

Are dingoes a trophic regulator in arid Australia? A comparison of mammal communities on either side of the dingo fence

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Abstract The direct and indirect interactions that large mammalian carnivores have with other species can have far-reaching effects on ecosystems. In recent years there has been growing interest in the role that Australia's largest terrestrial predator, the dingo, may have in structuring ecosystems. In this study we investigate the effect of dingo exclusion on mammal communities, by comparing mammal assemblages where dingoes were present and absent. The study was replicated at three locations spanning 300 km in the Strzelecki Desert. We hypothesized that larger species of mammal subject to direct interactions with dingoes should increase in abundance in the absence of dingoes while smaller species subject to predation by mesopredators should decrease in abundance because of increased mesopredator impact. There were stark differences in mammal assemblages on either side of the dingo fence and the effect of dingoes appeared to scale with body size. Kangaroos and red foxes were more abundant in the absence of dingoes while Rabbits and the Dusky Hopping-mouse *Notomys fuscus* were less abundant where dingoes were absent, suggesting that they may benefit from lower red fox numbers in the presence of dingoes. Feral cats and dunnarts (*Sminthopsis* spp.) did not respond to dingo exclusion. Our study provides evidence that dingoes do structure mammal communities in arid Australia; however, dingo exclusion is also associated with a suite of land use factors, including sheep grazing and kangaroo harvesting that may also be expected to influence kangaroo and red fox populations. Maintaining or restoring populations of dingoes may be useful strategies to mitigate the impacts of mesopredators and overgrazing by herbivores.

Key words: dingo, fox, kangaroo, mesopredator, top predator, trophic cascade.

INTRODUCTION

The disruption or total cessation of interactions between large mammalian carnivores and their prey species can have dramatic effects on the organization and function of terrestrial ecosystems (Crooks & Soulé 1999; Berger *et al.* 2001; Hebblewhite *et al.* 2005). The most obvious population level effects that top predators have are the suppression of large herbivores and smaller predator (mesopredator) populations through predation or competition. Following the removal of top predators, the release of large herbivore and mesopredator populations that occurs can unleash a cascade of 'indirect' effects on lower trophic groups. In the absence of top predators, changes in vegetation structure resulting from increased grazing pressure can lead to the decline of plant species and in turn affect small vertebrates dependent on dense vegetation (Berger *et al.* 2001; Hebblewhite *et al.* 2005). Similarly, in the absence of top predators, increased levels of predation by mesopredators can suppress popula-

tions of small prey species (Crooks & Soulé 1999). Because top predators can shape ecosystems through both direct and indirect interactions with other species their ecological effects can be harnessed to manipulate ecological processes and species abundances for the benefit of biodiversity conservation (Sergio *et al.* 2006; Beyer *et al.* 2007; Ripple & Beschta 2007).

In Australia, there has been considerable debate over the role that the continent's largest terrestrial predator, the dingo (body-weight 11–22 kg), has in structuring terrestrial ecosystems (Caughley *et al.* 1980; Pople *et al.* 2000; Newsome *et al.* 2001). Much of this debate has stemmed from field observations of dingo predation on kangaroos (Shepherd 1981; Marsack & Campbell 1990), and large-scale population surveys showing that kangaroos and emu were far more abundant in areas 'inside' the dingo fence where dingoes are rare because of intensive control than they were 'outside' the dingo fence (Caughley *et al.* 1980; Caughley & Grigg 1982; Grice *et al.* 1985). Consequently, several studies have suggested that dingoes may regulate kangaroo and emu populations (Caughley *et al.* 1980; Pople *et al.* 2000). Despite the strong correlative evidence suggesting that dingoes regulate kangaroo

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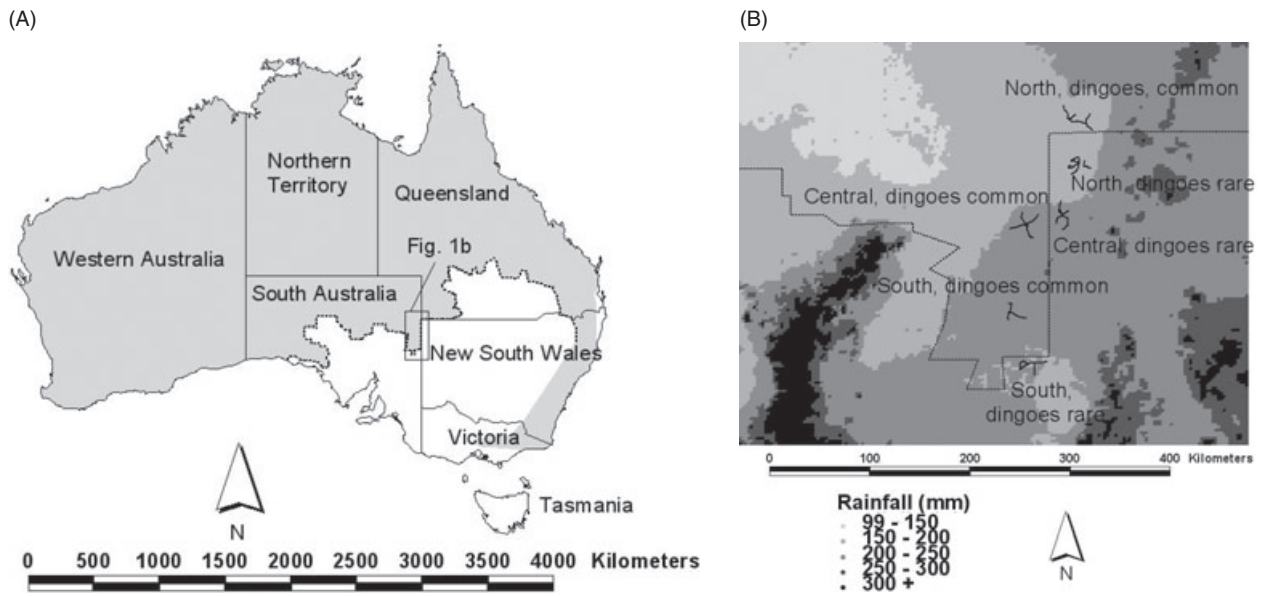


Fig. 1. Maps showing (A) the location of the dingo fence (hashed), and areas where dingoes are common (shaded) within Australia (modified after Fleming *et al.* 2006), and (B) the location of the spotlight transects on either side of the dingo fence at the North, Central and South sites and mean annual rainfall (mm) in the region (source: Australian Bureau of Meteorology).

and emu populations, some authors have questioned the generality of these results, contending that the observed differences may in some instances be due to differences in land use and geomorphology on either side of the dingo fence (Dawson 1995; Newsome *et al.* 2001).

Several authors have also suggested that the regulatory effects of dingoes may cascade through trophic webs (Read 1997; Newsome *et al.* 2001; Moseby *et al.* 2006; Glen *et al.* 2007; Letnic 2007). In evidence of this, field and desktop studies have found negative relationships between dingo and fox abundance (Newsome *et al.* 2001; Letnic 2007) and positive relationships between dingo abundance and the persistence of medium sized marsupials and native rodents (Smith & Quin 1996; Johnson *et al.* 2007; Southgate *et al.* 2007; Letnic *et al.* 2009). However, few field studies have investigated the interactions between dingoes, herbivores, mesopredators and their prey in arid Australia (Newsome *et al.* 2001; Letnic *et al.* 2009).

In a recent review paper, Glen *et al.* (2007) called for studies to investigate the role of dingoes as a keystone trophic regulator in Australian ecosystems. They suggested three questions must be investigated to understand the ecological role of dingoes. These were: (i) Do dingoes limit the abundance of other species? (ii) Do dingoes influence the ecological relationships of other predators or prey? (iii) Do changes in the abundance of dingoes entrain a trophic cascade? Although Glen *et al.* (2007) suggested that an experimental approach would best elucidate the ecological role of dingoes, they acknowledged that conducting such an experiment

would be logistically difficult because of the large spatial and temporal scales required. They proposed an alternative, and logistically less complex approach to investigate the ecological role of dingoes – a comparison of populations of species hypothesized to interact with dingoes in multiple areas with and without dingoes at a single point in time.

In this study we investigate the effect of dingo exclusion on mammal communities in arid Australia. We did this by conducting snapshot comparisons of mammal assemblages on either side of the dingo fence in the Strzelecki Desert in the southern arid zone of Australia. The dingo barrier fence excludes dingoes from predominantly sheep grazing lands and, in combination with dingo population control, has successfully reduced sheep losses because of dingo predation (Allen & Sparkes 2001, Fig. 1). Dingoes are rare on one side of the fence because of intensive pest-control and are common on the other side (Fleming *et al.* 2006) providing an opportunity to examine their role in structuring ecosystems. Because the impacts that predators have on their prey usually scale with body size (Sinclair *et al.* 2003), we hypothesized that the effect of dingoes on the abundances of mammal species should scale with body size (Table 1). We predicted that larger mammal species subject to direct interactions with dingoes such as predation or competition should increase in abundance in the absence of dingoes. In contrast, we predicted that smaller species are more likely to have strong interactions with mesopredators and should therefore decrease in abundance in the absence of dingoes because of increased mesopredator activity.

Table 1. The hypothesized responses of mammal species to dingo exclusion

Species	Body weight (g)	Hypothesized population response to dingo exclusion
Red fox [†]	4 600 ^{††}	Increase due to cessation of competition and predation by dingoes
Feral cat [†]	3 500 ^{††}	Increase due to cessation of competition and predation by dingoes
Red Kangaroo [‡]	35 000 ^{¶¶}	Increase due to cessation of predation by dingoes
Grey kangaroo [‡]	35 000 ^{¶¶}	Increase due to cessation of predation by dingoes
Rabbit [‡]	1 058 ^{##}	Decrease due to increased predation by foxes and cats.
<i>Notomys fuscus</i> [§]	35 ^{§§}	Decrease due increased predation by foxes and cats
<i>Sminthopsis</i> spp. [¶]	15 ^{§§}	Decrease due increased predation by foxes and cats

The approximate body size and diet of each mammal species is also presented. [†]Carnivore, [‡]Herbivore, [§]Omnivore, [¶]Insectivore. ^{††}Read and Bowen (2001), ^{##}Belovsky *et al.* (1991), ^{§§}Strahan (1995), ^{¶¶}Dawson (1995).

Study system

The difference in dingo density on either side of the dingo fence allowed us to conduct a natural experiment using either side of the dingo fence as the treatments (Fig. 1A). The study was replicated at three sites spanning 300 km. Each of the three study sites, North, Central and South, consisted of a pair of sub-sites located on pastoral properties that were near the dingo fence in the dunefield of the Strzelecki Desert. The sub-sites were located in South Australia, New South Wales and Queensland. At each study site there was a sub-site located 'inside' (no dingoes) and 'outside' (dingoes) the dingo fence (Fig. 1B). The sub-sites were selected for similarity of long-term annual rainfall, landform and vegetation type. Each study site was sampled once and we thus assumed that the differences between sub-sites at each site should be retained, regardless of season. All the sites were rangelands where commercial cattle and sheep grazing was conducted in natural vegetation, which may have been modified by livestock grazing, but had not been deliberately cleared and had been used for grazing since the 1870s.

The Strzelecki Desert is topographically uniform and is dominated by longitudinal sand dunes 3–8 m high, running in a NE-SW direction. At all sites the vegetation on dune crests and slopes was dominated by scattered trees and shrubs and perennial understorey vegetation was sparse. Following rain many ephemeral herbs and forbs are present. The plains between the sand dunes have clay soils with vegetation dominated by ephemeral forbs and short grasses. *Callitris glaucophylla*, *Casuarina pauper*, *Acacia aneura* and *A. ligulata* were the dominant overstorey plants at the South study site. *Dodonaea viscosa*, *A. ligulata*, *C. pauper*, *A. aneura* and *Senna artemisioides* were the dominant overstorey plants at the Central study site. *Hakea leucoptera*, *A. ligulata* and *Atalaya hemiglauca* were the dominant overstorey plants at the North study site.

The study area has an arid climate (<250 mm annual rainfall). Mean annual rainfall at the study sites ranged from 180 to 220 mm. The mean annual

maximum temperature at the nearest weather station to the study area (Tibooburra, 29.43°S, 142.01°E) is 27°C and the mean annual minimum temperature is 13°C. In summer, maximum temperatures may be >45°C and in winter minima may be <0°C (source: Australian Bureau of Meteorology). Elevation above sea level (a.s.l.) in the study areas decreased from north to south and east to west, and ranged between 68 m a.s.l. at South site to 124 m a.s.l. at North site.

METHODS

Spotlight surveys have been used in previous studies of small, medium and large mammals in the Australian arid zone (Morton 1978; Read & Bowen 2001; Moseby *et al.* 2006) and were suitable for estimating the abundance of a range of mammal species of different body sizes in the Strzelecki Desert because the understorey vegetation was sparse and allowed a largely uninterrupted view of the landscape. We derived an index of abundance for each mammal species using 3–4 nocturnal, spotlight transects at each sub-site. Each spotlight transect was undertaken on a different section of road and consequently, each transect was treated as a replicate in analyses. During spotlight surveys mammals were counted by an observer using a 50 W spotlight while sitting on the roof (approximately 2.3 m above ground level) of a four-wheel-drive vehicle moving at 15 km h⁻¹. Where necessary, binoculars were used to confirm the identification of species. Because of the difficulty in distinguishing between *Macropus giganteus* and *M. fuliginosus* during spotlight surveys (Dawson 1995), all observations of these species were classified as grey kangaroo for the purpose of analyses. Similarly, all observations of insectivorous marsupials of the genus *Sminthopsis* were classified as *Sminthopsis* spp. because *S. crassicaudata* and *S. macroura* could not be reliably distinguished during spotlight surveys. The spotlight transects varied in length from 10–20 km and commenced at dusk. The total length of spotlight transects conducted in each sub-site ranged from 45–60 km. An index of population density for each mammal species on each transect was calculated as the number of animals sighted divided by the number of kilometres surveyed.

To provide an indication of livestock grazing pressure at the time of sampling, livestock sightings were recorded during spotlight surveys. Density estimates for livestock were standardized by converting cattle and sheep densities into

dry sheep equivalents (DSE) and summing the total number of DSE sighted on each transect. One wether was assumed to equal 1 DSE. A cow was assumed to be equal to 8 DSE (Jansen & Robertson 2001).

Analyses

An ordination of mammal abundances recorded on spotlight transects was performed using the multidimensional scaling (MDS) procedure in Primer V. 5 (Clarke 1993). Dissimilarity indices were computed using the Bray–Curtis coefficient. Because the likelihood of sighting each mammal species in spotlight surveys varied between species, raw abundance indices do not allow direct comparison of abundance between species. Consequently, we standardized mammal variables before performing multivariate analyses. Mammal variables were square root transformed prior to analyses. Dingo abundance was not included in MDS analyses. Minimum stress configurations were computed from 20 starts. To interpret the results of the ordinations two-dimensional biplots of the ordinations were presented. For biplots of the spotlight transects, transects were labelled by dingoes (present, absent).

The ANOSIM procedure of Primer was used to test in a multivariate space for differences in the composition of mammal assemblages sampled during spotlight transects performed on either side of the dingo fence. If a significant result was obtained using ANOSIM, the Simper procedure of Primer was used to identify the species characteristic of each treatment. This exploratory method calculates the average similarity between every plot in each treatment. The average similarity is then broken down into separate contributions for each species to give the average contribution, as a percentage, by each species within each group.

Comparisons of the abundance of each mammal species between sites and on either side of the dingo fence were conducted using analysis of variance (ANOVA), with Dingoes (dingoes, no dingoes), and site nested within Dingoes (North, Central, South), as the factors. The data were subject to a $\sqrt{(x+1)}$ transformation prior to analysis. Fisher's protected least squares difference test (Fisher's PLSD) was used to conduct planned comparisons of mean mammal abundances on either side of the dingo fence, at each site, after significant *F* tests for the site nested within fence factor.

We investigated the hypothesis that the effect of dingoes on mammal species would scale with body size by calculating estimates of dingo effect on each species and plotting estimates of effect size against the log of body size for each mammal species at each site. Standardized estimates of dingo effect on mammal species were calculated using the log response ratio $\ln((X_c + 1)/(X_e + 1))$ where X_c was the mean abundance of each mammal species in the absence of dingoes, and X_e was the same variable in the presence of dingoes (Wootton 1997). The log response ratio thus represents the proportional change in species abundance and allowed direct comparison of the effects of the presence of dingoes between species. If the abundance of a mammal species increased in the absence of dingoes, the log response ratio would be positive. Conversely, if the abundance of a species decreased in the absence of dingoes the log response ratio would be negative. We used locally weighted regression scatterplot smoothing to explore the relationship between the

effect of dingoes and mammal body size (Quinn & Keough 2002). If the response of mammal species of different body sizes was consistent between sites we would expect that the form of the line describing the functional relationship between body size and effect size would be qualitatively similar at all three study sites.

RESULTS

Mammal assemblages

Assemblages of mammal species on either side of the dingo fence showed clear separation (Fig. 2, ANOSIM dingoes *vs.* no dingoes, Global $R = 0.748$, $P < 0.001$). Red kangaroos, grey kangaroos, rabbits and foxes were characteristic of transects conducted where dingoes were absent (Table 2). Rabbits and *Notomys fuscus* were characteristic of transects conducted where dingoes were present (Table 2).

Mammal abundances

Predators

Dingoes were only observed 'outside' (dingoes) the dingo fence and were most abundant at South site and least abundant at North site (Tables 3,4). Foxes or their spoor were recorded on both sides of the dingo fence. Overall foxes were more abundant inside the dingo fence where dingoes were absent (Tables 3,4). Cat spoor was recorded on both sides of the dingo fence; however, cats were only sighted where dingoes were common (Tables 3,4). Overall, cat sightings were infrequent and cat abundance did not differ significantly on either side of the dingo fence.

Kangaroos

Red kangaroos were more abundant in the absence of dingoes (Tables 3,4). No red kangaroos were observed during spotlight surveys at two of the sub-sites where dingoes were common; however, red kangaroos were sighted at all sub-sites during the daytime (Table 3). Grey kangaroos were more abundant in the absence of dingoes and were only sighted inside the dingo fence (Tables 3,4).

Rabbits

Rabbit abundance on each side of the dingo fence varied between sites (Tables 3,4) and was consistently greater in the presence of dingoes (North site, Fisher's

PLSD, $P = 0.007$, (Central site, Fisher's PLSD, $P = 0.02$; South site, Fisher's PLSD, $P < 0.001$).

Small mammals

Overall, the abundance of *N. fuscus* was greater where dingoes were common but varied among sites on either side of the dingo fence (Tables 3,4). *Notomys fuscus* were sighted at two of the three sub-sites where dingoes were common and only at one sub-site where dingoes were absent. Comparisons of mean sighting rates at each site indicated that *N. fuscus* was more abundant outside the dingo fence at South (Fisher's PLSD, $P < 0.02$) and Central sites (Fisher's PLSD, $P = 0.01$). The abundance of *Sminthopsis* spp. did not differ on either side of the dingo fence or between sites within treatments (Tables 3,4).

Livestock

Livestock abundance was highly variable but did not differ on either side of the dingo fence or between sites

Table 2. Results of Simper analyses of mammal abundance on spotlight transects conducted in the presence and absence of dingoes

No dingoes		Dingoes	
Species	C (%)	Species	C (%)
Red kangaroo	33.06	Rabbit	86.73
Grey kangaroo	27.86	<i>Notomys fuscus</i>	9.19
Rabbit	26.52		
Fox	10.14		

The table presents the percentage contribution to the multidimensional scaling solution (C) made by species characteristic of mammal assemblages in the presence and absence of dingoes.

Table 3. Mean abundance (sightings per kilometre) (± 1 standard error) of mammals at each sub-site

Variable	Site					
	North		Central		South	
	No dingoes	Dingoes	No dingoes	Dingoes	No dingoes	Dingoes
Dingo	0.00	0.02 (0.02)	0.00	0.02 (0.02)	0.00	0.05 (0.03)
Red fox	0.03 (0.03)	0.02 (0.02)	0.04 (0.03)	0.00 [†]	0.20 (0.10)	0.00 [†]
Feral cat	0.00 [†]	0.18 (0.16)	0.00 [†]	0.00 [†]	0.00 [†]	0.27 (0.23)
Red Kangaroo	0.30 (0.18)	0.07 (0.05)	0.09 (0.04)	0.00 [†]	0.51 (0.20)	0.00 [†]
Grey kangaroo	0.22 (0.08)	0.00	0.28 (0.14)	0.00	0.05 (0.05)	0.00
Rabbit	0.05 (0.04)	0.47 (0.09)	0.09 (0.03)	0.45 (0.11)	0.42 (0.15)	1.55 (0.30)
<i>Notomys fuscus</i>	0.00	0.00 [†]	0.03 (0.02)	0.14 (0.03)	0.00	0.10 (0.07)
<i>Sminthopsis</i> spp.	0.02 (0.02)	0.02 (0.02)	0.07 (0.05)	0.02 (0.02)	0.00 [†]	0.00 [†]
Livestock DSE	1.70 (1.70) [§]	6.66 (4.00) [¶]	0.17 (0.17) [‡]	0.00	3.64 (0.37) [¶]	0.79 (0.79) [¶]

[†]Detected, but not during formal spotlight surveys. [‡]Sheep and cattle. [§]Sheep only. [¶]Cattle only. DSE, dry sheep equivalents.

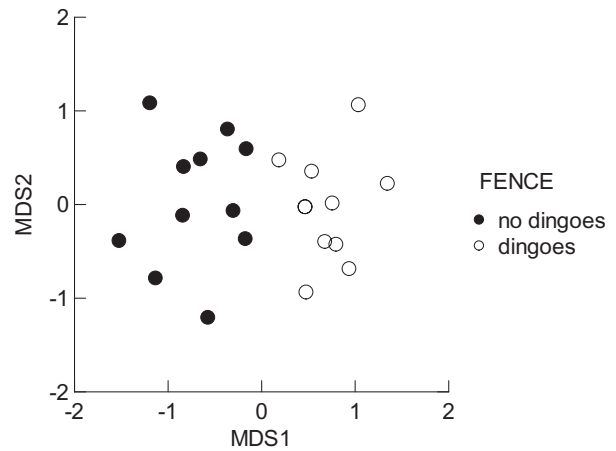


Fig. 2. Multidimensional scaling (MDS) ordination of mammal abundances, comparing mammal assemblages observed during spotlight-transects conducted in the presence and absence of dingoes. Stress = 0.14.

Table 4. F values from analyses of variance (ANOVA) comparing the effects of Dingoes (dingo/no dingo) and Site nested within Dingoes on the abundance of mammal species

Species	Effect	
	Dingoes (d.f. = 1,16)	Site (Dingoes) (d.f. = 4,16)
Dingo	6.33*	0.47
Red fox	8.09***	2.86
Feral cat	3.25	0.89
Red Kangaroo	10.86***	1.96
Grey kangaroo	10.05**	1.20
Rabbit	45.10***	12.67***
<i>Notomys fuscus</i>	11.13***	4.49**
<i>Sminthopsis</i> spp.	0.68	0.90
Livestock DSE	0	2.278

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

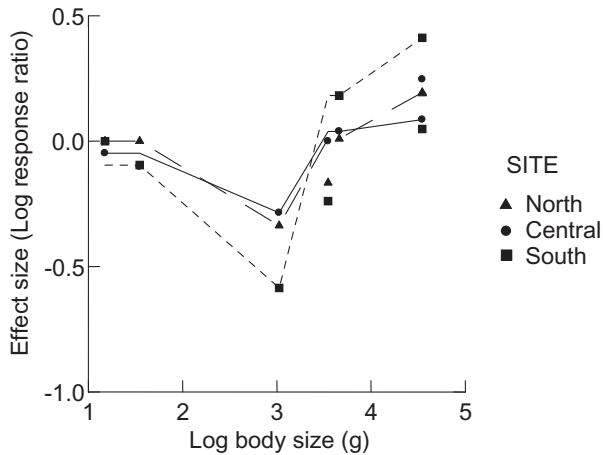


Fig. 3. Log body size of mammal species plotted against the mean effect (log response ratio) of dingo exclusion at each site. A LOWESS smoothing function was fitted to the data from each site. Positive effect sizes indicate variables that increased where dingoes were absent. Negative effect sizes indicate variables that decreased where dingoes were absent. LOWESS, locally weighted regression scatterplot smoothing.

on each side of the dingo fence (Tables 3,4). Sheep were only encountered on transects where dingoes were absent (Table 3).

Effect size versus body size

At all three sites, there was an apparently non-linear response relationship between body size and the effect of dingoes on mammal species abundances (Fig. 3). Large mammals (>30 kg) showed a strong increase in abundance in the absence of dingoes. Medium sized mammals (1–5 kg) showed varying responses to dingoes, with rabbits (1058 g) showing a strong decrease in the absence of dingoes. Cats (3500 g) displayed little response, while larger foxes (4600 g) responded positively to the absence of dingoes. Small mammals (<50 g) showed generally weak responses to the presence/absence of dingoes.

DISCUSSION

The effect of dingo exclusion in the Strzelecki Desert

So stark were the differences in kangaroo, rabbit, fox and dingo abundances on either side of the dingo fence in the Strzelecki Desert that Newsome *et al.* (2001) described the two adjacent landscapes as separate ecological universes. The results of our study also conducted in the Strzelecki Desert more than 20 years later were qualitatively similar to those of Newsome *et al.* (2001) and Caughley *et al.* (1980) for dingoes, foxes,

cats, rabbits and kangaroos. Our surveys also revealed differences in the abundance of *Notomys fuscus* that were consistent with a trapping study conducted at the same time but at a smaller spatial scale (Letnic *et al.* 2009).

Overall, our results indicate that the effects of the dingo fence on mammal community structure in the Strzelecki Desert were consistent across study sites and varied as a non-linear function of body size. As hypothesized (Table 1), the abundance of red kangaroos, grey kangaroos and foxes increased in the absence of dingoes, while the abundance of rabbits and *N. fuscus* decreased in the absence of dingoes. Contrary to our predictions, neither feral cat nor dunnart abundance differed on either side of the dingo fence. These results with apparently alternating effects on the abundance of five of the mammal taxa predicted to be directly and indirectly affected by dingoes lend support to the notion that dingoes are trophic regulators in arid ecosystems.

The weak response of feral cats and dunnarts to the presence of dingoes indicated that the presence/absence of dingoes may not influence the abundance of all mammal species in the Strzelecki Desert. One explanation for the weak response of feral cats is that their populations may be suppressed, to some extent, by both dingoes and foxes, with the latter species being the dominant predator in the absence of dingoes (Risbey *et al.* 2000; Burrows *et al.* 2003; Glen & Dickman 2005). An alternative explanation is that cat populations in the arid zone are driven by spatial and temporal variation in the availability of their primary prey species, rabbits and rodents (Read & Bowen 2001; Holden & Mutze 2002; Letnic *et al.* 2005) more so than the presence of dingoes. Further study investigating the factors driving cat populations is required.

In the case of dunnarts (*Sminthopsis* spp.), previous studies of fox and dingo diets indicate that they are rarely eaten and this may be the reason for their weak response to the presence/absence of dingoes (Corbett & Newsome 1987; Risbey *et al.* 2000; Holden & Mutze 2002; Paltridge 2002). One explanation for the low occurrence of dunnarts in fox and dingo diets is that because of their small body size they are less preferred as prey than larger rabbits and hopping mice. This explanation is also supported by dietary studies, which show that rabbits and rodents including *Notomys* spp. occur more frequently than dunnarts in the diet of foxes (Read & Bowen 2001; Holden & Mutze 2002; Paltridge 2002).

While our results support the body size model and suggest that dingoes do structure mammal communities in the Strzelecki Desert, there are other plausible explanations for the differences we observed. For example, Newsome *et al.* (2001) suggested that the differences in rabbit and fox abundance on either side of the dingo fence in the Strzelecki Desert were likely due to dingoes, but disagreed with the assertion of

Caughley *et al.* (1980) that predation by dingoes was the only cause for the dramatic difference in kangaroo numbers. Instead, Newsome *et al.* (2001) argued that because of differences in geomorphology, landscapes in New South Wales were more likely to retain moisture and produce forage for kangaroos than those in South Australia; consequently, landscapes in New South Wales could support higher populations of kangaroos than those in South Australia. However, as they acknowledge in their paper, the hypothesis to explain disparate kangaroo abundance on either side of the dingo fence was specific to their study location in the central Strzelecki Desert (Newsome *et al.* 2001). Other studies conducted at larger scales in South Australia and Queensland indicate that the disparity in red kangaroo numbers on either side of the dingo fence exists throughout the Australian arid zone (Caughley & Grigg 1982; Pople *et al.* 2000).

An examination of rainfall data (Fig. 1B) and land use patterns from arid Australia suggest at least two other explanations in addition to dingo predation to explain the differences in mammal communities on either side of the dingo fence. The first of these explanations is that there is a general tendency for rainfall to decrease northwards and eastwards across the dingo fence. Thus, it is possible that a large-scale rainfall gradient could contribute to the observed differences in mammal assemblages, particularly if higher density populations to the east and south of the dingo fence spillover westwards and their populations are checked by the dingo fence (see Caughley *et al.* 1988). Such a pattern has been proposed to explain the distribution and abundance of grey kangaroos, which have expanded their range in the last 50 years and do not appear to occur north or west of the dingo fence in the Strzelecki Desert (Caughley *et al.* 1980, 1988; Newsome *et al.* 2001). If such a large-scale pattern in rainfall was the primary factor shaping mammal communities we would expect that red kangaroo, fox, cat, rabbit, rodent and dunnart populations would also be greater south and east of the fence where annual rainfall is generally greater. While red kangaroo (Caughley *et al.* 1980; Pople *et al.* 2000) and fox (Saunders *et al.* 1995) population densities are greater in higher rainfall regions east and south of the fence, this explanation is not supported for all the mammal species we observed. Rabbits and *N. fuscus* were more abundant 'outside' the dingo fence where rainfall is generally lower, and dunnart and cat abundance did not differ on either side of the fence.

The other explanation is that land use and its intensity differ on either side of the dingo fence affecting the availability of food and water for mammals. In Sweden and Israel, increased availability of nutrients as a by-product of agricultural production are thought to have subsidized the diets of red foxes and led to increases in their populations (Elmhagen & Rushton

2007; Shapira *et al.* 2008). In Sweden, these bottom-up effects of agricultural production are thought to have had a greater impact on fox populations than the removal of top-down population control by wolves (Elmhagen & Rushton 2007).

In our study area, several lines of evidence suggest that land use and the availability of resources for mammal species differ on either side of the dingo fence. These differences include observations that: (i) sheep grazing was limited to areas where dingoes were absent; (ii) the density of artificial waters was greater in the absence of dingoes (Landsberg *et al.* 1997); and (iii) commercial kangaroo shooting was confined to areas where dingoes were absent. While the occurrence of sheep grazing and kangaroo harvesting are themselves likely due to the absence of dingoes, it is conceivable that the greater availability of surface water in the absence of dingoes may favour medium and large sized mammals such as kangaroos (Dawson *et al.* 2006), cats and foxes that have the mobility to utilize these resources. In addition, the availability of carrion from kangaroo harvesting (Read & Wilson 2004) and mass death of kangaroos during drought that has been documented to occur in areas without dingoes (Caughley *et al.* 1985) may subsidize the diet of foxes, allowing the maintenance of higher fox populations than areas with fewer kangaroos. However, the provision of additional water cannot explain the greater abundance of rabbits and *N. fuscus* in the presence of dingoes, as there were fewer artificial waters. Moreover, individuals of these species because of their relatively small body size and thus poor mobility are less likely to utilize dams and troughs to obtain water than larger mammal species.

In this study, stocking rates (measured as DSE per kilometre) at the time of the surveys did not differ consistently on either side of the dingo fence and lend little support to the hypothesis that contemporary stocking rates were the reason for the disparate mammal assemblages on either side of the dingo fence. However, we cannot account for the impact of past stocking rates and consider it likely that areas inside the dingo fence were grazed more intensively for longer periods of time than areas outside the dingo fence. The reason for this is that sheep grazing is generally considered to be a more intensive land use than cattle grazing (Ludwig *et al.* 1997). Our observations that rabbit and *N. fuscus* populations were lower inside the dingo fence support this hypothesis as they may compete directly with livestock for herbage and seeds (Letnic 2004). However, if historical livestock grazing intensity was the primary factor influencing herbivore and granivore assemblages we would also expect that populations of red kangaroos would be lower inside the dingo fence, which they were not.

Viewed collectively, our results and those of previous studies (Caughley *et al.* 1980; Caughley & Grigg 1982;

Pople *et al.* 2000) suggest that predation by dingoes was the most likely cause for the differences in red kangaroo numbers observed on either side of the dingo fence. Grey kangaroo population responses were likely the product of population spillover from more mesic regions (Caughley *et al.* 1988) with the dingo fence preventing further westward and northward population expansion (Caughley *et al.* 1980). While there is evidence that fox numbers decline in the presence of dingoes (Newsome *et al.* 2001; Letnic 2007), it is also plausible that fox populations may, at a larger scale, respond to carrion availability and land-use, which themselves appear to be a product of dingo exclusion. In turn, it is likely that the greater abundances of rabbits and *N. fuscus* observed in the presence of dingoes (Newsome *et al.* 2001; Moseby *et al.* 2006) were due to a reduction in predation pressure by red foxes and possibly release from competition for food resources with kangaroos and livestock.

Top predators and biodiversity conservation

Our results were consistent with studies conducted in North America, which have shown that large mammalian carnivores are trophic regulators that suppress herbivore and mesopredator populations (Crooks & Soulé 1999; Hebblewhite *et al.* 2005; Berger *et al.* 2008). The suppression of herbivores and mesopredators by top predators can have positive benefits for biodiversity conservation, and suggests that dingoes and other top predators can play an important functional role in biodiversity conservation programmes (Crooks & Soulé 1999; Johnson *et al.* 2007; Ripple & Beschta 2007). However, it is likely that the top predators only become functionally effective above a certain threshold population density (Soulé *et al.* 2003; White & Garrott 2005). Determining these thresholds, and managing the adverse impacts that top predators have on people will be critical issues for conservation programmes that aim to incorporate the ecological functions of top predators.

Conclusion

Mammal assemblages differed markedly in the presence and absence of dingoes. The effect of dingoes on the abundances of mammal species scaled with body size and was consistent with the hypothesis that dingoes are trophic regulators in arid ecosystems. However, the absence of dingoes was also associated with a suite of land use factors, including sheep grazing, kangaroo harvesting and a greater density of artificial waters that could also explain some of the variation in mammal assemblages. Predation by dingoes and land uses associated with dingo exclusion appear to be major factors

influencing mammal assemblages in the Strzelecki Desert. Maintaining or restoring populations of dingoes and other top-order predators may be useful strategies to mitigate the impacts of mesopredators and overgrazing by herbivores.

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