingoes. We compared the effect on marsupial persistence of dingo overlap with a range of other factors that have been shown in previous studies to have been correlated with range decline, in particular, body mass, habitat, geographical position and overlap with foxes. As it has been argued that habitat degradation by introduced herbivores, especially sheep and the European rabbit *Oryctolagus cuniculus*, was involved in declines (Morton 1990; Lunney 2001; Fisher *et al.* 2003), we also tested the effects of overlap with these species.

2. MATERIAL AND METHODS

(a) *Data*

For all ground-dwelling marsupials, we measured the extent of range decline on mainland Australia (excluding Tasmania) since European settlement and the proportion of the original range overlapping with the present distribution of high-density dingo populations (i.e. areas in which dingoes were classified as 'common' or 'generally common' rather than 'uncommon', 'naturally sparse' or 'absent' in Fleming *et al.* 2001). Range decline was expressed as 'persistence', defined as present range, as a proportion of the original range at European arrival. Past and present distributions of marsupials were taken from Strahan (1995) and Maxwell *et al.* (1996). We also compiled information for all taxa on: proportional overlap of the original range with the present distributions of sheep (Fleming *et al.* 2001), rabbits (Williams *et al.* 1995) and the red fox (Saunders *et al.* 1995); body mass (Strahan 1995); mean annual rainfall in the centre of the range; mid-latitudinal position of the range; and predominant habitat (Strahan 1995; habitats were classified as grassland, savannah/open woodland, open forest, shrubland/heath or closed forest and scored from 1 to 5 in that order to represent a transition from open to closed habitats). Range overlaps were calculated by transcribing species distributions onto gridded base maps, in which grid squares were 1 : 250 000 map sheets (as used in Maxwell *et al.* 1996), and by overlaying maps and counting grid squares.

We omitted strictly arboreal species because they would have been immune from impacts of terrestrial predators and herbivores, and because most have not declined significantly since European settlement; species (such as the two *Trichosurus* species) that den in trees, but spend substantial foraging time on the ground were included in the analysis. Geographical sub-species (Maxwell *et al.* 1996) were treated as distinct taxa ($n=137$ taxa).

(b) *Statistical analysis*

We constructed a set of least squares regression models using various combinations of variables to predict persistence of marsupials and selected the best performing model by comparing Akaike Information Criterion (AIC) values. The candidate models included: (i) overlap with dingo, (ii) overlap with introduced herbivores (sheep+rabbit), (iii) overlap with fox, and (iv) overlap with dingo+overlap with sheep. We tested the dingo+sheep model because the distributions of dingoes and sheep are strongly negatively related. Overlap with cats was not explicitly considered because cats are ubiquitous in Australia. As the effects of predation or competition are likely to be influenced by body mass and habitat, we included these variables in all models, with mass entered as mass and mass^2 to accommodate a quadratic relationship of persistence to mass (Burbidge & Mckenzie 1989; Morton 1990; Johnson *et al.* 2002). We also evaluated two null models, as follows: (i) intercept alone and (ii) a model including latitude, rainfall and body mass to describe the geographical pattern of range decline.

All the models were tested using both the raw data and phylogenetically independent contrasts to evaluate their robustness to non-independence owing to phylogeny. For the contrasts analysis, a species-level phylogeny was constructed in PDTREE (v. 5), an extension of the program PDAP (Garland *et al.* 1999), based on the marsupial supertree (Cardillo *et al.* 2004) with geographical subspecies classed as sister taxa and added to the tree. Each of the variables used in the analysis was assessed for phylogenetic signal using the program PHYSIG.M in MatLab (Blomberg *et al.* 2003). The majority of traits showed a strong phylogenetic signal and for these traits, independent contrasts were calculated in PDAP. For the few traits which showed no signal, contrasts were calculated in PDAP, assuming that they evolved along a star phylogeny (a phylogeny with equal branch lengths radiating from a single ancestor).

3. RESULTS

In the analysis of the raw data, the best performing model included dingo, mass and habitat. This was marginally superior (ΔAIC$=1.48$) to dingo+sheep+mass+habitat, and clearly superior (ΔAIC$=23.76$) to the next-ranked model (sheep+rabbit+mass+habitat). The other models performed poorly (ΔAIC>25). The relationships of persistence to mass and dingo overlap are shown in figure 1: persistence first declined and then increased with increasing body mass and was positively related to overlap with dingoes (figure 1*a*,*b*). Persistence was also positively related to vegetation density (table 1). In the analysis of contrasts, the preferred model included dingo+sheep+mass+habitat and was clearly superior to the next-ranked model with sheep+rabbit+mass+habitat (ΔAIC$=8.43$). Again, the other models performed poorly (ΔAIC>30).

We compared the effect sizes of sheep, dingoes, body mass and habitat in models that included all these variables (table 1). The effect of dingoes exceeded that of sheep in the analysis on raw data, while the effects of the two species were of similar strength (but opposite

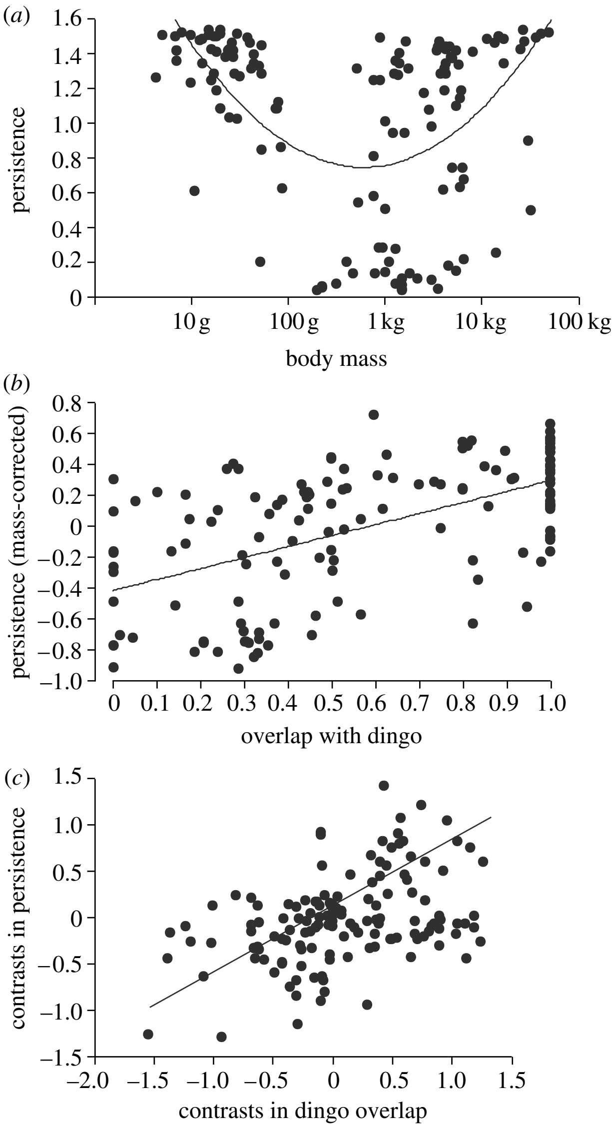

Figure 1. (*a*) Body mass and persistence (present range as a proportion of the original) in ground-dwelling Australian marsupials of mainland Australia. The fitted curve is a quadratic. Persistence is measured as proportion of the original range still occupied, subject to Anscombe transformation (Fisher *et al.* 2003); (*b*) relationship between overlap with dingoes and the residual values of persistence from the mass-persistence quadratic in (*a*) and (*c*) relationship between independent contrasts in dingo overlap and marsupial persistence.

direction, dingoes being associated with persistence and sheep with decline) in the analysis of contrasts. Effects of both mass and mass^2 were strong and consistent in both analyses, demonstrating a quadratic relationship of mass to persistence (see figure 1*a*). Habitat had a moderate positive effect in both analyses: persistence was higher in habitats with greater vegetation density. The distributions of high-density dingo populations and sheep across Australia are compared with the geographical pattern of marsupial decline in figure 2.

4. DISCUSSION

This analysis identified overlap with dingoes as a significant extrinsic factor that acted to protect ground-dwelling marsupials from decline and extinction. The effect of dingoes was independent of latitude, habitat and the distribution of other threats, such as sheep and rabbits, and was consistent in analyses of raw data and phylogenetically independent contrasts. It also had more power to predict the pattern of marsupial decline than did simple overlap with foxes, even though there is very strong evidence that foxes were directly involved in many extinctions (Short 1998; Short & Calaby 2001). Our interpretation of this is that the presence of foxes did not inevitably lead to extinctions, but did so only when foxes reached very high abundance; abundance of foxes was, in turn, strongly affected by the presence of dingoes. In addition, cats occur throughout Australia and contributed to extinctions, so their influence also reduced the association of fox distribution alone with the extinction pattern.

Table 1. Comparison of standardized effect sizes, measuring the effect of a proportional change in dingo overlap, sheep overlap and habitat structure (open to closed) on persistence of marsupial species.

model term	parameter estimate	standard error
raw data		
log mass	−3.03	0.34
log mass^2	2.91	0.35
dingo	0.31	0.06
sheep	−0.07	0.07
habitat	0.18	0.06
phylogenetically independent contrasts		
log mass	−1.14	0.31
log mass^2	1.13	0.27
dingo	0.22	0.08
sheep	−0.37	0.09
habitat	0.26	0.08

Presumably, direct estimates of the densities of cats and foxes would provide even stronger explanation of local extinction rates, but in the absence of such information, the distribution of dingoes accounts for the large-scale pattern of extinction. The abundance of foxes and cats is likely to be also affected by factors other than the presence of dingoes. In particular, the availability of rabbits as prey, and habitat characteristics, may be important. The fact that we found such a strong and general relationship between persistence and overlap with dingoes without formally controlling for other factors suggests that the effects of dingoes on the threat from mesopredators are powerful enough to override them.

We found evidence that overlap with sheep also affected persistence. This could suggest that habitat changes caused by sheep grazing contributed to marsupial declines, perhaps because such changes increased the exposure of marsupials to predation. An alternative explanation for the role of sheep is that because rabbits are typically very abundant where sheep are grazed and foxes prey heavily on rabbits, fox populations are especially large where they overlap with sheep and are therefore more likely to cause extinction of some prey by hyperpredation (Smith & Quin 1996; Courchamp *et al.* 2000). In addition, suppression of dingoes was and is especially intense where sheep are grazed (Fleming *et al.* 2001), and this is another factor contributing to very high fox density in sheep country. Our analysis of the relationship of persistence to mass among ground-dwelling marsupials shows a strong effect, with persistence lowest for medium-sized species in the

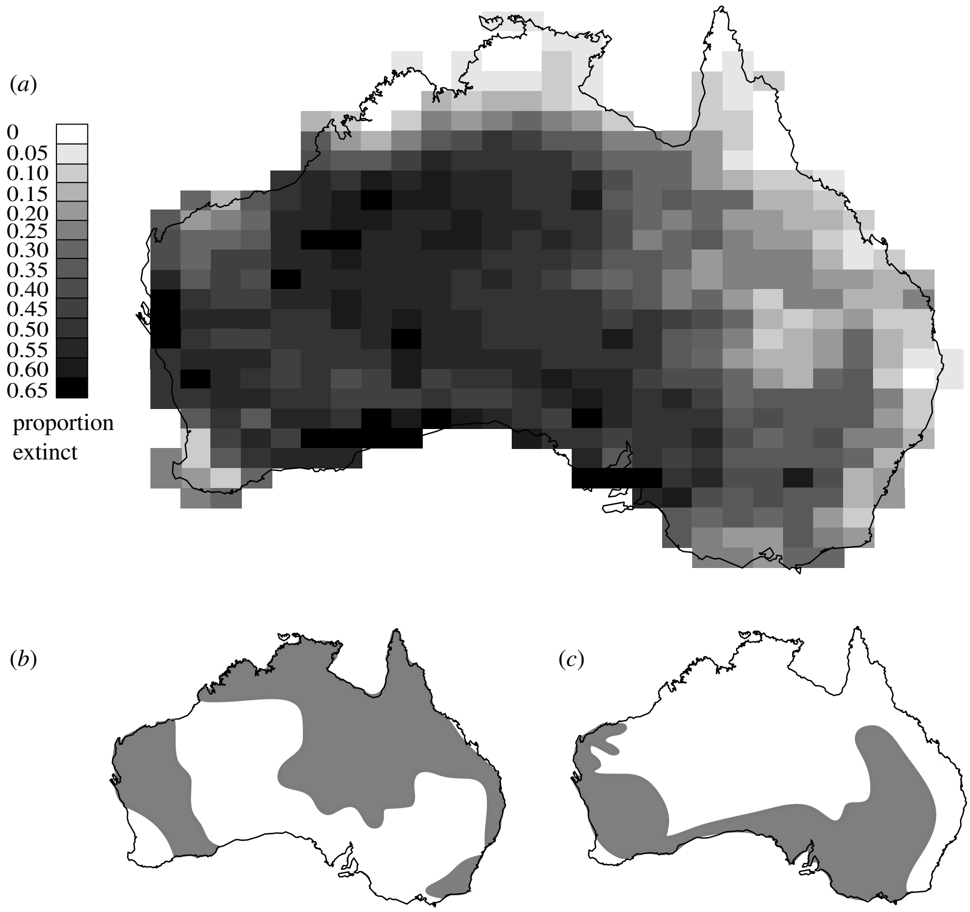

Figure 2. Maps showing (*a*) the geographical pattern in the proportions of ground-dwelling marsupials that have gone locally extinct over the last 200 years, (*b*) the distribution of high-density dingo populations (Fleming *et al.* 2001) and (*c*) the distribution of sheep (Fleming *et al.* 2001) over mainland Australia.

combined prey-size range of foxes and cats. The effect of habitat on persistence is also consistent with predation as the cause of decline, because species in more open habitats would be more exposed to predation and therefore likely to decline most severely.

Australia's marsupial declines began in the nineteenth century, and many species had gone extinct by the middle of the twentieth century. Our analysis of the pattern of decline used the present distributions of threatening or protective factors as explanatory variables. A potential problem with this is that these distributions may not be relevant to the times when the declines took place. However, the present distribution of dingoes was established early in the history of settlement, especially as land was taken up for sheep grazing, and has since been maintained by continued control (and in some regions, is held in place by dingo barrier fences; Fleming *et al.* 2001). In addition, there is historical evidence that suppression of the dingo was followed by marsupial declines. In New South Wales, the suppression of dingoes began in about 1880 and peaked in the last decade of the nineteenth century (Glen & Short 2000). This was followed by rapid establishment of large fox populations between 1900 and 1915, which in turn was followed within a few years by extinctions of rat-kangaroos (Short 1998).

Persecution of dingoes is widespread in southern Australia and accounts for the rarity or absence of dingoes throughout much of the south. In parts of the central and northwestern deserts, the present rarity of dingoes is probably owing to environmental conditions rather than human interference (Fleming *et al.* 2001). In our analysis, the absence of dingoes from such areas accounts for declines in medium-sized mammals, just as it does over much of the south. There is direct evidence that in the absence of dingoes, cats are a serious threat to medium-sized mammals in the central and northwestern deserts (Gibson *et al.* 1994). The general point is that the rarity of top predators, however it is caused, leaves prey species vulnerable to over predation by mesopredators.

Our results constitute the first evidence that removal of a top predator and the consequent release of mesopredators in terrestrial ecosystems can lead to the collapse of prey faunas at a continental scale. They should also prompt a rethink of the ecological role of the dingo in Australia. The dingo reached Australia approximately 3500–4000 years ago (Corbett 1995; Savolainen *et al.* 2004), almost certainly as a result of transport by seafaring people from Southeast Asia. The thylacine, *Thylacinus cynocephalus*, and devil, *Sacophilus harrisii*, went extinct on the mainland soon after. Whether the arrival of the dingo triggered these extinctions is debateable (Johnson & Wroe 2003), but whatever the cause, the result was that the dingo stepped into the role of the top non-human predator on mainland Australia. There is evidence that dingo predation presently regulates population size of large macropods and emus (Pople *et al.* 2000). The dingo clearly occupies a stable and significant role in Australian ecosystems, but it is not generally regarded as a native species in Australia. Rather, it is treated as an introduced pest, with the goal of dingo management typically being to hold numbers at very low density or achieve local eradication. This hostile attitude is intensified by occasional attacks by dingoes on people.

The major implication of our study is that the dingo is a keystone species protecting mammal biodiversity in Australia and is the most significant constraint on the destructive power of exotic predators. This means that positive management of dingoes should be seen as an essential element of biodiversity conservation in Australia and should be given very high priority.

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