Top predators as biodiversity regulators: the dingo *Canis lupus dingo* as a case study

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ABSTRACT

Top-order predators often have positive effects on biological diversity owing to their key functional roles in regulating trophic cascades and other ecological processes. Their loss has been identified as a major factor contributing to the decline of biodiversity in both aquatic and terrestrial systems. Consequently, restoring and maintaining the ecological function of top predators is a critical global imperative. Here we review studies of the ecological effects of the dingo *Canis lupus dingo*, Australia's largest land predator, using this as a case study to explore the influence of a top predator on biodiversity at a continental scale. The dingo was introduced to Australia by people at least 3500 years ago and has an ambiguous status owing to its brief history on the continent, its adverse impacts on livestock production and its role as an ecosystem architect. A large body of research now indicates that dingoes regulate ecological cascades, particularly in arid Australia, and that the removal of dingoes results in an increase in the abundances and impacts of herbivores and invasive mesopredators, most notably the red fox *Vulpes vulpes*. The loss of dingoes has been linked to widespread losses of small and medium-sized native mammals, the depletion of plant biomass due to the effects of irrupting herbivore populations and increased predation rates by red foxes. We outline a suite of conceptual models to describe the effects of dingoes on vertebrate populations across different Australian environments. Finally, we discuss key issues that require consideration or warrant research before the ecological effects of dingoes can be incorporated formally into biodiversity conservation programs.

Key words: biodiversity, conservation, dingo, *Canis lupus dingo*, intra-guild predation, trophic cascade, mesopredator, top predator, red fox, *Vulpes vulpes*, competition.

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I. INTRODUCTION

The loss of top-order predators has been identified as a key factor contributing to continuing species extinctions and the global biodiversity-loss crisis (Duffy, 2003; Ray, 2005). Consequently, restoring and maintaining the ecological function of top predators is a critical goal in many systems (Heithaus *et al.*, 2008; Hayward & Somers, 2009). Top predators typically exert top–down control on ecosystems through their direct predatory and competitive interactions with herbivores and smaller predators (Frank *et al.*, 2005; Frank, 2008; Ritchie & Johnson, 2009). The disruption or cessation of these interactions can have cascading effects on lower trophic groups, and result in declines in small species of animal prey (Crooks & Soulé, 1999) and the depletion of plant species diversity and biomass (Estes & Duggins, 1995; Terborgh *et al.*, 2001). The dramatic reorganisation of ecosystems and losses of biodiversity that frequently follow the loss of top predators have provided insight into the pivotal role they can play in maintaining healthy ecosystems in marine, aquatic and terrestrial environments (Soulé *et al.*, 2003). Increasingly, ecologists are realising that top predators shape the ecosystems around them and that their effects have the potential to be harnessed to manipulate ecological processes and species abundances for the benefit of biodiversity conservation (Soulé *et al.*, 2003).

Due to the widespread loss of top-order predators, frequent opposition to their reintroduction and sometimes even indifference about maintaining existing populations (Coman & Evans, 2007), there are relatively few opportunities to evaluate the role that true top predators have in structuring ecosystems, particularly at large geographical scales. This is especially so in terrestrial ecosystems where top predators can conflict strongly with livestock production and endanger human life (Musiani *et al.*, 2004; Frump, 2006). With a few exceptions (Caughley *et al.*, 1980; Pople *et al.*, 2000; Sinclair, Mduma & Brashares, 2003; Ripple & Beschta, 2006; Letnic *et al.*, 2009b; Wallach *et al.*, 2010), most studies investigating the ecological roles of true top predators in terrestrial ecosystems have been conducted at relatively small (i.e. <2000 km^2) spatial scales (Sinclair *et al.*, 2000; Fortin *et al.*, 2005; Beyer *et al.*, 2007; Kauffman *et al.*, 2007; Berger, Gese & Berger, 2008; Trewby *et al.*, 2008) or in fragmented landscapes and island ecosystems (McLaren & Peterson, 1994; Crooks & Soulé, 1999; Terborgh *et al.*, 2001).

While these studies demonstrate that top predators can exert strong effects on ecosystems (Beyer *et al.*, 2007; Ripple & Beschta, 2007; Berger & Conner, 2008; Berger *et al.*, 2008), we still have a poor understanding of the extent to which these predators can structure ecosystems at larger spatial scales and how their effects filter through trophic webs (Schmidt, 2003). This is particularly true in human-modified systems, where the return of a top predator can threaten native species with which they coexisted in the pre-disturbance state (Lovari *et al.*, 2009). Hence, understanding predator function is of fundamental importance for biodiversity conservation and pest control at regional, national and even continental scales as it considers the ecological role that top predators have in maintaining functional and biodiverse ecosystems.

In Australia, the role and historical importance of top terrestrial predators has been controversial. Flannery (1994) proposed that large reptilian predators may have dominated terrestrial systems over much of the Quaternary, but there were also many species of large carnivorous marsupials over this period (Wroe, Argot & Dickman, 2004). The largest carnivorous marsupial of recent times, the thylacine *Thylacinus cynocephalus* (∼30 kg), became extinct in Tasmania in the early twentieth century (Paddle, 2000), leaving the Tasmanian devil *Sarcophilus harrisii* (10 kg) as the largest living predatory marsupial. On the Australian mainland the largest of the extant marsupial predators, the spotted-tailed quoll *Dasyurus maculatus*, is smaller still and seldom achieves a mass of more than 5 kg. However, the continent's largest, most widespread and important terrestrial predator is no longer a marsupial, but a canid—the dingo *Canis lupus dingo*. As for *Canis* spp. generally (Vanak & Gompper, 2009), the dingo appears to be a strongly interactive species with pervasive effects on trophic cascades and other ecological processes (Johnson, 2006).

There has been long-standing debate over the status and ecological role of the dingo in Australia (Etheridge, 1916; Wood Jones, 1921; Marlow, 1962; Rolls, 1969; Newsome, 1990; Catling & Burt, 1995; Dawson, 1995; Smith, 1999; Newsome *et al.*, 2001; Elledge *et al.*, 2006; Coman & Evans, 2007; Glen *et al.*, 2007; Claridge *et al.*, 2009). Dingoes were probably introduced to Australia by people 3500–5000 years before present (y BP) (Barker & Macintosh, 1979; Gollan, 1984; Savolainen *et al.*, 2004) and currently have ambiguous status in most areas where they occur (Coman & Evans, 2007; Claridge & Hunt, 2008; Hytten, 2009). They have

been a major pest to pastoralists for the last two centuries because they prey upon livestock (Parker, 2007), and thus are subject to ongoing extermination programs across much of the continent. Dingoes are culled in specific areas also where they are considered to pose risks to human health and safety (Healy, 2007). Due to their relatively recent arrival on the continent they are considered as an invasive species by some authors and classified as a noxious pest that landholders are legally obliged to destroy in some jurisdictions (Fleming *et al.*, 2006).

In contrast to these perceptions, dingoes were mainland Australia's largest extant terrestrial predator at the time of European settlement in 1788 when they existed both as free-ranging wild and commensal animals and were valued highly by Aboriginal people (Trigger *et al.*, 2008; Smith & Litchfield, 2009). Consequently, dingoes are considered by some laws and many people to be a native species worthy of protection in their own right (Corbett, 1995*b*; Dickman & Lunney, 2001*b*; Hytten, 2009). In addition, because the dingo is Australia's largest terrestrial predator some authors have suggested that the species likely has a positive ecological role by regulating trophic pathways (Glen *et al.*, 2007). Indeed, dramatic differences in kangaroo abundance and in the composition of mammal assemblages in the presence and absence of dingoes have been known for a long time and many authors have speculated as to whether these differences were linked to the predatory effects of dingoes (Krefft, 1871; Marlow, 1962; Rolls, 1969; Jarman, 1986; Newsome, 1990).

The status of the dingo is also clouded by the issue of hybridisation between it and domestic dogs *Canis lupus familiaris* and the fact that "pure-bred" dingoes are now rare in some regions such as the south-eastern portion of the continent (Wood Jones, 1921; Corbett, 1995*b*; Daniels & Corbett, 2003; Elledge *et al.*, 2006; Claridge & Hunt, 2008). In evidence of this, wild canids in Australia are referred to euphemistically as 'wild dogs' rather than dingoes in most legislation and policy documents concerning management strategies that aim to reduce wild canid numbers. Presumably, this is because the term 'dingo' is derived from an indigenous Australian language (Tench, 1788) and is likely to invoke more positive sentiment among the public than the phrase 'wild dog' (Hytten, 2009). Hybridisation occurs commonly between other wild forms of *Canis lupus* and domestic dogs in other parts of the world (Wayne & Jenks, 1991; Vilà *et al.*, 2003; Verardi, Lucchini & Randi, 2006; Iacolina *et al.*, 2010), causing concern for the retention of local genotypes of wild *Canis lupus*.

In this paper we begin by outlining the origins and natural history of the dingo. We then review studies that have investigated the effects of dingoes on different elements of ecosystems across Australia, paying particular attention to the considerable body of research that has been published since the beginning of this century. We then introduce and outline conceptual models to explain the trophic interactions of dingoes. The basic model is built upon observations of dingoes interacting with other species, which we believe are fundamental to understanding the roles of the dingo in

structuring Australian ecosystems. There is a strong focus on arid regions because this is where the trophic effects of dingoes are best understood. The arid biome comprises 70% of Australia's landmass and represents one of the world's largest desert regions, occupying approximately 7.5 million square kilometres (Byrne *et al.*, 2008). We conclude by discussing the potential benefits and problems that could arise from incorporating the ecological interactions of dingoes into biodiversity conservation programs. Throughout this paper we use the term dingo to refer to *Canis lupus dingo*, *C. l. dingo* × *C. l. familiaris* hybrids, and feral dogs. The reasons for this are that hybrids between dingoes and dogs are rare through most of the continent (Elledge *et al.*, 2006), and that this uniquely Australian word precedes the term wild dog.

II. NATURAL HISTORY OF THE DINGO

(1) Taxonomic status

Molecular studies indicate that the dingo (body mass 15–25 kg) is a primitive form of the domestic dog descended from the Asian wolf (*Canis lupus chanco*; Savolainen *et al.*, 2002; Savolainen *et al.*, 2004; vonHoldt *et al.*, 2010). Although the dingo was first described on the basis of a description given by the first Governor of Australia in his journal (Meyer, 1793), and has since been subject to various reclassifications and changes in nomenclature, no type specimen of the dingo has ever been lodged (ABRS, 2009). The absence of a definitive type specimen compounds taxonomic confusion regarding the identity of the dingo.

(2) Diet

Dingoes are generalist predators as, although they prey primarily upon mammals, they will readily switch their diet according to prey availability (Newsome, Catling & Corbett, 1983; Robertshaw & Harden, 1986; Corbett & Newsome, 1987; Thomson, 1992). Thus the predominant prey taxa of dingoes vary both spatially and temporally (Newsome & Coman, 1989; Corbett, 1995*b*; Pavey, Eldridge & Heywood, 2008; Cupples *et al.*, 2011). Where they are abundant, rabbits, macropodids and vombatids are important prey items (Whitehouse, 1977; Triggs, Brunner & Cullen, 1984; Robertshaw & Harden, 1985, 1986; Lunney *et al.*, 1990; Lunney, Law & Rummery, 1996; Brook & Kutt, 2011), but dingoes have also been observed to prey heavily on rodents, water birds and sea-turtle nests, and will kill and eat foxes, cats, lizards, birds and livestock (Newsome *et al.*, 1983; Marsack & Campbell, 1990; Vernes, Dennis & Winter, 2001; Paltridge, 2002; Allen & Fleming, 2004; Whiting *et al.*, 2007; Claridge, Mills & Barry, 2010; Glen *et al.*, 2011). During drought dingoes frequently consume carrion (Corbett, 1995*b*; Allen, 2010*b*) and in coastal areas they often scavenge on strand lines (Newsome *et al.*, 1983). Like other *Canis* spp. dingoes are social and frequently occur in packs. Packs facilitate the cooperative capture of large prey (Thomson,

1992; Webb, 1996), and some authors have suggested that such groups may also facilitate the competitive exclusion of mesopredators such as the red fox (Glen *et al.*, 2007). In arid areas, sources of water serve as focal areas for dingo social interactions (Wallach *et al.*, 2009) and dingoes frequently congregate and hunt near sources of water (Corbett, 1995*b*; Shepherd, 1981).

III. IMPACTS OF THE DINGO ON OTHER ANIMALS AND PLANTS

(1) Early impacts

The arrival of the dingo in mainland Australia coincided with an increase in human population size, the adoption of new technologies by Aboriginal people and the extinction of both the thylacine and Tasmanian devil as well as the flightless native hen *Gallinula mortierii* (Gollan, 1984; Baird, 1991; Mulvaney & Kamminga, 1999). The timing of these extinctions, being coincident with the arrival of the dingo, has led to speculation that dingoes contributed to the extinctions (Gollan, 1984; Baird, 1991; Corbett 1995*b*). This argument is strengthened by the fact that the thylacine and Tasmanian devil persisted on the island of Tasmania which dingoes never reached. However, other authors have suggested that these extinctions were more likely the product of climate change and improved hunting efficiency due to the adoption by people of new technologies such as edge-ground and hafted stone tools and perhaps the use of hunting dogs (Mulvaney & Kamminga, 1999; Johnson & Wroe, 2003; Brown, 2006; Johnson, 2006).

(2) Effects of dingoes on large prey (>10 kg)

Much of the debate over the ecological role of dingoes has stemmed from early anecdotal observations that kangaroo populations irrupt in the absence of dingoes (Krefft, 1871; Rolls, 1969). However, more recent field observations have been made of dingo predation on macropods (*Macropus* spp. and *Wallabia bicolor*, body mass 10–90 kg; Shepherd, 1981; Newsome *et al.*, 1983; Robertshaw & Harden, 1986; Marsack & Campbell, 1990), while longitudinal tracking of population dynamics has shown declines in kangaroo populations with increased frequency of dingo predation (Corbett & Newsome, 1987; Thomson, 1992). In addition, population studies have shown macropods to be abundant in areas where dingoes are uncommon but comparatively rare in areas where dingoes are common (Table 1; Caughley *et al.*, 1980; Robertshaw & Harden, 1986).

Some of the best evidence for the effects of dingoes on large prey comes from observations made either side of the dingo fence (Table 1). This fence is dingo-proof, over 5000 km in length (the longest man-made structure on earth) and was constructed to exclude dingoes from the predominantly sheep-grazing lands of south-eastern Australia (Fig.1; Bauer, 1964; McKnight, 1969). Dingoes are rare on the

sheep-grazing or "inside" side of the fence due both to the fence itself and intensive control of animals that manage to cross through (Wilson & Delahay, 2001), and are relatively common in the cattle grazing areas "outside" the fence where their numbers are controlled only sporadically (Fleming *et al.*, 2001). This difference in dingo numbers on either side of the fence has created a natural experiment that has in turn permitted much investigation of the ecological effects of dingoes. These studies have uncovered dramatic differences in the composition and numbers of large mammals and birds on either side of the fence.

Quantitative aerial surveys conducted by Caughley *et al.* (1980) and Newsome *et al.* (2001) on either side of the dingo fence in the Strzelecki Desert indicated that kangaroos and emus (*Dromaius novaehollandiae*; body mass ∼40–50 kg) were far more abundant in areas "inside" the fence where dingoes were rare than they were "outside". Caughley *et al.* (1980) suggested that the disparity in kangaroo and emu numbers on either side of the dingo fence provided evidence that dingoes regulate their populations. This was disputed by Dawson (1995) and Newsome *et al.* (2001), who questioned the generality of these results and contended that the observed differences may have been due to differences in land use and geomorphology on either side of the dingo fence. However, studies conducted at larger scales indicate that the disparity in red kangaroo *Macropus rufus* and emu numbers on either side of the dingo fence exists throughout the Australian arid zone and remains consistent regardless of whether land is used for the purposes of sheep or cattle grazing or conservation reserve (Caughley & Grigg, 1982; Grice, Caughley & Short, 1985; Pople *et al.*, 2000; Letnic *et al.*, 2009*b*). The disparity in kangaroo abundance also exists despite the fact that commercial harvesting of mainly adult kangaroos is limited to areas where dingoes are rare (Hale, 2004; Fillios *et al.*, 2010). Collectively, these observations provide compelling support for the argument that dingoes limit recruitment and thus regulate macropod populations. Regulation occurs most likely *via* preferential predation on juveniles and females (Robertshaw & Harden, 1986). The nature of the interaction between dingoes and emus has been studied less intensively, but it is likely that dingoes suppress emus through predation too (Seyfort, 2001).

A long-term study of kangaroo and emu population dynamics in adjacent areas with and without dingoes provides insight into how the effects of dingo predation may interact with climate variability (Fig. 2; Pople *et al.*, 2000). Where dingoes were rare, kangaroo and emu populations tended to increase following periods of high rainfall and consequent increases in primary productivity, and declined during periods of rainfall deficiency when food availability was presumed to decrease. These fluctuations were consistent with patterns observed in other studies conducted in the absence of dingoes (Caughley, Bayliss & Giles, 1984; Caughley, Grigg & Smith, 1985). Where dingoes were common, by contrast, fluctuations in kangaroo and emu populations were dampened, suggesting that dingoes were suppressing herbivore populations and may also have

Table 1. Empirical field studies that have examined whether dingoes influence the abundances or survival of prey species, competitors and vegetation. The effect of dingoes on indicator taxa is indicated as positive (+), negative (−) or neutral (0)

Study	Description	Species studied	Effect	Comment
Caughley *et al.* (1980)	Replicated comparisons of kangaroo and emu abundance on either side of the dingo fence in the arid zone.	Red kangaroo (*Macropus rufus*) Emu (*Dromaius novaehollandiae*)	− −	Kangaroos and emus less abundant in the presence of dingoes.
Thompson (1983)	Comparison of nesting success in semi-arid areas where dingoes were common and rare.	Short-necked turtles (*Emydura* spp.)	+	Nesting success was higher in the presence of dingoes.
Caughley & Grigg (1982)	Large-scale replicated comparison of kangaroo abundance on either side of the dingo fence in arid and semiarid areas.	Kangaroos (*Macropus* spp.)	−	Kangaroos were more abundant where dingoes were rare.
Grice *et al.* (1985)	Broadscale aerial survey estimates of emu population density in arid areas where dingoes were rare and common.	Emu (*D. novaehollandiae*)	−	Emus were rare in the presence of dingoes.
Robertshaw & Harden (1986)	Comparison of macropod abundances and dingo diet in three areas subject to different levels of dingo control in temperate forest.	Grey kangaroo (*M. giganteus*) Swamp wallaby (*Wallabia bicolor*) Red-necked wallaby (*M. rufogriseus*)	0 − −	Macropods were more abundant where dingoes were rare.
Thomson (1992)	Longitudinal monitoring of dingo populations, kangaroo abundance and dingo diet	Kangaroos (*M. rufus, M. robustus*)	−	Kangaroo abundance declined coincident with an increase in dingo abundance.
Pettigrew (1993)	Comparison of cat activity in relation to dingo activity in the arid zone.	Cat (*Felis catus*)	−	Negative correlation between indices of dingo and cat abundance.
Catling & Burt (1995)	Comparison of fox activity in relation to dingo activity and other variables predicted to influence fox abundance in temperate forest.	Fox (*Vulpes vulpes*)	−	Fox abundance negatively correlated with dingo abundance, but land use was a better predictor of fox abundance than dingo abundance.
Corbett (1995*a*)	Comparison of pig activity in relation to dingo activity in tropical savannah.	Pig (*Sus scrofa*)	−	Inverse relationship between indices of dingo and pig abundance.
Read (1997)	Comparison of small vertebrate abundance on islands with dingoes *versus* mainland areas where dingoes were rare in an arid salt pan.	House mouse (*Mus domesticus*) Planigale (*Planigale gilesi*) Painted dragon (*Ctenophorus pictus*) Skink (*Morethia adelaidensis*)	+ + + 0	Small mammals and painted dragons were more abundant and foxes and cats absent on islands where dingoes were abundant.
Pople *et al.* (2000)	Comparison of time series of emu and kangaroo abundance on either side of the dingo fence in three arid regions.	Red kangaroo (*M. rufus*) Emu (*D. novaehollandiae*)	− −	Kangaroo and emu abundance was suppressed in the presence of dingoes.
Newsome (2001)	Comparison of fox activity in relation to dingo activity in temperate forest.	Fox (*V. vulpes*)	−	Inverse relationship between dingo and fox abundance.
Newsome *et al.* (2001)	Comparisons of mammal abundance and activity on either side of the dingo fence in an arid region.	Red kangaroo (*M. rufus*) Rabbit (*Oryctolagus cuniculus*) Fox (*V. vulpes*) Cat (*F. catus*)	− + − 0	Alternative ecosystem states in the presence and absence of dingoes. Kangaroos interpreted to be influenced by geomorphology rather than dingoes.
Mitchell & Banks (2005)	Comparison of fox activity in relation to dingo activity in temperate forest.	Fox (*V. vulpes*)	0	Foxes avoided dingoes at a small scale but no relationship apparent at a large scale.

Table 1. *(Cont.)*

Study	Description	Species studied	Effect	Comment
Southgate *et al.* (2007*a*)	Comparison of bilby activity in relation to dingo activity and other variables predicted to influence bilby activity in an arid region.	Greater bilby (*Macrotis lagotis*)	+	Bilbies associated positively with dingoes and negatively with foxes.
Letnic *et al.* (2009*a*)	Comparison of dusky hopping mouse activity in relation to dingo activity and other variables predicted to influence dusky hopping mouse activity in an arid region.	Dusky hopping mouse (*Notomys fuscus*)	+	Abundance of a threatened rodent species was positively associated with dingo activity and negatively with foxes.
Letnic *et al.* (2009*b*)	Comparisons of mammal abundance and vegetation on either side of the dingo fence at eight paired locations in arid regions.	Kangaroos (*Macropus* spp.) Foxes (*V. vulpes*) Cats (*F. catus*) Rabbit (*O. cuniculus*) House mouse (*M. domesticus*) Native rodents Dunnarts (*Sminthopsis* spp.). Grasses	− − 0 0 + + + −	Effects of dingoes scaled with body size. Dingoes had a positive effect on small mammals and grasses and negative effects on foxes and kangaroos.
Johnson & VanDerWal (2009)	Comparison of fox activity in relation to dingo activity in temperate forest.	Foxes (*V. vulpes*)	−	Inverse relationship between dingo and fox abundance.
Wallach *et al.* (2009)	Comparison of threatened species persistence in relation to dingo activity in arid regions.	Malleefowl (*Lepoia ocellata*) Rock-wallaby (*Petrogale xanthopus*)	+ +	Positive association found between the occurrence of dingoes and rock-wallabies and malleefowl.
Wallach & O'Neill (2009*b*)	Comparison of kowari activity in an area where dingo populations were controlled *versus* an area where they were not controlled, in an arid region.	Kowari (*Dasyuroides byrnei*)	+	Positive association found between the occurrence of dingoes and kowaris.
Wallach *et al.* (2010)	Comparisons of mammal activity and vegetation in multiple areas where dingo populations were controlled *versus* areas where they were not controlled, in arid regions.	Large herbivores (>10 kg) Mesopredators (*V. vulpes, F. catus*) Rabbits (*O. cuniculus*) Small mammals (<50 g) Medium-sized mammals (>50−300 g) Vegetation cover	− − − + + +	Removal of dingoes was associated with increased abundance of invasive species and loss of vegetation cover.
Letnic & Koch (2010)	Comparisons of mammal activity in three areas on either side of the dingo fence in an arid region.	Red kangaroo (*M. rufus*) Grey kangaroo (*M. giganteus, M. fuliginosus*) Fox (*V. vulpes*) Cat (*F. catus*) Rabbit (*O. cuniculus*) Dusky hopping mouse (*N. fuscus*) Dunnarts (*Sminthopsis* spp.) Livestock	− − − 0 + + 0 0	Alternative ecosystem states in the presence and absence of dingoes. The effect of dingoes scaled with body size.
Letnic *et al.* (2011*b*)	Comparison of fox activity in relation to dingo activity at 26 study locations in arid regions.	Fox (*V. vulpes*)	−	Inverse relationship between abundances of dingoes and foxes.

Table 1. (*Cont.*)

| Study	Description	Species studied	Effect	Comment
Letnic & Dworjanyn (2011)	Comparison of dusky hopping mouse abundance, occurrence in predator scats and foraging behaviour on either side of the dingo fence in an arid region.	Fox (*V. vulpes*) Dusky hopping mouse (*N. fuscus*)	− +	Foxes less abundant in the presence of dingoes. Hopping mice more abundant.
Kennedy *et al.* (2011)	Comparison of cat activity in relation to dingo activity and dingo management strategies at multiple sites in tropical savannah	Cat (*F. catus*)	−	Negative relationship between dingo and cat abundances.
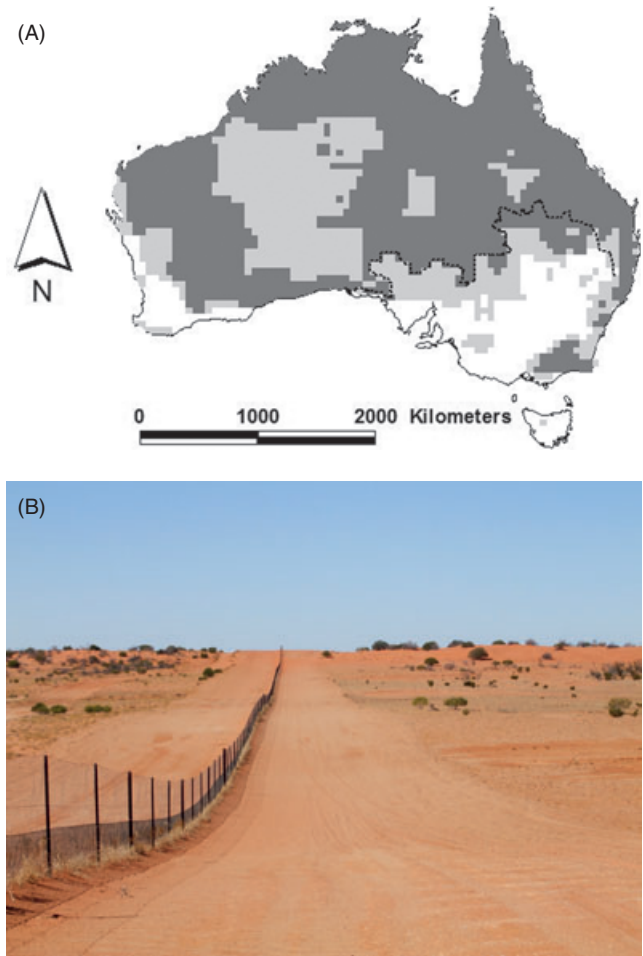
Fig. 1. A map (A) showing the route of the dingo fence (dashed line) through Australia and areas where dingoes and wild dogs are common (dark grey), rare (light grey) and absent (unshaded). Dingoes were never present on the island of Tasmania but feral dogs now exist there. Distributions are derived from maps published by the Australian Natural Resources Atlas and the National and Water Resources Audit (http://www.nlwra.gov.au/national-land-and-waterresources-audit/atlas, viewed 11th May 2011). (B) The dingo fence in the Strzelecki Desert on the border of New South Wales and South Australia. The specifications of the fence vary along its length, at this point the fence is approximately 2 m tall and is normally impenetrable to dingoes, foxes, kangaroos, rabbits and small mammals.

had stabilizing effects on their population dynamics (Pople *et al.*, 2000).

The contrasting dynamics of kangaroo and emu populations on either side of the dingo fence provide evidence that, in the presence of dingoes, predation as an additive source of mortality may be more important in regulating populations than the availability of food (Pople *et al.*, 2000). The view that kangaroo populations are regulated by the availability of food in the absence of dingoes is also supported by studies conducted in areas where dingoes are rare; these have reported mass deaths of
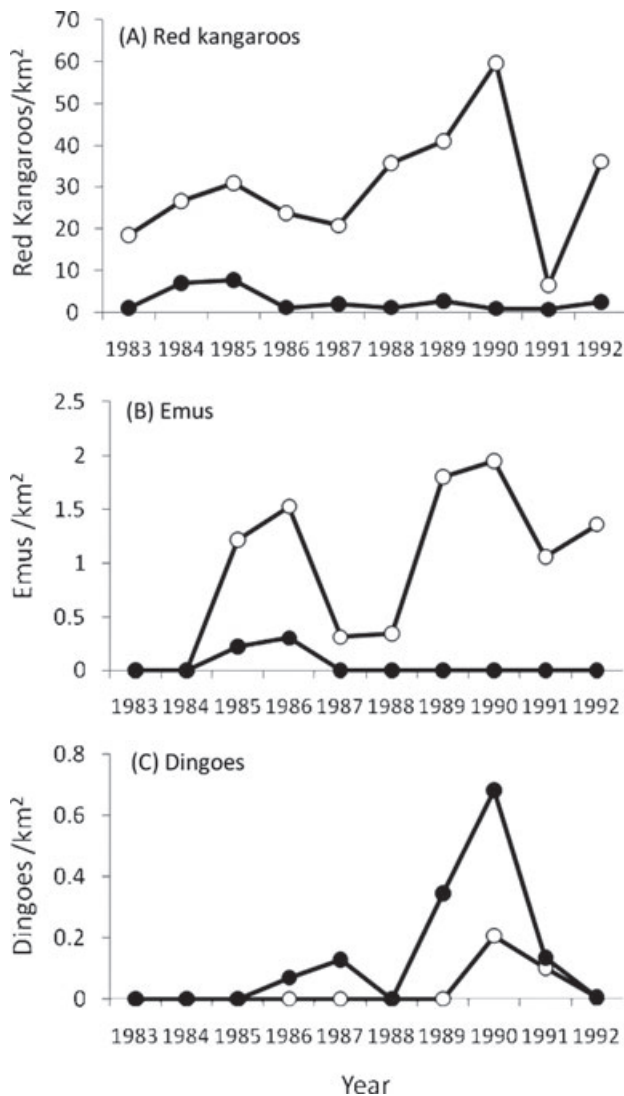
Fig. 2. The density of (A) red kangaroos, (B) emus and (C) dingoes at sites on either side of the dingo fence during aerial surveys conducted in north-eastern South Australia between 1983 and 1992. The symbols denote sites where dingoes were common (shaded symbols) and rare (open symbols). Fluctuations in kangaroo and emu abundances appeared to be dampened in the presence of dingoes, suggesting the existence of top-down regulation by dingoes. (Adapted from Fig. 3, Pople *et al.*, 2000).

kangaroos due to food shortages, often in combination with extreme temperatures (Ealey, 1967; Newsome & Corbett, 1975; Robertson, 1984; Holden & Mutze, 2002; Read & Wilson, 2004; Fillios *et al.*, 2010; Morgan & Pedler, 2010). Although mortality of kangaroos during drought also occurs in areas with dingoes, we are aware of only one report in the literature of mass mortality in an area where dingoes were moderately abundant (Newsome, 1965). The ability of dingoes to moderate the effects of drought on kangaroo populations is supported by the results of an eight year experimental simulation of natural predation of western grey kangaroos (*Macropus fuliginosus*) in semi-arid Victoria. In this

study, simulated predation improved vegetation condition and reduced the extent of starvation-related mortality of kangaroos (Morgan & Pedler, 2010).

Feral livestock exist in many regions of Australia and are frequently identified as a major threat to biodiversity and agricultural enterprises. Field surveys and mapping indicate that the distributional ranges of goats (*Capra hircus*, body mass 15–40 kg) and feral pigs (*Sus scrofa*, body mass 25–175 kg) show little overlap with that of dingoes in the arid regions of the continent, except in areas where dingoes are scarce (Newsome, 1990; Wilson *et al.*, 1992). This lack of spatial overlap suggests that dingoes may regulate their populations and limit their distributions (Newsome, 1990; Newsome *et al.*, 2001). There is also some evidence of the capacity for dingoes to suppress pig populations where the two species coexist in northern Australia (Corbett, 1995a). Indeed, analyses of bounty records show that increased dingo numbers coincide with decreased pig numbers (Woodall, 1983).

By contrast, studies of the population dynamics, and distribution maps showing extensive overlap with dingoes, suggest that predation by dingoes has little influence on populations of larger feral animals (>100 kg), namely camels (body mass 600–1000 kg), horses (*Equus callabus*; body mass >300 kg), cattle (*Bos taurus/indicus*; body mass 500–900 kg) and donkeys (*Equus asinus;* body mass 300–350 kg) (Freeland & Choquenot, 1990; Wilson *et al.*, 1992; Dobbie, Berman & Braysher, 1993; Edwards *et al.*, 2000). This is not to say that dingoes do not prey on large species, as there are observations of groups of dingoes attacking and successfully killing cattle and horses (Newsome *et al.*, 1983; Thomson, 1992). In the case of cattle, groups of dingoes have been observed to prey successfully on calves (Thomson, 1992). However, large mammals are presumably riskier and more difficult to hunt than smaller prey, and most dietary studies of dingoes suggest that very large feral mammals are not taken frequently (e.g. Whitehouse, 1977; Newsome *et al.*, 1983; Corbett, 1995b; Brook & Kutt, 2011; Glen *et al.*, 2011).

(3) Effects of dingoes on mesopredators (1–7 kg)

The mesopredator release hypothesis (MRH) has been invoked to explain the decline of some small prey species by suggesting that the elimination of large carnivores results in an increase in the abundance and consequently impact of smaller predators (Ritchie & Johnson, 2009). According to the MRH large predators will be able to suppress populations of smaller predators *via* several mechanisms including direct killing, interference competition, competition for food and shelter, and fear-mediated changes in habitat use and activity patterns (Crooks & Soulé, 1999; Switalski, 2003; Berger & Gese, 2007; Thompson & Gese, 2007). The fundamental criterion for a prey species to benefit from the presence of a larger predator is that the prey species' intrinsic rate of increase should exceed the sum of the *per capita* rate of predation by both the large predator and mesopredator. This criterion is likely to be met if the prey species is more vulnerable to predation by the mesopredator, and

the top predator limits the *per capita* rate of killing by the mesopredator (Courchamp, Langlais & Sugihara, 1999). In simple terms, this is the familiar concept that my enemy's enemy is my friend.

Since European settlement of Australia in 1788, two introduced eutherian carnivores, the red fox *Vulpes vulpes* and feral cat *Felis catus* have largely supplanted the similar-sized endemic marsupial predators of the genus *Dasyurus* from temperate, arid, subtropical and tropical regions of the continent. The eastern quoll *Dasyurus viverrinus* has become extinct from the mesic areas of continental eastern Australia, although the larger spotted-tailed quoll *D. maculatus* remains common in some of the more heavily forested areas along the Great Dividing Range (Glen & Dickman, 2011). The formerly extensive geographical range of the western quoll *Dasyurus geoffroii* has been reduced by about 98% and the species now occupies a small area in south-western Australia (Jones *et al.*, 2003). For most of the period of European settlement of Australia, the northern quoll, *D. hallucatus* remained quite common outside of the range of the fox. The range of the northern quoll began to decline towards the end of the 20th Century. In some parts of its range their decline has been linked to the invasion of cane toads (*Bufo marinus*), but in other areas northern quolls declined prior to the arrival of cane toads suggesting that other factors, perhaps interactions with feral cats may have contributed to their decline (Braithwaite & Griffiths, 1994; Oakwood, 2000; Johnson, 2006; O'Donnell, Webb & Shine 2010).

Red foxes and feral cats have been identified as major threats to biodiversity in Australia and their presence has been linked to the extinction or endangerment of many species of Australian vertebrates (Smith & Quin, 1996; McKenzie *et al.*, 2007), including the four species of quoll (Jones *et al.*, 2003; Morris *et al.*, 2003; Glen & Dickman, 2008). The MRH predicts that the abundance of both red foxes (mean body mass 5–7 kg) and cats (body mass 3–5 kg) should increase in the absence of the dingo (Glen & Dickman, 2005).

In support of the MRH, several studies have speculated on or reported negative relationships between indices of dingo and fox abundance (Table 1, Fig. 3; Jarman, 1986; Newsome,1990, 2001; Lundie-Jenkins, Corbett & Phillips, 1993; Catling & Burt, 1995; Saunders *et al.*, 1995; Letnic *et al.*, 2009b, 2011b; Wallach *et al.*, 2010; Brawata & Neeman, in press). The MRH is supported also by dietary studies showing that foxes prefer smaller prey than dingoes

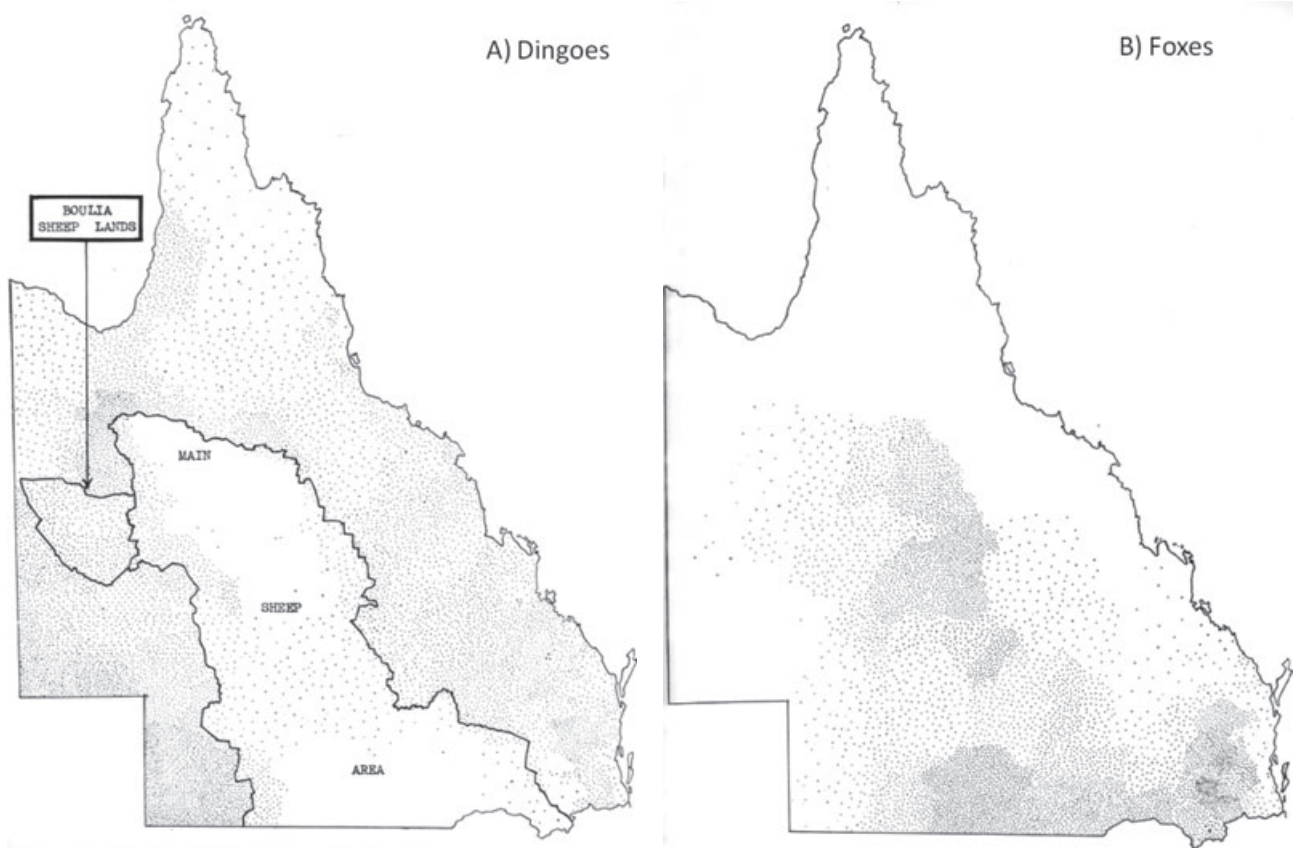**Fig. 3.** Bounty returns for (A) dingoes and (B) foxes in Queensland for the 1951–52 financial year (source: Queensland Parliamentary Papers 1951–52). Each dot represents five dingoes or five foxes. The distribution of fox bounties shows an inverse spatial relationship with that of dingo bounties, suggesting that dingoes may have suppressed fox numbers over large geographical areas. (Adapted from Letnic *et al.*, 2011b).

(Letnic *et al.*, 2009*b*; Claridge *et al.*, 2010; Glen *et al.*, 2011), observations of dingoes killing foxes (Moseby *et al.*, in press), observations of foxes occurring in the diets of dingoes (Newsome & Coman, 1989; Marsack & Campbell, 1990) and studies reporting extensive dietary overlap and thus potential for competition between sympatric dingoes and foxes (Paltridge, 2002; Mitchell & Banks, 2005; Pavey *et al.*, 2008; Glen *et al.*, 2011; Cupples *et al.*, 2011). However, unequivocal evidence for an inverse relationship between dingo and fox numbers is lacking, as none of the above studies manipulated dingo abundance, and studies conducted in mesic regions have found mixed support for the hypothesis that dingoes suppress the abundance of foxes.

In eastern Australia, several studies have reported a negative relationship between the abundances of dingoes and foxes at a landscape scale (Catling & Burt, 1995; Newsome *et al.*, 2001; Johnson & VanDerWal, 2009; Letnic *et al.*, 2011*b*). However, Catling & Burt (1995) found that land use was a better predictor of fox activity than dingo activity, while Mitchell & Banks (2005) showed that foxes appeared to avoid dingoes at a small scale, but found no evidence of an inverse relationship between indices of their abundance at a landscape scale.

One reason for the uncertainty regarding the numerical relationships between dingoes and foxes may be the use of inappropriate statistical approaches that assume normal error distributions to describe the relationship between the abundances of these species (Johnson & VanDerWal, 2009; Letnic *et al.*, 2011*b*). The ecological literature is replete with examples of non-linear, threshold-type relationships between the abundances of strongly interactive species (Estes & Duggins, 1995). Such strong interactions may be difficult to detect using traditional parametric statistical approaches. The potential shortcomings of parametric approaches to describe the numerical relationships between dingoes and foxes are exemplified by the non-linear relationship between indices of dingo and fox abundances evident from field studies and other data sources such as bounty records (Johnson & VanDerWal, 2009; Letnic *et al.*, 2011*b*). Johnson & VanDerWal (2009) explored the numerical association between the abundances of dingoes and foxes using semi-parametric and parametric techniques. Linear regression provided a poor fit to the data, but semi-parametric techniques suggested that dingoes may place an upper limit on the abundance of foxes, and that dingoes may not be the only factor influencing fox numbers (Johnson & VanDerWal, 2009). Similarly, Letnic *et al.* (2011*b*) found consistently negative relationships between indices of dingo and fox abundance using non-parametric and semi-parametric analyses at a near-continental scale.

Another factor that may influence the ability reliably to detect numerical relationships between coexisting dingoes and foxes is that both species occur commonly at low population densities and occupy large home ranges. In arid regions of Australia estimates of predator population densities range from 0.025–0.034 km^{-2} for dingoes (Thomson, Rose & Kok, 1992; Corbett, 1995*b*) and 0.9–2 km^{-2} for foxes

in the absence of dingoes (Saunders *et al.*, 1995). No studies have reported population densities of foxes in the presence of dingoes but, as indicated above, several have noted that fox numbers tend to be suppressed in the presence of dingoes. At such low densities, obtaining reliable population estimates is problematic and predator abundances are frequently gauged using indices calculated from counts of tracks or scats or by quantifying visitation to lures (Allen, Engeman & Krupa, 1996; Mahon, Banks & Dickman, 1998; Edwards *et al.*, 2000; Sharp *et al.*, 2001). Because these predators typically occur at such low densities it is conceivable that the act of a dingo killing one fox could have a marked effect on a local fox population, and such effects would be magnified if dingoes killed or attempted to kill foxes whenever they encountered them (Moseby *et al.*, in press). Understanding the ecological interaction of dingoes and foxes may require studies to be conducted at large spatial scales so that abundance indices can be calculated across the home ranges of many individuals.

Studies investigating the numerical relationship between dingoes and feral cats generally have produced equivocal results (Table 1). Cats are likely to be killed in close encounters with dingoes (Moseby *et al.*, in press) and are reported as dietary items of dingoes throughout the continent (Newsome & Coman, 1989; Corbett, 1995*b*; Cupples *et al.*, 2011). Dingoes appear to suppress cat numbers in northern Australia (Kennedy *et al.*, 2011). However, correlations between dingo and cat activity in the arid zone are less clear, reporting negative associations (Pettigrew, 1993; Wallach *et al.*, 2010; Brawata & Neeman, 2011), positive associations (Letnic *et al.* 2009*b*) or no association (Newsome, 2001; Letnic *et al.*, 2009*b*) between the two predators. Few studies have reported on the numerical relationships between dingoes and cats in the mesic forests of eastern Australia where they coexist (May & Norton, 1996; Purcell, 2010). Given that dingoes and foxes are predators of cats it is likely that interactions with both predators influence cat abundance (Risbey, Calver & Short, 1999; Paltridge, 2002). As an example, it is not inconceivable in some circumstances that cats may experience a net benefit of dingo predation on foxes, as the latter species may interact more strongly with cats due to its greater overlap in body size and diet (Ritchie & Johnson, 2009). Another mechanism by which dingoes, and perhaps foxes, may affect cats is by causing fear-induced changes to their activity and habitat use (i.e. changes in behaviour or movements in relation to cover/protection). This could explain in part why cats are particularly nocturnal in the presence of the more crepuscular dingo. An alternative explanation for the weak and inconsistent relationship between dingo and cat abundances is that cat populations may be determined by other factors, particularly the abundance of their primary rodent prey (Letnic, Tamayo & Dickman, 2005). In addition, habitat probably plays an important role. For example, cats may be more likely to show an inverse numerical or spatial relationship with dingoes in treeless areas or other structurally simple habitats where it is difficult for cats to avoid the larger predator than in forested or rocky environments that offer structurally more complex habitat with refuges (Pettigrew, 1993).

Cats are secretive by nature and can be difficult to detect and census. Few techniques are available that can be used effectively to census cat populations, particularly when they occur at low population densities or in structurally dense habitats (Catling, Burt & Kooyman, 1997; Mahon *et al.*, 1998; Read & Eldridge, 2010). The difficulty in obtaining reliable abundance indices and/or population estimates for cats has hampered our ability to understand the numerical relationships between dingoes and cats in many parts of the continent. Also it is possible that indices of cat and dingo abundance could display a non-linear relationship similar to that reported for dingoes and foxes and hence may require investigation with non-parametric statistical techniques (Johnson & VanDerWal, 2009).

(4) Effects of dingoes on small and medium-sized prey (<10 kg)

Since British colonisation of Australia in 1788, there have been mass extinctions and range reductions of native mammals weighing less than 10 kg, particularly in the semi-arid and arid regions of the continent (Burbidge & McKenzie, 1989; Morton, 1990; Dickman *et al.*, 1993; McKenzie *et al.*, 2007; Johnson & Isaac, 2009). Many ground-nesting birds have also undergone major range declines (Reid & Fleming, 1992; Smith, Pressey & Smith, 1994). In the arid and temperate regions of the continent the mammal fauna is now dominated by invasive species and relict assemblages of large (>15 kg) and small (<0.1 kg) native species (Letnic & Dickman, 2006). The mammal species that have undergone the greatest declines in range and abundance are indigenous rodents and 'medium-sized' marsupials weighing between 0.1 kg and 5.5 kg (Burbidge & McKenzie, 1989; Johnson, Isaac & Fisher, 2007; McKenzie *et al.*, 2007). Predation by red foxes and feral cats has been identified as a key factor contributing to the decline of native mammals and ground-nesting birds (Dickman *et al.*, 1993; Smith *et al.*, 1994; Smith & Quin, 1996; Kinnear, Sumner & Onus, 2002; Short, Kinnear & Robley, 2002).

Macroecological studies of the continental distributions of extant indigenous rodents and marsupials suggest that their persistence is associated with the presence of dingoes and the absence or low abundance of foxes (Smith & Quin, 1996; Johnson *et al.*, 2007). These continental-scale patterns are consistent with predictions made by the MRH and provide evidence that dingoes may facilitate the conservation of native mammals by suppressing fox populations (Johnson *et al.*, 2007).

The MRH is supported further by field surveys in arid regions of the continent showing that the abundances and persistence of native species vulnerable to predation by red foxes, including small mammals and threatened species such as the bilby (*Macrotis lagotis*, body mass 0.8–2.5 kg), dusky hopping mouse (*Notomys fuscus*, body mass 0.03–0.045 kg), yellow-footed rock-wallaby (*Petrogale xanthopus*, body mass 5 kg–10 kg), malleefowl (*Leipoa ocellata*; body mass 1.3 kg) and kowari (*Dasyuroides byrnei*, body mass 0.07–0.17 kg), were associated positively with the abundance of dingoes

and negatively with the abundance of red foxes (Table 1; Southgate *et al.*, 2007*a*; Letnic, Crowther & Koch, 2009*a*; Wallach & O'Neill, 2009*a*; Wallach *et al.*, 2010). The notion that dingoes provide prey with refuge from predation by foxes is given mechanistic support by findings that the lethal and non-lethal impacts of foxes on dusky hopping mice are alleviated in presence of dingoes (Letnic & Dworjanyn, 2011). In this case, both the abundance of foxes and the frequency of dusky hopping mouse remains in predator scats were lower in the presence of dingoes; correspondingly, dusky hopping mice were more abundant and foraged less apprehensively in the presence of dingoes (Fig. 4; Letnic & Dworjanyn, 2011).

Large-scale natural experiments created by the dingo fence and natural barriers elsewhere provide compelling evidence that dingoes benefit small mammals by suppressing the impacts of foxes. Letnic *et al.* (2009*b*) contrasted 16 sites on each side of the dingo fence, and found widespread and consistent differences in the abundances and species richness of small mammals depending on which side of the fence was sampled (Table 1). The abundances of native rodents (<0.05 kg), the introduced house mouse (*Mus musculus*; body mass 0.015 kg) and dasyurid marsupials (<0.02 kg) were on average greater in the presence than in the absence of dingoes. The species richness of native small mammals (body mass <50 g) was also greater in the presence of
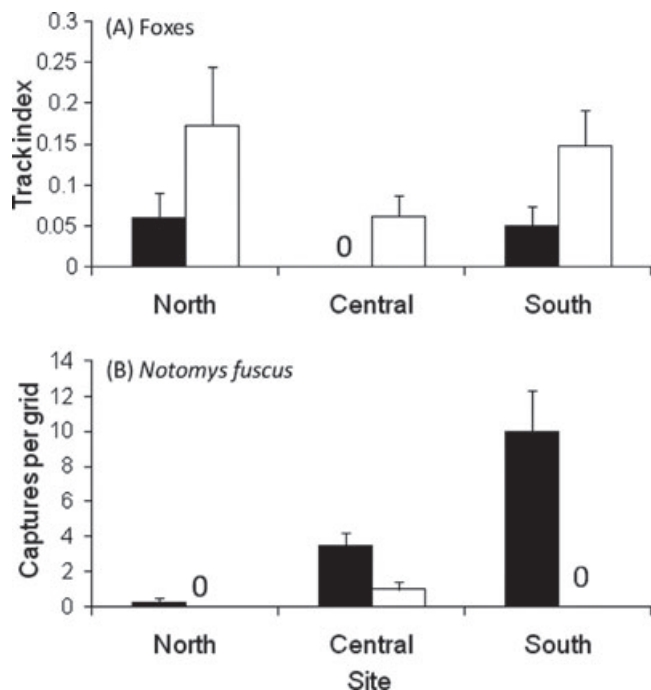

Fig. 4. Indices of the abundance of (A) red foxes *Vulpes vulpes* and (B) dusky hopping mice *Notomys fuscus* at three locations (north, central, south) in the Strzelecki Desert, central Australia. Data are means + 1 standard error. Open bars represent sites where dingoes were absent, shaded bars indicate sites where dingoes were present, and 0 indicates no activity recorded (source, Letnic *et al.*, 2009*a*). Foxes were less abundant and hopping mice were more abundant in the presence of dingoes.
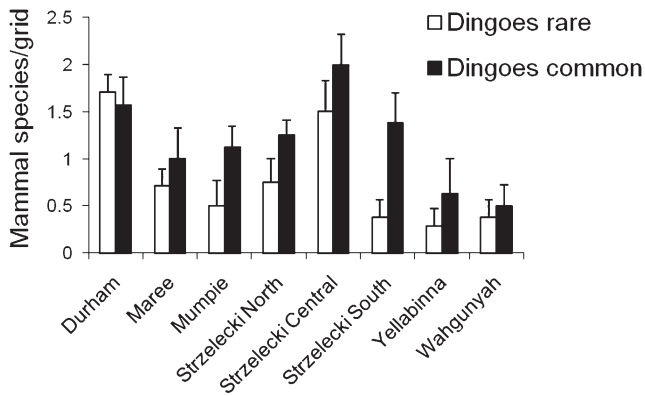
Fig. 5. The species richness of native small mammals (mean + 1 standard error) on study grids set on either side of the dingo fence at eight paired locations in arid Australia (source Letnic *et al.*, 2009*b*). The species richness of small mammals was generally greater where dingoes were common compared to where they were rare.

dingoes (Fig. 5) and, consistent with the MRH, was correlated negatively with the abundance of foxes. Other evidence that dingoes may benefit species preyed upon by mesopredators comes from fauna surveys of ephemeral islands within the arid Lake Eyre salt-pan in central Australia where dingoes were present and cats and foxes were absent (Table 1). On islands where dingoes were present, house mice, the dasyurid marsupial *Planigale gilesi* (body mass 0.007–0.012 kg) and an agamid lizard, the painted dragon (*Ctenophorus pictus*; body mass 0.008–0.016 kg) were more abundant than on adjacent mainland areas where dingoes were comparatively rare and cats and foxes were present (Read, 1997).

In southern Australia nest predation by foxes has been identified as a major threat to freshwater turtles (Thompson, 1983; Spencer & Thompson, 2005). In a comparative study of nest survival in short-necked turtles (*Emydura* spp.), Thompson (1983) found that at sites on the Murray River where dingoes were absent, foxes preyed upon 93% of nests and that the overall nest predation rate was 97%. By contrast, no nest predation was observed at a site on Cooper Creek where dingoes were present. An explanation put forward to explain reduced nest predation in the presence of dingoes was that dingoes suppressed fox numbers through direct killing (Thompson, 1983).

Studies comparing the abundance of the invasive European rabbit in the presence and absence of dingoes provide mixed support for the MRH (Table 1). In sand dune habitats of the Strzelecki Desert foxes were less abundant and rabbits were more abundant in the presence *versus* absence of dingoes (Newsome *et al.*, 2001; Letnic & Koch, 2010). However, other studies in stony desert and mallee woodland biomes have found the effects of dingo population control on rabbit populations to be variable (Letnic *et al.*, 2009*b*; Wallach *et al.*, 2010).

(5) Effects of dingoes on vegetation

Trophic cascades occur when a predator alters the abundance of species across more than one link in a food web and indirectly influences plant biomass (Polis, 1999). An increasing body of evidence suggests that large mammalian predators can induce trophic cascades and influence plant communities in terrestrial ecosystems either directly by suppressing herbivore populations through predation or indirectly by affecting herbivore foraging behaviour (McLaren & Peterson, 1995; Fortin *et al.*, 2005; Frank, 2008; Fey *et al.*, 2009).

Because the availability of food appears to be the principal factor regulating herbivore populations in the absence of dingoes, some authors have suggested that in the arid regions of the continent there is an inherent risk of overgrazing in areas where dingoes have been exterminated (Ludwig *et al.*, 1997). Evidence that the removal of dingoes induces a trophic cascade was provided by Letnic *et al.* (2009*b*) and Wallach *et al.* (2010) who found that grazing activity by herbivores, particularly kangaroos, was greater in the absence of dingoes. In turn, grass cover (Letnic *et al.*, 2009*b*) and overall vegetation cover (Wallach *et al.*, 2010) tended to be greater where dingoes were present (Fig. 6).

(6) Trophic effects of dingoes and the human economy

In arid regions of Australia, differences in land use in areas with and without dingoes demonstrate that people alter their economic activities owing to the predatory impacts of dingoes (Fennessy, 1962; Rowley, 1970). To reduce the impact of dingo predation on sheep (*Ovis aries*), government agencies and private landholders have 'controlled' dingo populations using a combination of methods including fencing, poisoning, trapping and shooting (Figs 1, 2; Bauer, 1964; McKnight, 1969; Fleming *et al.*, 2001). Sheep are grazed primarily in areas where dingoes have been exterminated or are rare.
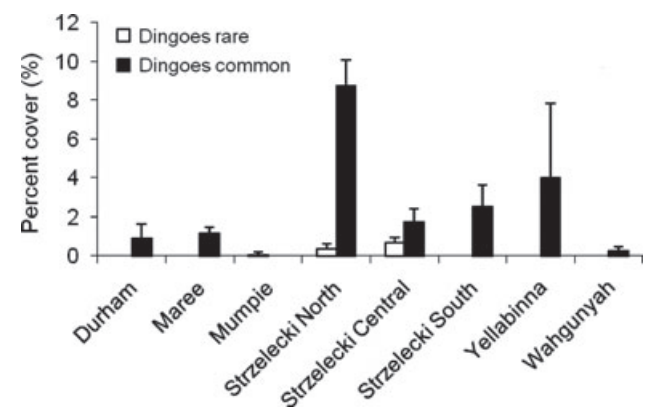

Fig. 6. Percentage grass cover (mean + 1 standard error) on study grids set on either side of the dingo fence at eight paired locations in arid Australia (source Letnic *et al.*, 2009*b*). Grass cover was greater in the presence of dingoes.

Few sheep are grazed in areas where dingoes are common due to the risk of predation (Rowley, 1970; Fleming *et al.*, 2001), unless guardian animals or intensive poison baiting are used as protective measures (Van Bommel, 2010). Cattle are less vulnerable to dingo predation than sheep (Thomson, 1992) and are grazed in areas where dingoes are both rare and common.

Commercial kangaroo harvesting also is restricted largely to places where dingoes are rare, as kangaroos are often too scarce in areas where dingoes are common to make harvesting economically viable (Fillios *et al.*, 2010). The underlying reason for the disparity in kangaroo numbers in the presence/absence of dingoes may be that human hunters and dingoes remove different components of the kangaroo population and thus have different effects on the reproductive potential of kangaroo populations. For economic reasons, harvests are biased towards larger animals which are predominantly males (Hale, 2004). As smaller males are usually available to compensate for the loss of large and dominant animals, male-biased harvests have less impact on the reproductive potential of kangaroo populations than female-biased harvests (McLeod, Hacker & Druhan, 2004); dingoes, by contrast, are more likely to kill juveniles and females than large males (Shepherd, 1981).

The strong linkage between sheep grazing, kangaroo harvesting and dingo exclusion indicates that the structuring effects of dingo predation extend to the human economy. Indeed this shift in land use in the presence/absence of dingoes provides evidence that, in the case of sheep husbandry, humans modify their use of the landscape to avoid economic losses incurred by dingoes, and in the case of kangaroo harvesting, conduct less harvesting in the presence of dingoes due to direct competition for the same resource: kangaroos.

(7) Experimental considerations

One problem affecting studies investigating the effects of dingoes is that of sampling and experimental design (Glen *et al.*, 2007; Allen, 2010*a*; Allen, Engeman & Allen, 2011). No published studies investigating the ecological effects of dingoes have used planned experimental manipulations, and those that have compared abundances or response variables in a mensurative manner on either side of the dingo fence or in areas with and without dingo control are by necessity spatially segregated or unreplicated (Caughley *et al.*, 1980; Pople *et al.*, 2000; Newsome *et al.*, 2001; Letnic *et al.*, 2009*a*, *b*; Wallach & O'Neil, 2009*b*; Wallach *et al.*, 2010; Letnic & Koch, 2010; Letnic & Dworjayn, 2011). They can thus be considered pseudoreplicated (Hurlbert, 1984) or confounded (Letnic *et al.*, 2009*b*). Indeed, few studies investigating the ecological effects of dingoes or other large predators have met the requirements for experimental design stipulated by Hurlbert (1984). Does this mean that the trends in abundance and distribution of species with regard to taxon and body size that we have described in preceding sections could be due to other sources of variation than just the trophic effects of dingoes? Oksanen

(2001) has argued that Hurlbert's (1984) strict approach to experimental design should not be applied to large-scale studies where it is not feasible or even possible to have replication, and that where replication is not possible, experiments should aim to test predictions generated by theory and use inferential statistics to guide the interpretation of the results. In this vein, we contend that studies of the effects of dingoes show clearly that this predator has marked and consistent effects on ecological communities that accord with the theories of animal population regulation, trophic cascades and foraging theory (Caughley *et al.*, 1980; Pople *et al.*, 2000; Newsome *et al.*, 2001; Johnson *et al.*, 2007; Letnic *et al.*, 2009*b*; Wallach *et al.*, 2010; Letnic & Dworjanyn, 2011; Letnic *et al.*, 2011*a*, *b*). To assist in directing future research to further clarify the role of the dingo in Australian systems, in the section below we construct models of dingo impact that should allow researchers to design comparative and experimental studies to test explicit predictions that the models generate.

IV. THE ECOLOGICAL INTERACTIONS OF DINGOES: A CONCEPTUAL MODEL

(1) Element 1: the effects of dingoes on other species scale with body size

The effects of dingoes on the abundances of other animals appear to scale with body size (Fig. 7; Johnson *et al.*, 2007; Letnic *et al.*, 2009*b*). These effects are consistent among studies and at spatial scales ranging from local to continental (Table 1). Species weighing 5–100 kg such as kangaroos, emus and foxes typically decrease in abundance in the presence of dingoes (Caughley *et al.*, 1980; Newsome *et al.*, 2001; Pople *et al.*, 2000; Letnic *et al.*, 2009*b*). Presumably the suppressive effects of dingoes on these taxa are due to
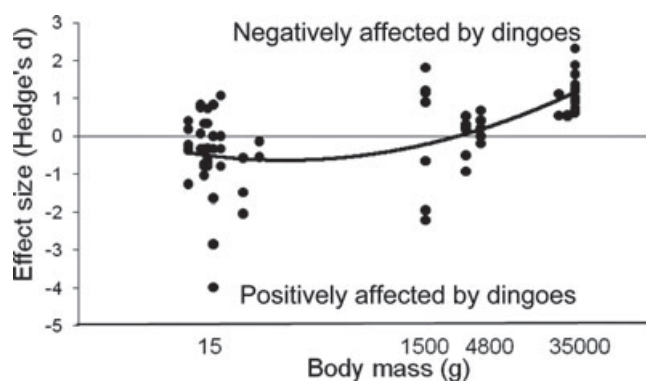
Fig. 7. The natural logarithm (Ln) of the body mass (g) of mammal species plotted against the mean effect size (Hedge's *d*) of dingo exclusion at eight paired sites in arid Australia (adapted from Letnic *et al.*, 2009*b*). A quadratic function was fitted to the data ($r^2 = 0.338$, $F = 18.361$ $P < 0.001$). Positive effect sizes indicate species whose abundance increased where dingoes were absent. Negative effect sizes indicate species whose abundance decreased where dingoes were absent.

direct interactions such as predation and, in the case of foxes, interference competition also. Conversely, populations of species weighing less than 1 kg generally appear to increase in the presence of dingoes (Smith & Quin, 1996; Newsome *et al.*, 2001; Johnson *et al.*, 2007; Letnic *et al.*, 2009*b*; Letnic & Koch, 2010; Wallach *et al.*, 2010). Such small species most likely benefit indirectly from the suppressive effects of dingoes on herbivores and mesopredators, especially foxes and, in the tropical north of Australia, feral cats. This is probably because they are released from predation by foxes and from competition for food with large herbivores; alternatively, in the absence of dingoes, they may be affected detrimentally by herbivores grazing down the cover of vegetation that is required both as food but also as shelter from predators. Species weighing 1–10 kg show mixed responses to the presence/absence of dingoes (Newsome *et al.*, 2001; Letnic *et al.*, 2009*b*; Wallach *et al.*, 2010), perhaps indicating that they have strong context-dependent interactions with herbivores, foxes and dingoes. Species with adults weighing more than 100 kg are subject to only occasional predation by dingoes and do not appear to be regulated by them (Newsome & Coman, 1989).

(2) Element 2: the influence of resource pulses and prey switching on dingo interactions

Throughout Australia, and particularly in the arid regions of the continent, temporal fluctuations in plant and animal populations in relation to rainfall have strong effects on the flux of energy through communities and food-web architecture (Nicholls, 1991; Letnic & Dickman, 2010). Such temporal and spatial variation in ecosystem productivity is likely to moderate the strength of the interactions that large predators have with other taxa (Oksanen *et al.*, 2001; Elmhagen & Rushton, 2007; Ritchie & Johnson, 2009). Indeed, studies that have monitored temporal variation in the diets of dingoes and the abundance of their prey provide evidence that the direct and indirect interactions between dingoes and other animal species scale with the energy state of ecosystems, which in turn is dictated by the amount of rainfall. These interactions between rainfall and the ecological effects of dingoes are best understood in the arid regions of the continent (Corbett & Newsome, 1987; Lundie-Jenkins *et al.*, 1993; Paltridge, 2002; Pavey *et al.*, 2008; Letnic *et al.*, in press; Letnic & Dworjanyn, 2011) but are also supported by studies from the northern tropics (Corbett, 1995*a*) and the forests of south-eastern Australia (Newsome *et al.*, 1983; Robertshaw & Harden, 1985, 1986). We address the effects of dingoes in these regions in detail below.

In arid areas of Australia the availability of water typically limits primary productivity (Ludwig *et al.*, 1997), and rainfall-driven pulses in primary productivity can have an overriding effect on the population dynamics of vertebrates (Letnic & Dickman, 2010). In evidence of this, populations of rodents and kangaroos fluctuate in response to rainfall with time lags of approximately six months to a year (Caughley *et al.*, 1984; Pople *et al.*, 2000; Morgan & Pedler, 2010; Letnic &

Dickman, 2010), while predators such as dingoes, red foxes and feral cats show numerical responses to resource pulses with time lags of about a year (Letnic *et al.*, 2005; Pavey *et al.*, 2008).

Following rainfall-driven booms in primary productivity, the suppressive effects of dingoes on kangaroos and mesopredators are likely to diminish due to several factors (Fig. 8A). Firstly, dingoes typically exhibit prey-switching and are likely to increase their consumption of irruptive prey such as rodents, rabbits and locusts, and reduce their consumption of large prey (Corbett & Newsome, 1987; Paltridge, 2002). Secondly, populations of mesopredators and kangaroos are likely to disperse from drought-refugia into the broader landscape after rain, hence reducing their *per capita* risk of encounter with dingoes. Thirdly, populations of these species are less likely to be limited by food resources in the aftermath of flooding rains. Competition for prey between dingoes and sympatric mesopredators also may be reduced when prey such as rodents and locusts are abundant (Lundie-Jenkins *et al.*, 1993). Indeed, Donadio & Buskirk (2006) argued that competition for food resources may be a factor that motivates interspecific killing in carnivores, and thus according to this argument, the motivation for dingoes to kill competitors may be reduced during periods of prey surfeit.

As a consequence of reduced predation and competition with dingoes, and an increase in recruitment, the numbers of kangaroos and mesopredators are expected to increase in the wake of resource pulses (Corbett & Newsome, 1987; Pople *et al.*, 2000; Letnic *et al.*, 2005). Following flooding rains the beneficial effects that dingoes have on small and medium-sized mammal species may be expected to diminish due to an increase in mesopredator populations and impact (Fig. 8A). In evidence of this, small mammal populations which are typically regulated by food availability undergo catastrophic declines in numbers coincident with an increase in fox and feral cat populations after flooding rains (Letnic *et al.*, 2005; Letnic & Dickman, 2006; Pavey *et al.*, 2008; Letnic *et al.*, in press). These dramatic declines have been attributed in part to the onset of top-down population control when mesopredators become abundant and the relaxation of interactions between dingoes and mesopredators due to the ready availability of food resources (Letnic *et al.*, 2005).

In the tropics, water also limits primary productivity but this limitation occurs seasonally as part of a wet/dry cycle and therefore is largely predictable with a gradual drying out of the landscape each year following monsoonal rains, and arid-like conditions occurring towards the end of the dry season in most years (Woinarski *et al.*, 2007). This means that species interactions in the tropics can be expected to be less prone to the large extremes that are associated with the unpredictable 'boom and bust' prey cycles that characterise arid ecosystems, but rather will vary during the course of the year due to intra-annual variability in resource availability. The effects of dingoes on the abundances of other animal species are predicted to be similar to those observed in the arid zone (Fig. 8B), although in this case their effects on prey and competitors are expected to be greatest during
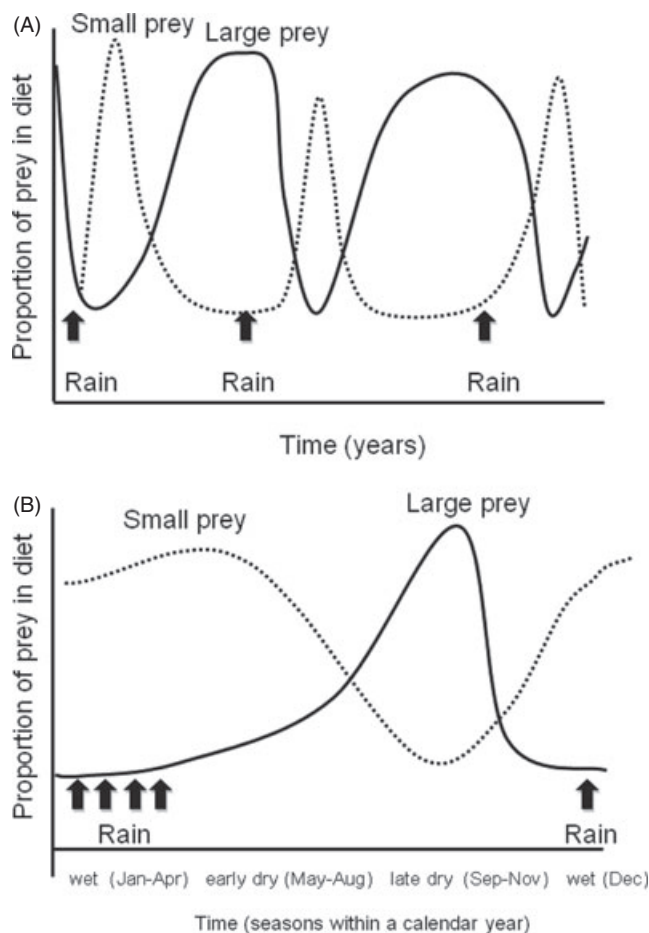
Fig. 8. Conceptual models of the dietary functional responses of dingoes in response to climate variability and hence resource availability in (A) arid Australia, and (B) the tropical savannas of northern Australia. Large prey are defined as animals weighing >10 kg. (A) The dynamics of arid systems are driven by unpredictable rainfall events that drive pulses of primary productivity. In these environments, the suppression of large herbivores (e.g. kangaroos and emus) by dingoes will often be sustained for periods of several years between rains. This suppression may be temporarily relaxed for periods of 1–2 years following resource pulses that are linked to irregular large rainfall events that prompt irruptions of small prey (e.g. grasshoppers and small mammals). Dingoes typically switch their diets to irrupting prey. As numbers of irruptive prey decline, dingoes switch their diets back to larger prey. (B) Tropical systems: These systems are driven primarily by seasonal rainfall, with abundant small prey (e.g. grasshoppers, rodents) peaking in abundance shortly after the cessation of the wet season (December–February), but then declining steadily in their availability during an extended dry season (March–November) when little to no rain falls. Resources (prey) are most depleted at the end of the dry season (September–November). It is during the late-dry season that we predict dingoes to have comparatively larger effects on large herbivore prey such as pigs and kangaroos. This is firstly because smaller/alternate prey are less available, and secondly herbivores are forced to drink more often (due to high temperatures) at increasingly patchily distributed and smaller waterholes, thereby increasing their susceptibility to attack by dingoes.

the late dry season when water and food resources become limiting for herbivores (Freeland & Boulton, 1990; Corbett, 1995a; Ritchie et al., 2008, 2009) and presumably also for mesopredators.

In the mesic forests of south-eastern Australia, periodic droughts precipitate collapses in small and medium sized prey populations and are linked to devastating wildfires (Newsome et al. 1983). During droughts, dingoes increase their consumption of large prey such as macropods (body size >10 kg) and wombats (Vombatus ursinus, body size 22–39 kg) and appear to have a greater effect on their populations during these periods (Newsome et al., 1983; Robertshaw & Harden, 1985, 1986). However, in these forested environments subject to year-round rainfall, limitation of moisture during dry periods is not as extreme as in the arid zone or the wet-dry tropics, and it is possible the effects of dingoes on the abundance of prey are not as great because surface waters tend not to be a focal point for activity by dingoes or prey species. The relatively high species diversity and complexity of vegetation in productive forested environments may also attenuate the predatory impacts of dingoes by diffusing their impacts across a larger number of interaction pathways and by providing prey and competitors with shelter, respectively (Duffy, 2003; Duffy et al., 2007).

If the effects of environmental resource pulsing and prey switching by dingoes are generalised, we can derive a model that predicts stronger suppressive effects by dingoes on medium-sized mammals and stronger beneficial effects on small species when resources are scarce compared to when they are more abundant (Fig. 9). In this model, which is an extension of the empirical findings presented in Fig. 7 and the conceptual syntheses in Fig. 8, the effects of dingoes are predicted to scale with increasing prey body size in the form of a sine wave (Fig. 9). Our conceptual model predicts that both the amplitude of the wave and the body size intercept at which the effect of dingoes switches from positive to negative, and vice versa, can be expected to vary according to resource conditions and the distribution of prey body sizes that is available. However, effect sizes for very small (<0.01 kg) and very large prey animals (>100 kg) are likely to remain negligible under all conditions; very small animals are probably little affected by increases or decreases in the activity of mesopredators, while very large prey are seldom hunted or killed by dingoes.

(3) Element 3: large predators induce trophic cascades

Trophic cascade theory predicts that removing a top predator will have alternating positive and negative effects on lower trophic levels and will indirectly depress plant biomass (Polis, 1999). These effects on plant biomass may stem from changes in both the population density and behaviour of herbivores following the cessation of interactions with the predator (Fortin et al., 2005; Frank, 2008; Beschta & Ripple, 2009). Lower total grazing pressure and increased grass cover and density in the presence of dingoes are consistent with the predictions made by trophic cascade theory. The consistent
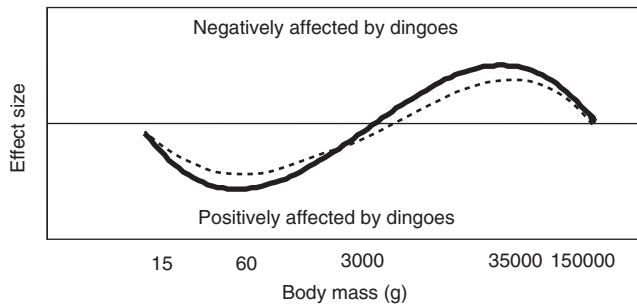
Fig. 9. Conceptual model of mammalian body size *versus* effect size arising from the presence of dingoes under periods of low resource availability (solid line) and high resource availability (dashed line). Positive effect sizes indicate species whose abundance is expected to be suppressed due to predation by dingoes. Negative effect sizes indicate species whose abundance is expected to increase in the presence of dingoes due to the suppression by dingoes of red foxes, feral cats and large herbivores. The suppressive effects of dingoes on medium-sized mammals (1–10 kg) are moderated during periods of high resource availability due to prey switching by dingoes to eruptive small prey such as rodents and locusts. The beneficial effects of dingoes on small mammal prey are diminished during periods of high resource availability due to increased predation pressure from foxes, cats and dingoes, owing in part to the breakdown of competitive and predatory interactions between dingoes and mesopredators and increases in mesopredator populations.

effects that dingoes have on the abundances of taxa at several trophic levels suggest that they may induce community-wide cascades (Polis, 1999; Letnic *et al.*, 2009b; Wallach *et al.*, 2010).

The regulatory effects of dingoes on herbivore populations have further implications for ecosystem function. In the absence of dingoes, herbivore populations will irrupt due to the absence of predation and are likely to deplete the biomass of palatable plants, particularly during periods of drought when forage becomes limiting (Oksanen *et al.*, 2001). These effects of herbivory have the potential to limit the magnitude of rainfall-driven resource pulses by reducing the production of seeds and consequently the abundance of seeds available for germination (Ludwig *et al.*, 1997). In addition, soil erosion resulting from overgrazing can lead to the loss of essential mineral resources and reduce the capacity of soil to absorb and retain moisture, further limiting the capacity of ecosystems to respond to rainfall events (Ludwig *et al.*, 1997).

The shift in plant community structure and seed bank characteristics associated with the irruption of herbivore populations is likely to have repercussions for animal species. Firstly, large herbivores can directly limit the production of herbage and seeds (Letnic, 2004) and consequently remove food resources that would otherwise be available for granivores. This is likely to impose constraints on food resources throughout all stages of the pulse-resource cycle and could potentially dampen the responses of granivore populations to rainfall events. Secondly, herbivores often simplify or degrade understorey habitat structure by defoliation and trampling (Short, 1985; Eccard, Walther

& Milton, 2000; Read, 2002; Letnic, 2004). Thus grazers and browsers may increase the exposure of ground-dwelling species to their predators by reducing the amount of available cover.

(4) Synthesis and application of the model

Studies investigating the effects of dingoes suggest that this predator has marked effects on Australian ecosystems that accord with trophic cascade theory and the MRH. Our conceptual model (Figs 8, 9) explicitly recognises that the effects of dingoes on other animals scale with both body size and rainfall-driven pulses in primary productivity. The strong relationship between body size and the effect of dingoes suggests that dingoes structure ecosystems through two distinct interaction pathways: (1) predation by dingoes reduces the abundance of herbivores weighing between 10 and 100 kg. In turn, in the absence of dingoes grazing by abundant herbivores reduces grass cover and biomass. (2) Dingoes reduce the abundance of invasive mesopredators (foxes in southern Australia and cats in northern Australia) through predation and competition. In turn, predation by invasive mesopredators in the absence of dingoes can suppress the abundance of smaller species. Both of these interaction pathways appear to have profound effects on the structure and function of arid ecosystems, and perhaps also in other systems with more predictable climates (Visser *et al.*, 2009). These effects have led some authors to label the dingo a keystone species, whose removal has far-reaching effects on the architecture and functioning of ecosystems (Johnson *et al.*, 2007; Dickman, Glen & Letnic, 2009; Letnic *et al.*, 2009b; Wallach *et al.*, 2010).

With increasing realisation that top predators are very often strongly interactive, and even keystone species, conservation biologists have expressed growing interest in utilising their trophic and behavioural interactions with other species as a means of managing ecological processes (Soulé *et al.*, 2003; Beschta & Ripple, 2009). Such 'ecological process management' has been trialled following the reintroduction of wolves into Yellowstone National Park, USA, and has been hailed as a success due to the recovery of plant and animal communities following the suppression of deer populations by wolves (Beschta & Ripple, 2009). Could the keystone effects of dingoes be used in a similar manner to achieve biodiversity conservation goals in Australia?

The link between the presence of dingoes and ecosystem attributes valued by conservation biologists suggests that dingoes already benefit biodiversity conservation across the large areas of the Australian continent where they currently occur (Smith & Quin, 1996; Johnson *et al.*, 2007). However, continuation of these benefits into the future is likely to require formal articulation and recognition of the dingo's ecological functions in legislation, policy and planning documents to ensure that their trophic and behavioural interactions with other species are maintained in the face of political pressures to cull them (Soulé *et al.*, 2005). Using formal documents, land-management agencies could plan to maintain existing dingo populations or reintroduce dingoes

as a 'passive' tool to achieve explicit biodiversity conservation goals such as mitigating the predatory impacts of red foxes, or relieving overgrazing by kangaroos, feral pigs and feral goats.

While the presence of dingoes may afford some benefit to animal species that are vulnerable to predation by foxes and cats, the mass extinction of mammals from Australia's deserts that has occurred in the last 100 years (McKenzie *et al.*, 2007), despite the presence of dingoes, and the apparent failure of dingoes to regulate populations of large feral livestock, make it clear that dingoes are not a 'silver bullet' for biodiversity conservation. Dingo predation frequently has adverse impacts on livestock producers and may impact also on some native animal species of conservation concern, particularly if the killing of breeding females by dingoes significantly reduces the reproductive capacity of the population concerned (Fisher, Hoyle & Blomberg, 2000; Whiting *et al.*, 2007; Claridge *et al.*, 2010). These potentially adverse impacts of dingoes make their reintroduction and even the maintenance of existing populations a complex issue that encompasses economic, social and ecological considerations.

V. DINGO INTERACTIONS: FROM CONCEPTUAL MODEL TO A PRACTICAL CONSERVATION TOOL

Questions that must be considered before the ecological interactions of dingoes can be incorporated formally into biodiversity conservation programs are many, and include: (1) will dingoes have adverse effects on native species, and how will they affect exotic species (Fisher *et al.*, 2000); (2) at what population density will dingoes become ecologically effective (Soule *et al.*, 2003; Letnic *et al.*, 2011*b*); (3) do artificial waters facilitate the trophic effects of dingoes (Wallach & O'Neil, 2009*a*); (4) what effects will dingoes have on livestock producers and can these effects be mitigated (Dickman *et al.*, 2009; Van Bommel, 2010); and (5) what effect does hybridisation with domestic dogs have on the ecological role of dingoes in ecosystems? If dingoes cannot be integrated effectively into programs of biodiversity conservation, it is of interest, finally, to ask if their beneficial ecological effects can be simulated in the absence of the species itself.

(1) Native species adversely affected by dingoes

Our body-size model of dingo-wildlife interactions explicitly recognises that dingoes are likely to suppress populations of animals weighing more than 7 kg through direct predation or competition and may have context-dependent effects on species weighing between 1 and 7 kg. Dingoes certainly prey on threatened native species weighing less than 7 kg (Lundie-Jenkins *et al.*, 1993; Claridge *et al.*, 2010; Letnic & Dworjanyn, 2011) and thus may well have detrimental effects on their populations. Nonetheless, the fact that dingoes have coexisted with extant Australian animals for at least 3500 years suggests that dingo predation alone is unlikely

to pose a major threat to any extant species. However, it is conceivable that dingo predation may interact with other processes and could compound the threat posed to species that are subject to additional threats such as habitat modification and interactions with invasive species (Fisher *et al.*, 2000; Whiting *et al.*, 2007). In the case of some critically endangered species, such as the northern hairy-nosed wombat *Lasiorhinus latifrons* or bridled nailtail wallaby *Onychogalea fraenata*, predators including dingoes may need to be excluded or culled to maximise the conservation potential of threatened populations (McCallum, Timmers & Hoyle, 1995; Fisher *et al.*, 2000).

(2) Functionally effective dingo populations

It is likely that the interactions of top-order predators only become ecologically effective above a certain threshold population density (Soulé *et al.*, 2003; White & Garrott, 2005). However, if the fear of top predators by mesopredators is a strong motivator of changes to their activity and behaviour, perhaps even quite small numbers of top predators may precipitate significant ecosystem-level effects (Ritchie & Johnson, 2009). The effects of predators on their prey/competitors will to a degree be determined by the frequency of their encounters with a predator (Dickman, 1991). For example, if dingoes reduce the predatory impacts of red foxes, presumably there is a threshold population density of dingoes above which dingoes exert strong impacts on fox populations with positive flow-on effects for fox prey. Such threshold relationships are likely to be non-linear and location-specific (Soulé *et al.*, 2003). Determining these thresholds will be a critical issue for conservation managers aiming to maintain or restore ecosystems with effective densities of top-order predators.

The suppressive effects of dingoes on foxes and possibly cats in tropical northern regions have important implications for the operation of wildlife conservation programs in Australia (Newsome, 1990; Letnic *et al.*, 2011*b*; Kennedy *et al.*, 2011). To protect threatened native mammals and ground-nesting birds, conservation agencies frequently aim to control fox and sometimes dingo populations by distributing meat baits impregnated with poison from aircraft or along vehicular tracks (Fleming *et al.*, 2001; Burrows *et al.*, 2003; Saunders, Gentle & Dickman, 2010). Dingoes consume these baits and are frequently killed. If we are correct in contending that dingoes can have positive effects on small and medium-sized native mammals and other vertebrate species *via* mesopredator suppression, poisoning programs that kill dingoes may actually be detrimental for biodiversity conservation if they do not effectively suppress mesopredator populations.

A poignant example of counter-productive predator control was provided by Lundie-Jenkins *et al.* (1993) who witnessed the extinction of a population of the critically endangered mala (*Lagorchestes hirsutus*: body mass 1−3 kg) following an increase in cat activity and the invasion of a single fox into their study area. The invasion of the fox and an increase in cat activity coincided with a poisoning program

directed at dingoes. The authors suspected that suppression of dingoes facilitated an increase in the activity and impacts of mesopredators and indirectly led to the extinction of the mala population.

(3) The effects of dingoes on livestock production

Winning the support of local communities and industries that are affected adversely by large carnivores must be a major consideration for biodiversity conservation programs that aim to maintain or restore their populations (Treves & Karanth, 2003; Bradley *et al.*, 2005; Gusset *et al.*, 2008). In the case of the dingo, there is widespread opposition to the predator's existence across much of Australia due to predation on livestock or its perceived threat to livestock (Dickman & Lunney, 2001*a*; Allen & Fleming, 2004; Coman & Evans, 2007). The widespread antagonism towards top predators and the existence of formal control programs can pose a major obstacle for wildlife agencies responsible for their conservation (Dickman & Lunney, 2001*a*), let alone management at ecologically functional densities. Indeed, it is likely that the threshold population density required for top-order predators to have an ecologically effective role in ecosystems will be above the threshold density at which predators have or are perceived to have an adverse impact on livestock production or pose a direct threat to people (Treves & Karanth, 2003; Bradley *et al.*, 2005).

Programs that incorporate the ecological functions of dingoes could be implemented most readily in areas that have been set aside already as conservation reserves and, pending their success in biodiversity conservation and livestock production terms, extended subsequently to the broader landscape. Due to conflicts with livestock producers (Fleming *et al.*, 2001; Allen & Fleming, 2004), such expanded programs clearly would have to be balanced with the needs of agriculture and would require the implementation of diverse strategies to minimise the impacts of dingoes on livestock. Such strategies would need to be tailored for different areas, but could include dingo-proof fencing around dingo-conservation areas, compensation or insurance schemes for the loss of livestock, livestock-aversion training for dingoes, buffer zones, and the use of shepherds or shepherd dogs (Wagner, Schmidt & Conover, 1997; Andelt *et al.*, 1999; O'Neill, 2002; Dickman *et al.*, 2009). In recent work, Marucco & McIntire (2010) identified a promising further avenue to reduce carnivore-livestock conflict. These authors successfully constructed models to explain the spatio-temporal distribution of wolves moving through the Italian Alps. By projecting movements into the future, these authors were then able to predict areas where depredation on livestock was likely to be most intense, hence allowing tailored local and regional management plans to be developed. Any strategy that aims to maintain or reintroduce dingo populations would inevitably incur costs for livestock producers and land management agencies. Budgeting for these costs must be an essential component of any plan to restore the ecological function of dingoes.

While much of the discussion of the economic impacts of dingoes has focused on the costs of dingo predation on livestock, dingoes could potentially provide indirect benefits for some livestock producers by reducing the abundance and hence impact of wild herbivores on pastures. At present, large numbers of kangaroos are harvested primarily in the absence of dingoes, in large part to reduce competition for forage between kangaroos and livestock (McLeod *et al.*, 2004). Given the strong effects that dingoes have on populations of kangaroos and feral goats, it is probable that dingoes help to relieve total grazing pressure and thus contribute positively to pasture and soil management strategies (Letnic *et al.*, 2009*b*; Wallach *et al.*, 2010). Ecological studies coupled with cost-benefit analyses are required to evaluate the economic effects of dingoes, particularly with regard to the offset between livestock losses and pasture gains.

(4) Hybridisation

Hybridisation between domestic dogs and dingoes is a key problem influencing the management of dingoes in Australia (Daniels & Corbett, 2003; Claridge & Hunt, 2008); it also affects the management of other *Canis* spp. elsewhere (e.g. Wayne & Jenks, 1991). In some parts of south-eastern Australia wild canids consist mainly of dingo-feral dog hybrids, and 'pure-bred' dingoes are rare (Elledge *et al.*, 2006). The existence of hybrids poses a major challenge for conservation agencies charged with the responsibility of conserving native species and biodiversity more generally. Under some legislation the dingo is classified as, or is eligible for classification as, a protected native species (Dickman & Lunney, 2001*b*). Thus in some jurisdictions there are moves to identify and conserve pure dingo populations, and manage the genetics of dingo populations by removing dingo-feral dog hybrids if they can be identified (Elledge *et al.*, 2006). However, confusion exists over how to discriminate dingoes and their hybrids because there is no holotype specimen against which the identities of putative hybrid and pure dingoes can be assessed (ABRS, 2009). The lack of an adequate species description hampers efforts to identify and conserve populations of dingoes and prevents development of clear policies for their management.

Another complexity posed by the existence of hybrids is that dingoes/wild dogs appear to have positive effects on the conservation of native mammals (Johnson *et al.*, 2007; Letnic *et al.*, 2009*a*; Glen, 2010; Wallach *et al.*, 2010). Here lies a quandary for wildlife managers. How should they prioritise their management of dingoes? Should they strive to conserve pure dingoes or maintain the ecological function of the dingo even if the animals are not pure-bred? There is emerging evidence that the richness of predators, including genotypes, can have broader cascading effects within ecological systems than those of single predator species (Duffy *et al.*, 2007; Bruno & Cardinale, 2008), so it is possible that mixed populations of hybrid and pure-bred animals have particularly strong impacts. Evidence of this for dingoes/wild dogs is presently lacking. However, because dingoes as top-order predators provide a clear conservation benefit for Australian fauna and

flora, we argue that the primary focus of dingo management should be to maintain their ecological function while at the same time reduce their impact on agricultural producers. In our opinion, maintaining the genetic integrity of dingo populations should be a secondary priority to be pursued more fully once dingo populations become ecologically effective. However, we are sure that others may not agree with this viewpoint.

Clarification of these issues will require research to determine if dingoes, dingo/dog hybrids and feral dogs fulfill similar or different ecological functions. Further research is also required to clarify the taxonomic identity of the dingo, paying particular attention to the relationships between modern dingoes and specimens obtained from pre-historic and 19th Century sources when presumably hybridisation with domestic dogs was less prevalent than it is today.

(5) The role of artificial water

Understanding how biotic and abiotic factors influence the strength of interactions among species is a key knowledge gap in population and community ecology (e.g. Noy-Meir, 1973; Oksanen & Oksanen, 2000; Morton *et al.*, 2011). Water is a limiting resource for primary productivity and many animal species, particularly in desert and seasonally dry tropical environments, and its presence can influence the strength of interspecific interactions (Noy-Meir, 1973; Huxman *et al.*, 2004; Woinarski, *et al.*, 2007; Fensham & Fairfax, 2008). Many animals require drinking water while others will drink water if it is available (Florance *et al.*, 2011). In the pastoral regions of arid and tropical Australia, artificial sources of water have been developed to provide drinking water for livestock (James, Landsberg & Morton, 1999), and many remain in conservation reserves that were used previously for livestock grazing.

Although dingoes can live in waterless areas where they presumably meet all their water requirements from their prey, they frequently drink, particularly during the hot summer months and droughts when prey are scarce, and focus their activities around water sources (Green & Catling, 1977; Corbett, 1995*b*). If water becomes a limiting resource for dingoes during periods of hot, dry weather or prey shortage such that dingoes need to drink, the provision of artificial waters is likely to represent a significant resource subsidy and may allow dingo populations to occupy areas that they would otherwise not be able to inhabit if water was absent (Corbett, 1995*b*). Hence, the presence of artificial water could amplify the strength of interactions they have with other species and extend their role in structuring communities (Wallach & O'Neill, 2009*b*; Brawata & Neeman, 2011). The role that surface water has in facilitating dingo populations and the interactions of this predator with other species is poorly undertsood; however, there is some field evidence which suggests that foxes and cats avoid artificial water sources that are frequented by dingoes (Brawata & Neeman, in press). Similarly, broadscale surveys have found that dingoes are relatively rare in waterless desert areas while foxes are relatively common suggesting that foxes

may be released from suppression by dingoes in waterless areas (Southgate *et al.*, 2007*b*). Thus decisions to establish, maintain or remove artificial waters may be crucial for managers of arid conservation reserves. Research is required to understand the role that artificial waters may play in facilitating the trophic and other effects of dingoes.

(6) Simulation of the effects of dingoes

Due to conflict with livestock producers it is unlikely that dingo populations will be re-established or even maintained in all areas of the continent, particularly in the heart of sheep-grazing areas. However, it is in these areas where dingoes have been exterminated that the populations and impacts of red foxes and wild herbivores are greatest (Thompson, 1983; Smith & Quin, 1996; Johnson *et al.*, 2007; Dickman *et al.*, 2009).

Given the extent of species losses in areas where dingoes have been exterminated and the deep-rooted threats to the remaining biodiversity in these areas (Smith & Quin, 1996; Johnson *et al.*, 2007), an ecological triage approach to conservation may be to consign deeply degraded areas to the "biodiversity scrapheap" and reallocate resources to areas where conservation goals are more likely to be attained. However, an alternative approach to achieving biodiversity conservation goals using our model of dingo interactions and knowledge of dingo behaviour would be to simulate the effects of dingoes. Such a strategy could entail culling of red foxes and herbivores, with herbivore culling focused specifically on limiting the reproductive potential of herbivore populations through removal of juveniles and females. Carcasses would have to be removed to prevent the influx of facultative scavengers and thus reduce their predatory impact on secondary species *via* hyper-predation (Sinclair *et al.*, 1998). In areas with critically endangered populations of animals threatened by foxes, trained guard dogs could be deployed in much the same way as shepherd dogs, to alleviate the impacts of fox predation through interference and direct killing.

VI. CONCLUSIONS

(1) Dingoes have pervasive effects on ecological communities in Australia, especially in the arid regions of the continent. In general, animal species weighing more than 100 kg appear to be unaffected by dingoes, species weighing 7–100 kg decline in the presence of dingoes, species weighing 1–7 kg show context-dependent responses to dingoes, and species weighing less than 1 kg typically benefit from the presence of dingoes. There is evidence that dingoes induce trophic cascades and influence plant communities by regulating herbivore populations.

(2) The effectiveness of dingoes as ecosystem architects appears to depend on the energy state of ecosystems. Following rainfall-driven resource pulses when rates of plant growth and biomass are high, there is likely to be a surfeit of resources

for dingoes and other animal consumers. We predict that the effect of dingoes on ecosystems will diminish during these periods. Conversely, during dry conditions we expect that the effects of dingoes on ecosystems will be magnified due to reduced availability of food resources and increased reliance on large prey such as macropods as food and intensification of competitive and/or predatory relationships between dingoes and mesopredators.

(3) The ecological interactions of dingoes have the potential to be utilised as a tool to manage ecological processes. In particular, dingoes could be used in programs aimed at reducing the predatory impacts of foxes and of herbivores weighing 7–100 kg.

(4) Harnessing the positive ecological effects of dingoes while at the same time minimising their impacts on agriculture will present a major socio-political challenge. Further research on the taxonomy and ecological function of dingoes and wild dogs will help to resolve such contentious issues. Research into dingo-management strategies that allow for the preservation of dingoes and protection of livestock is urgently required.

VII. ACKNOWLEDGEMENTS

VIII. REFERENCES

ABRS (2009). *Australian Faunal Directory*. Australian Biological Resources Study, Canberra. Viewed 11 May 2011. http://www.environment.gov.au/biodiversity/abrs/online-resources/fauna/afd/index.html

ALLEN, B. L. (2010a). Did dingo control cause the elimination of kowaris through mesopredator release effects? A response to Wallach and O'Neill. *Animal Biodiversity and Conservation* 33, 1–4.

ALLEN, B. L. (2010b). Skin and bone: observations of dingo scavenging during a chronic food shortage. *Australian Mammalogy* 32, 207–208.

ALLEN, B. L., ENGEMAN, R. & ALLEN, L. (2011). Wild dogma: An examination of recent "evidence" for dingo regulation of invasive mesopredator release in Australia. *Current Zoology* 57, 568–583

ALLEN, L., ENGEMAN, R. & KRUPA, H. (1996). Evaluation of three relative abundance indices for assessing dingo populations. *Wildlife Research* 23, 197–206.

ALLEN, L. R. & FLEMING, P. J. S. (2004). Review of canid management in Australia for the protection of livestock and wildlife - potential application to coyote management. *Sheep and Goat Research Journal* 19, 97–104.

ANDELT, W. F., PHILLIPS, R. L., GRUVER, K. S. & GUTHRIE, J. W. (1999). Coyote predation on domestic sheep deterred with electronic dog-training collar. *Wildlife Society Bulletin* 27, 12–18.

BAIRD, R. F. (1991). The dingo as a possible factor in the disappearance of *Gallinula mortierii* from the Australian mainland. *Emu* 91, 121–122.

BARKER, B. C. W. & MACINTOSH, A. (1979). The dingo - a review. *Archaeology and Physical Anthropology in Oceania* 14, 27–53.

BAUER, F. H. (1964). Queensland's new dingo fence. *Australian Geographer* 9, 244–246.

BERGER, K. M. & CONNER, M. M. (2008). Recolonizing wolves and mesopredator suppression of coyotes: impacts on pronghorn population dynamics. *Ecological Applications* 18, 599–612.

BERGER, K. M. & GESE, E. M. (2007). Does interference competition with wolves limit the distribution and abundance of coyotes? *Journal of Animal Ecology* 76, 1075–1085.

BERGER, K. M., GESE, E. M. & BERGER, J. (2008). Indirect effects and traditional trophic cascades: a test involving wolves, coyotes, and pronghorn. *Ecology* 89, 818–828.

BESCHTA, R. L. & RIPPLE, W. J. (2009). Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation* 142, 2401–2414.

BEYER, H. L., MERRILL, E. H., VARLEY, N. & BOYCE, M. S. (2007). Willow on Yellowstone's northern range: evidence for a trophic cascade? *Ecological Applications* 17, 1563–1571.

BRADLEY, E. H., PLETSHER, D. H., BANGS, E. E., KUNKEL, K. E., SMITH, D. W., MACK, C. M., MEIER, T. J., FONTAINE, J. A., NIEMAYER, C. C. & JIMENEZ, M. D. (2005). Evaluating wolf translocation as a nonlethal method to reduce livestock conflicts in the northwestern United States. *Conservation Biology* 19, 1498–1508.

BRAITHWAITE, R. W. & GRIFFITHS, A. D. (1994). Demographic variation and range contraction in the northern quoll, *Dasyurus hallucatus* (Marsupialia: Dasyuridae). *Wildlife Research* 21, 203–217.

BRAWATA, R. & NEEMAN, T. (2011). Is water the key? Dingo management, intraguild interactions and predator distribution around water points in arid Australia. *Wildlife Research* 38, 426–436.

BROOK, L. A. & KUTT, A. S. (2011). The diet of the dingo (*Canis lupus dingo*) in northeastern Australia with comments on its conservation implications. *The Rangeland Journal* 33, 79–85.

BROWN, O. J. F. (2006). Tasmanian devil (*Sarcophilus harrisii*) extinction on the Australian mainland in the mid-Holocene: multicausality and ENSO intensification. *Alcheringa* 30, 49–57.

BRUNO, J. F. & CARDINALE, B. J. (2008). Cascading effects of predator richness. *Frontiers in Ecology and the Environment* 10, 539–546.

BURBIDGE, A. A. & McKENZIE, N. L. (1989). Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. *Biological Conservation* 50, 143–198.

BURROWS, N. D., ALGAR, D., ROBINSON, A. D., SINAGRA, J., WARD, B. & LIDDELOW, G. (2003). Controlling introduced predators in the Gibson Desert of Western Australia. *Journal of Arid Environments* 55, 691–713.

BYRNE, M., YEATES, D. K., JOSEPH, L., KEARNEY, M., BOWLER, J., WILLIAMS, M. A. J., COOPER, S., DONNELLAN, S. C., KEOGH, J. S., LEYS, R., MELVILLE, J., MURPHY, D. J., PORCH, N. & WYRWOLL, K. H. (2008). Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. *Molecular Ecology* 17, 4398–4417.

CATLING, P. C. & BURT, R. J. (1995). Why are red foxes absent from some eucalypt forests in eastern New South Wales? *Wildlife Research* 22, 535–546.

CATLING, P. C., BURT, R. J. & KOOYMAN, R. (1997). A comparison of techniques used in a ground survey of the ground dwelling and arboreal mammals in forests of north-eastern New South Wales. *Wildlife Research* 24, 417–432.

CAUGHLEY, G. & GRIGG, G. C. (1982). Numbers and distribution of kangaroos in the Queensland pastoral zone. *Australian Wildlife Research* 9, 365–371.

CAUGHLEY, G., GRIGG, G. C., CAUGHLEY, J. & HILL, G. J. E. (1980). Does dingo predation control the densities of kangaroos and emus? *Australian Wildlife Research* 7, 1–12.

CAUGHLEY, G., GRIGG, G. C. & SMITH, L. (1985). The effect of drought on kangaroo populations. *Journal of Wildlife Management* 49, 679–685.

CAUGHLEY, G., BAYLISS, P. & GILES, J. (1984). Trends of kangaroo populations in western New South Wales and their relationship to rainfall. *Australian Wildlife Research* 11, 415–422.

CLARIDGE, A. W. & HUNT, R. (2008). Evaluating the role of the dingo as a trophic regulator: additional practical suggestions. *Ecological Management and Restoration* 9, 116–119.

CLARIDGE, A. W., MILLS, D. J. & BARRY, S. C. (2010). Prevalence of threatened native species in canid scats from coastal and near-coastal landscapes in south-eastern Australia. *Australian Mammalogy* 32, 117–126.

CLARIDGE, A. W., MILLS, D. J., HUNT, R., JENKINS, D. J. & BEAN, J. (2009). Satellite tracking of wild dogs in south-eastern mainland Australian forests: implications for management of a problematic top-order carnivore. *Forest Ecology and Management* 258, 814–822.

COMAN, B. J. & EVANS, E. (2007). The loaded dog. *Quadrant* 51, 10–15.

CORBETT, L. K. (1995a). Does dingo predation or buffalo competition regulate feral pig populations in the Australian wet-dry tropics? An experimental study. *Wildlife Research* 22, 65–74.

CORBETT, L. K. (1995b). *The dingo in Australia and Asia*. University of NSW Press, Sydney.

CORBETT, L. K. & NEWSOME, A. E. (1987). The feeding ecology of the dingo. 3. Dietary relationships with widely fluctuating prey populations in arid Australia - an hypothesis of alternation of predation. *Oecologia* 74, 215–227.

COURCHAMP, F., LANGLAIS, M. & SUGIHARA, G. (1999). Cats protecting birds: modelling the mesopredator release effect. *Journal of Animal Ecology* 68, 282–292.

CROOKS, K. R. & SOULÉ, M. E. (1999). Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400, 563–566.

CUPPLES, J., CROWTHER, M., STORY, G. & LETNIC, M. (2011). Dietary overlap and prey selectivity among sympatric carnivores: could dingoes suppress foxes through competition for prey? *Journal of Mammalogy* **92**, 590–600.

DANIELS, M. J. & CORBETT, L. (2003). Redefining introgressed protected mammals: when is a wild cat a wild cat and a dingo a wild dog? *Wildlife Research* **30**, 213–218.

DAWSON, T. J. (1995). *Kangaroos*. University of NSW Press, Sydney.

DICKMAN, C. R. (1991). Mechanisms of competition among insectivorous mammals. *Oecologia* **85**, 464–471.

DICKMAN, C. R., GLEN, A. S. & LETNIC, M. (2009). Reintroducing the dingo: can Australia's conservation wastelands be restored? In: *Reintroduction of top-order predators* (eds M. W. HAYWARD and M. J. SOMERS), pp. 238–269. Wiley-Blackwell, London.

DICKMAN, C. R. & LUNNEY, D., editors (2001a). *A symposium on the dingo*. Royal Zoological Society of New South Wales, Sydney.

DICKMAN, C. R. & LUNNEY, D. (2001b). Last howl of the dingo: the legislative, ecological and practical issues arising from the kill-or-conserve dilemma. In: *A symposium on the dingo* (eds C. R. DICKMAN and D. LUNNEY), pp. 95–107. Royal Zoological Society of New South Wales, Sydney.

DICKMAN, C. R., PRESSEY, R. L., LIM, L. & PARNABY, H. E. (1993). Mammals of particular conservation concern in the Western Division of New South Wales. *Biological Conservation* **65**, 219–248.

DOBBIE, W. K., BERMAN, D. M. & BRAYSHER, M. L. (1993). *Managing vertebrate pests: feral horses*. Bureau of Resource Sciences, Australian Government Publishing Service, Canberra.

DONADIO, E. & BUSKIRK, S. W. (2006). Diet, morphology, and interspecific killing in Carnivora. *American Naturalist* **167**, 524–536.

DUFFY, J. E. (2003). Biodiversity loss, trophic skew and ecosystem functioning. *Ecology Letters* **6**, 680–687.

DUFFY, J. E., CARDINALE, B. J., FRANCE, K. E., MCINTYRE, P. B., THÉBAULT, E. & LOREAU, M. (2007). The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters* **10**, 522–538.

EALEY, E. H. M. (1967). Ecology of the euro, *Macropus robustus* (Gould), in north-western Australia. I. The environment and changes in euro and sheep populations. *CSIRO Wildlife Research* **12**, 9–25.

ECCARD, J. A., WALTHER, R. B. & MILTON, S. J. (2000). How livestock grazing affects vegetation structures and small mammal distribution in the semi-arid Karoo. *Journal of Arid Environments* **46**, 103–106.

EDWARDS, G. P., DE PREU, N. D., SHAKESHAFT, B. J. & CREALY, I. V. (2000). An evaluation of two methods of assessing feral cat and dingo abundance in central Australia. *Wildlife Research* **27**, 143–149.

ELLEDGE, A. E., LEUNG, L. K. P., ALLEN, L. R., FIRESTONE, K. & WILTON, A. N. (2006). Assessing the taxonomic status of dingoes *Canis familiaris dingo* for conservation. *Mammal Review* **36**, 142–156.

ELMHAGEN, B. & RUSHTON, S. P. (2007). Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? *Ecology Letters* **10**, 197–206.

ESTES, J. A. & DUGGINS, D. O. (1995). Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecological Monographs* **65**, 75–100.

ETHERIDGE, R. (1916). *The warrigal, or 'dingo', introduced or indigenous?* Memoirs of the Geological Survey of New South Wales, Ethnological Series 2. Government Printer, Sydney.

FENNESSY, B. V. (1962). Competitors with sheep: mammal and bird pests of the sheep industry. In: *The simple fleece* (ed. A. BARNARD), pp. 221–240. Cambridge University Press, London.

FENSHAM, R. J. & FAIRFAX, R. J. (2008). Water-remoteness for grazing relief in Australian arid-lands. *Biological Conservation* **141**, 1447–1460.

FEY, K., BANKS, P. B., OKSANEN, L. & KORPIMÄKI, E. (2009). Does removal of an alien predator from small islands in the Baltic Sea induce a trophic cascade? *Ecography* **32**, 546–552.

FILLIOS, M. A., GORDON, C., KOCH, F. & LETNIC, M. (2010). The effect of a top predator on kangaroo abundance in arid Australia and its implications for archaeological faunal assemblages. *Journal of Archaeological Science* **37**, 986–993.

FISHER, D. O., HOYLE, S. D. & BLOMBERG, S. P. (2000). Population dynamics and survival of an endangered wallaby: a comparison of four methods. *Ecological Applications* **10**, 901–910.

FLANNERY, T. F. (1994). *The Future Eaters*. Reed Books, Melbourne.

FLEMING, P., CORBETT, L., HARDEN, R. & THOMSON, P. (2001). *Managing the impacts of dingoes and other wild dogs*. Bureau of Rural Sciences, Canberra.

FLEMING, P. J. S., ALLEN, L. R., LAPIDGE, S. J., ROBLEY, A., SAUNDERS, G. R. & THOMSON, P. C. (2006). A strategic approach to mitigating the effects of wild canids: proposed activities of the Invasive Animals Cooperative Research Centre. *Australian Journal of Experimental Agriculture* **46**, 753–762.

FLORANCE, D., WEBB, J. K., DEMPSTER, T., KEARNEY, M. R., WORTHING, A. & LETNIC, M. (2011). Excluding access to invasion hubs can contain the spread of an invasive vertebrate. *Proceedings of the Royal Society B: Biological Sciences* **278**, 2900–2908.

FORTIN, D., BEYER, H. K., BOYCE, M. S., SMITH, D. W., DUCHESNE, T. & MAO, J. S. (2005). Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* **86**, 1320–1330.

FRANK, D. A. (2008). Evidence for top predator control of a grazing ecosystem. *Oikos* **117**, 1718–1724.

FRANK, K. T., PETRIE, B., CHOI, J. S. & LEGGETT, W. C. (2005). Trophic cascades in a fomerly cod-dominated ecosystem. *Science* **308**, 1621–1623.

FREELAND, W. J. & BOULTON, W. J. (1990). Feral water buffalo (*Bubalus bubalis*) in the major floodplains of the 'Top End', Northern Territory, Australia: population growth and the brucellosis and tuberculosis eradication campaign. *Australian Wildlife Research* **17**, 411–420.

FREELAND, W. J. & CHOQUENOT, D. (1990). Determinants of herbivore carrying-capacity - plants, nutrients, and *Equus asinus* in northern Australia. *Ecology* **71**, 589–597.

FRUMP, R. R. (2006). *The man-eaters of Eden: life and death in Kruger National Park*. Lyons Press, Guilford, Connecticut.

GLEN, A. S. (2010). Hybridisation between dingoes and domestic dogs: a comment on Jones (2009). *Australian Mammalogy* **32**, 76–77.

GLEN, A. S. & DICKMAN, C. R. (2005). Complex interactions among mammalian carnivores in Australia, and their implications for wildlife management. *Biological Reviews* **80**, 387–401.

GLEN, A. S. & DICKMAN, C. R. (2008). Niche overlap between marsupial and eutherian carnivores: does competition threaten the endangered spotted-tailed quoll? *Journal of Applied Ecology* **45**, 700–707.

GLEN, A. S. & DICKMAN, C. R. (2011). Why are there so many spotted-tailed quolls *Dasyurus maculatus* in parts of north-eastern New South Wales? *Australian Zoologist* **35**, 711–718.

GLEN, A. S., DICKMAN, C. R., SOULÉ, M. E. & MACKEY, B. G. (2007). Evaluating the role of the dingo as a trophic regulator in Australian ecosystems. *Austral Ecology* **32**, 492–501.

GLEN, A. S., PENNAY, M., DICKMAN, C. R., WINTLE, B. A. & FIRESTONE, K. B. (2011). Diets of sympatric native and introduced carnivores in the Barrington Tops, eastern Australia. *Austral Ecology* **36**, 290–296.

GOLLAN, K. (1984). The Australian dingo: in the shadow of man. In: *Vertebrate zoogeography & evolution in Australasia* (eds M. ARCHER and G. CLAYTON), pp. 921–927. Hesperian Press, Perth.

GREEN, B. & CATLING, P. C. (1977). The biology of the dingo. In: *Australian animals and their environment* (eds H. MESSEL and S. T. BUTLER), pp. 49–60. MacArthur Press, Sydney.

GRICE, D., CAUGHLEY, G. & SHORT, J. (1985). Density and distribution of emus. *Australian Wildlife Research* **12**, 69–73.

GUSSET, M., RYAN, S. J., HOFMEYR, M., VAN DYK, G., DAVIES-MOSTERT, H. T., GRAF, J. A., OWEN, C., SZYKMAN, M., MACDONALD, D. W., MONFORT, S. L., WILDT, D. E., MADDOCK, A. H., MILLS, M. G. L., SLOTOW, R. & SOMERS, M. J. (2008). Efforts going to the dogs? Evaluating attempts to re-introduce endangered wild dogs in South Africa. *Journal of Applied Ecology* **45**, 100–108.

HALE, P. T. (2004). Genetic effects of kangaroo harvesting. *Australian Mammalogy* **26**, 75–86.

HAYWARD, M. W. & SOMERS, M. J., editors (2009). *Reintroduction of top-order predators*. Wiley-Blackwell, London.

HEALY, S. (2007). Deadly dingoes: 'wild' or simply requiring 'due process'? *Social Studies of Science* **37**, 443–471.

HEITHAUS, M. R., FRID, A., WIRSING, A. J. & WORM, B. (2008). Predicting ecological consequences of marine top predator declines. *Trends in Ecology and Evolution* **23**, 202–210.

HOLDEN, C. & MUTZE, G. (2002). Impact of rabbit haemorrhagic disease on introduced predators in the Flinders Ranges, South Australia. *Wildlife Research* **29**, 615–626.

HURLBERT, S. H. (1984). Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* **54**, 187–211.

HUXMAN, T. E., SNYDER, K. A., TISSUE, D., LEFFLER, A. J., OGLE, K., POCKMAN, W. T., SANDQUIST, D. R., POTTS, D. L. & SCHWINNING, S. (2004). Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia* **141**, 254–268.

HYTTEN, K. F. (2009). Dingo dualism: exploring the ambiguous identity of Australian dingoes. *Australian Zoologist* **35**, 18–27.

IACOLINA, L., SCANDURA, M., GAZZOLA, A., CAPPAI, N., CAPITANI, C., MATTIOLI, L., VERCILLO, F. & APOLLONIO, M. (2010). Y-chromosome microsatellite variation in Italian wolves: a contribution to the study of wolf-dog hybridization patterns. *Mammalian Biology* **75**, 341–347.

JAMES, C. D., LANDSBERG, J. & MORTON, S. R. (1999). Provision of watering points in the Australian arid zone: a review of effects on biota. *Journal of Arid Environments* **41**, 87–121.

JARMAN, P. (1986). The red fox - an exotic large predator. In: *The ecology of exotic animals and plants* (ed. R. L. KITCHING), pp. 43–61. John Wiley and Sons, Brisbane.

JOHNSON, C. N. (2006). *Australia's mammal extinctions: a 50,000 year history*. Cambridge University Press, Cambridge.

JOHNSON, C. N. & ISAAC, J. L. (2009). Body mass and extinction risk in Australian marsupials: the critical weight range revisted. *Austral Ecology* **34**, 35–40.

Johnson, C. N., Isaac, J. L. & Fisher, D. O. (2007). Rarity of a top predator triggers continent-wide collapse of mammal prey: dingoes and marsupials in Australia. *Proceedings of the Royal Society B: Biological Sciences* **274**, 341–346.

Johnson, C. N. & VanDerWal, J. (2009). Evidence that dingoes limit abundance of a mesopredator in eastern Australian forests. *Journal of Applied Ecology* **46**, 641–646.

Johnson, C. N. & Wroe, S. (2003). Causes of extinction of vertebrates during the Holocene of mainland Australia: arrival of the dingo, or human impact? *Holocene* **13**, 941–948.

Jones, M. E., Oakwood, M., Belcher, C. A., Morris, K., Murray, A. J., Woolley, P. A., Firestone, K. B., Johnson, B. & Burnett, S. (2003). Carnivore concerns: problems, issues and solutions for conserving Australasia's marsupial carnivores. In: *Predators with pouches: the biology of carnivorous marsupials* (eds M. E. Jones, C. R. Dickman and M. Archer), pp. 422–434. CSIRO Publishing, Melbourne.

Kauffman, M. J., Varley, N., Smith, D. W., Stahler, D. R., MacNulty, D. R. & Boyce, M. S. (2007). Landscape heterogeneity shapes predation in a newly restored predator-prey system. *Ecology Letters* **10**, 690–700.

Kennedy, M., Phillips, B., Legge, S., Murphy, S. & Faulkner, R. (2011). Do dingoes suppress the activity of cats in northern Australia? *Austral Ecology*. published online 27 April 2011.

Kinnear, J. E., Sumner, N. R. & Onus, M. L. (2002). The red fox in Australia - an exotic predator turned biocontrol agent. *Biological Conservation* **108**, 335–359.

Krefft, G. (1871). *The mammals of Australia*. Government Printer, Sydney.

Letnic, M. (2004). Cattle grazing in a hummock grassland regenerating after fire: the short-term effects of cattle exclusion on vegetation in south-western Queensland. *Rangeland Journal* **26**, 34–48.

Letnic, M., Crowther, M. S. & Koch, F. (2009a). Does a top-predator provide an endangered rodent with refuge from an invasive mesopredator? *Animal Conservation* **12**, 302–312.

Letnic, M., Crowther, M. S., Dickman, C. R. & Ritchie, E. (2011a). Demonising the dingo: how much wild dogma is enough? *Current Zoology* **57**, 668–670.

Letnic, M. & Dickman, C. R. (2006). Boom means bust: interactions between the El Niño/Southern Oscillation (ENSO), rainfall and the processes threatening mammal species in arid Australia. *Biodiversity and Conservation* **15**, 3847–3880.

Letnic, M. & Dickman, C. R. (2010). Resource pulses and mammalian dynamics: conceptual models for hummock grasslands and other Australian desert habitats. *Biological Reviews* **85**, 501–521.

Letnic, M. & Dworjanyn, S. A. (2011). Does a top predator reduce the predatory impact of an invasive mesopredator on an endangered rodent? *Ecography* **34**, 827–835.

Letnic, M., Greenville, A., Denny, E., Dickman, C. R., Tischler, M. K., Gordon, C. & Koch, F. (2011b). Does a top predator suppress the abundance of an invasive mesopredator at a continental scale? *Global Ecology and Biogeography* **20**, 343–353.

Letnic, M. & Koch, F. (2010). Are dingoes a trophic regulator in arid Australia? A comparison of mammal communities on either side of the dingo fence. *Austral Ecology* **35**, 167–175.

Letnic, M., Koch, F., Gordon, C., Crowther, M. S. & Dickman, C. R. (2009b). Keystone effects of an alien top-predator stem extinctions of native mammals. *Proceedings of the Royal Society B: Biological Sciences* **276**, 3249–3256.

Letnic, M., Story, P., Story, G., Field, J., Brown, O. J. F. & Dickman, C. R. (2011c). Resource pulses, switching trophic control and the dynamics of small mammal assemblages in arid Australia. *Journal of Mammalogy* **92**, 1210–1222.

Letnic, M., Tamayo, B. & Dickman, C. R. (2005). The responses of mammals to La Niña (El Niño Southern Oscillation)-associated rainfall, predation, and wildfire in central Australia. *Journal of Mammalogy* **86**, 689–703.

Lovari, S., Boesi, R., Minder, I., Mucci, N., Randi, E., Dematteis, A. & Ale, S. B. (2009). Restoring a keystone predator may endanger a prey species in a human-altered ecosystem: the return of the snow leopard to Sagarmatha National Park. *Animal Conservation* **12**, 559–570.

Ludwig, J., Tongway, D., Freudenberger, D., Noble, J. & Hodgkinson, K., editors (1997). *Landscape ecology, function and management: principles from Australia's rangelands*. CSIRO Publishing, Melbourne.

Lundie-Jenkins, G., Corbett, L. K. & Phillips, C. M. (1993). Ecology of the rufous hare-wallaby, *Lagorchestes hirsutus* Gould (Marsupialia: Macropodidae) in the Tanami Desert, Northern Territory. III Interactions with introduced mammal species. *Wildlife Research* **20**, 495–511.

Lunney, D., Law, B. & Rummery, C. (1996). Contrast between the visible abundance of the brush-tailed rock-wallaby, *Petrogale penicillata*, and its rarity in fox and dog scats in the gorges east of Armidale, New South Wales. *Wildlife Research* **23**, 373–379.

Lunney, D., Triggs, B., Eby, P. & Ashby, E. (1990). Analysis of scats of dogs *Canis familiaris* and foxes *Vulpes vulpes* (Canidae, Carnivora) in coastal forests near Bega, New South Wales. *Australian Wildlife Research* **17**, 61–68.

Mahon, P. S., Banks, P. B. & Dickman, C. R. (1998). Population indices for wild carnivores: a critical study in sand-dune habitat, south-western Queensland. *Wildlife Research* **25**, 11–22.

Marlow, B. J. (1962). Dingoes. *Australian Natural History* **14**, 61–63.

Marsack, P. & Campbell, G. (1990). Feeding behaviour and diet of dingoes in the Nullarbor region, Western Australia. *Australian Wildlife Research* **17**, 349–357.

Marucco, F. & McIntire, E. J. B. (2010). Predicting spatio-temporal recolonization of large carnivore populations and livestock depredation risk: wolves in the Italian Alps. *Journal of Applied Ecology* **47**, 789–798.

May, S. A. & Norton, T. W. (1996). Influence of fragmentation and disturbance on the potential impact of feral predators on native fauna in Australian forest ecosystems. *Wildlife Research* **23**, 387–400.

McCallum, H., Timmers, P. & Hoyle, S. (1995). Modelling the impact of predation on reintroductions of bridled nailtail wallabies. *Wildlife Research* **22**, 163–171.

McKenzie, N. L., Burbidge, A. A., Baynes, A., Brereton, R. N., Dickman, C. R., Gordon, G., Gibson, L. A., Menkhorst, P. W., Robinson, A. C., Williams, M. R. & Woinarski, J. C. Z. (2007). Analysis of factors implicated in the recent decline of Australia's mammal fauna. *Journal of Biogeography* **34**, 597–611.

McKnight, T. L. (1969). Barrier fencing for vermin control in Australia. *Geographical Review* **59**, 330–347.

McLaren, B. E. & Peterson, R. O. (1994). Wolves, moose, and tree-rings on Isle Royale. *Science* **266**, 1555–1558.

McLaren, B. E. & Peterson, R. O. (1995). Seeing the forest with the trees: using dendrochronology to investigate moose-induced changes to a forest understory. In: *Alces: North American moose conference and workshop proceedings* (eds M. W. Lankester and H. R. Timmermann), pp. 77–86. North American Moose Conference and Workshop, Thunder Bay.

McLeod, S. R., Hacker, R. B. & Druhan, J. P. (2004). Managing the commercial harvest of kangaroos in the Murray-Darling Basin. *Australian Mammalogy* **26**, 9–22.

Meyer, F. A. A. (1793). *Systematisch-Summarische Uebersicht der neuesten Zoologischen Entdeckungen in Neuholland und Afrika*. Nebst zwey andern Zoologischen Abhandlungen. Dykischen Buchhandlung, Leipzig.

Mitchell, B. D. & Banks, P. B. (2005). Do wild dogs exclude foxes? Evidence for competition from dietary and spatial overlaps. *Austral Ecology* **30**, 581–591.

Morgan, D. G. & Pedler, P. (2010). Managing a kangaroo population by culling to simulate predation:the Wyperfield trial. In: *Macropods: The biology of kangaroos, wallabies and rat-kangaroos* (eds G. Coulson and M. Eldridge), CSIRO Publishing, Melbourne. pp. 349–360.

Morris, K., Johnson, B., Orell, P., Gaikhorst, G., Wayne, A. & Moro, D. (2003). Recovery of the threatened chuditch (*Dasyurus geoffroii*): a case study. In: *Predators with pouches: the biology of carnivorous marsupials* (eds M. E. Jones, C. R. Dickman and M. Archer), pp. 435–451. CSIRO Publishing, Melbourne.

Morton, S. R. (1990). The impact of European settlement on the vertebrate animals of arid Australia: a conceptual model. *Proceedings of the Ecological Society of Australia* **16**, 201–213.

Morton, S. R., Stafford Smith, D. M., Dickman, C. R., Dunkerley, D. L., Friedel, M. H., McAllister, R. R. J., Reid, J. R. W., Roshier, D. A., Smith, M. A., Walsh, F. J., Wardle, G. M., Watson, I. W. & Westoby, M. (2011). A fresh framework for the ecology of arid Australia. *Journal of Arid Environments* **75**, 313–329.

Moseby, K., Neilly, H., Read, J.L. & Crisp, H. Interactions between a top order predator and exotic mesopredators in the Australian Rangelands. International Journal of Ecology (in press).

Mulvaney, J. & Kamminga, J. (1999). *Prehistory of Australia*. Allen & Unwin, Sydney.

Musiani, M., Muhly, T., Callaghan, C., Gates, C. C., Smith, M. E., Stone, S. & Tosoni, E. (2004). Wolves in rural agricultural areas of western North America: conflict and conservation. In: *People and predators: from conflict to coexistence* (eds N. Fascione, A. Delach and M. E. Smith), pp. 51–75. Island Press, Washington, D. C.

Newsome, A. (1990). The control of vertebrate pests by vertebrate predators. *Trends in Ecology and Evolution* **5**, 187–191.

Newsome, A. E. (1965). The abundance of red kangaroos, *Megaleia rufa* (Desmarest), in central Australia. *Australian Journal of Zoology* **13**, 735–759.

Newsome, A. E. (2001). The biology and ecology of the dingo. In: *A symposium on the dingo* (eds C. R. Dickman and D. Lunney), pp. 20–33. Royal Zoological Society of New South Wales, Sydney.

Newsome, A. E., Catling, P. C., Cooke, B. D. & Smyth, R. (2001). Two ecological universes separated by the dingo barrier fence in semi-arid Australia: interactions between landscapes, herbivory and carnivory, with and without dingoes. *Rangeland Journal* **23**, 71–98.

Newsome, A. E., Catling, P. C. & Corbett, L. K. (1983). The feeding ecology of the dingo. 2. Dietary and numerical relationships with fluctuating prey populations in southeastern Australia. *Australian Journal of Ecology* **8**, 345–366.

Newsome, A. E. & Coman, B. J. (1989). Canidae. In: *Fauna of Australia, volume 1B: Mammalia* (eds D. W. Walton and B. J. Richardson), pp. 993–1005. Australian Government Publishing Service, Canberra.

Newsome, A. E. & Corbett, L. K. (1975). Outbreaks of rodents in semi-arid and arid Australia: causes, preventions, and evolutionary considerations. In: *Rodents in desert environments* (eds I. Prakash and P. K. Ghosh), pp. 117–153. Dr W. Junk, The Hague.

Nicholls, N. (1991). The El Niño/Southern Oscillation and Australian vegetation. *Plant Ecology* **91**, 23–36.

Noy-Meir, I. (1973). Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* **4**, 25–51.

O'donnell, S., Webb, J. K. & Shine, R. S. (2010). Conditioned taste aversion enhances the survival of an endangered predator imperilled by a toxic invader. *Journal of Applied Ecology* **47**, 558–565.

O'Neill, A. (2002). *Living with the dingo*. Envirobook, Sydney.

Oakwood, M. (2000). Reproduction and demography of the northern quoll, *Dasyurus hallucatus*, in the lowland savanna of northern Australia. *Australian Journal of Zoology* **48**, 519–539.

Oksanen, L. (2001). Logic of experiments in ecology: is pseudoreplication a pseudoissue? *Oikos* **94**, 27–38.

Oksanen, L. & Oksanen, T. (2000). The logic and realism of the hypothesis of exploitation of ecosystems. *American Naturalist* **155**, 703–723.

Oksanen, T., Oksanen, L., Schneider, M. & Aunapuu, M. (2001). Regulation, cycles and stability in northern carnivore-herbivore systems: back to first principles. *Oikos* **94**, 101–117.

Paddle, R. (2000). *The last Tasmanian tiger: the history and extinction of the thylacine*. Cambridge University Press, New York.

Paltridge, R. (2002). The diets of cats, foxes and dingoes in relation to prey availability in the Tanami Desert, Northern Territory. *Wildlife Research* **29**, 389–403.

Parker, M. (2007). The cunning dingo. *Society and Animals* **15**, 69–78.

Pavey, C. R., Eldridge, S. R. & Heywood, M. (2008). Population dynamics and prey selection of native and introduced predators during a rodent outbreak in arid Australia. *Journal of Mammalogy* **89**, 674–683.

Pettigrew, J. D. (1993). A burst of feral cats in the Diamantina: a lesson for the management of pest species. In: *Cat management workshop proceedings* (eds G. Siepen and C. Owens), pp. 25–32. Queensland Department of Environment and Heritage, Brisbane.

Polis, G. A. (1999). Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos* **86**, 3–15.

Pople, A. R., Grigg, G. C., Cairns, S. C., Beard, L. A. & Alexander, P. (2000). Trends in the numbers of red kangaroos and emus on either side of the South Australian dingo fence: evidence for predator regulation? *Wildlife Research* **27**, 269–276.

Purcell, B. (2010). *Dingo*. CSIRO Publishing, Melbourne.

Ray, J. C. (2005). Large carnivorous animals as tools for conserving biodiversity: assumptions and uncertainties. In: *Large carnivores and the conservation of biodiversity* (eds J. C. Ray, K. H. Redford, R. S. Steneck and J. Berger), pp. 34–56. Island Press, Washington, D.C.

Read, J. L. (1997). Stranded on desert islands? Factors shaping animal populations in Lake Eyre South. *Global Ecology and Biogeography* **6**, 431–438.

Read, J. L. (2002). Experimental trial of Australian arid zone reptiles as early warning indicators of overgrazing by cattle. *Austral Ecology* **27**, 55–66.

Read, J. L. & Eldridge, S. (2010). An optimised rapid detection technique for simultaneously monitoring activity of rabbits, cats, foxes and dingoes in the rangelands. *Rangeland Journal* **32**, 389–394.

Read, J. L. & Wilson, D. (2004). Scavengers and detritivores of kangaroo harvest offcuts in arid Australia, *Wildlife Research* **31**, 51–56.

Reid, J. & Fleming, M. (1992). The conservation status of birds in arid Australia. *Rangeland Journal* **14**, 65–91.

Ripple, W. J. & Beschta, R. L. (2006). Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. *Forest Ecology and Management* **230**, 96–106.

Ripple, W. J. & Beschta, R. L. (2007). Restoring Yellowstone's aspen with wolves. *Biological Conservation* **138**, 514–519.

Risbey, D. A., Calver, M. C. & Short, J. (1999). The impact of cats and foxes on the small vertebrate fauna of Heirisson Prong, Western Australia. I. Exploring potential impact using diet analysis. *Wildlife Research* **26**, 621–630.

Ritchie, E. G. & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters* **12**, 982–998.

Ritchie, E. G., Martin, J. K., Krockenberger, A. K., Garnett, S. & Johnson, C. N. (2008). Large-herbivore distribution and abundance: Intra-and interspecific niche variation in the tropics. *Ecological Monographs* **78**, 105–122.

Ritchie, E. G., Martin, J. K., Johnson, C. N. & Fox, B. J. (2009). Separating the influences of environment and species interactions on patterns of distribution and abundance: competition between large herbivores. *Journal of Animal Ecology* **78**, 724–731.

Robertshaw, J. D. & Harden, R. H. (1985). The ecology of the dingo in north-eastern New South Wales II. Diet. *Australian Wildlife Research* **12**, 39–50.

Robertshaw, J. D. & Harden, R. H. (1986). The ecology of the dingo in north-eastern New South Wales IV. Prey selection by dingoes, and its effect on the major prey species, the swamp wallaby, *Wallabia bicolor* (Desmarest). *Australian Wildlife Research* **13**, 141–163.

Robertson, G. (1984). The mortality of kangaroos in drought. *Australian Wildlife Research* **13**, 349–354.

Rolls, E. C. (1969). *They all ran wild*. Angus and Roberston, Sydney.

Rowley, I. (1970). Lamb predation in Australia: incidence, predisposing conditions, and the identification of wounds. *C.S.I.R.O. Wildlife Research* **15**, 79–123.

Saunders, G., Coman, B., Kinnear, J. & Braysher, M. (1995). *Managing vertebrate pests: foxes*. Australian Government Publishing Service, Canberra.

Saunders, G. R., Gentle, M. N. & Dickman, C. R. (2010). The impacts and management of foxes *Vulpes vulpes* in Australia. *Mammal Review* **40**, 181–211.

Savolainen, P., Leitner, T., Wilton, A. N., Matisoo-Smith, E. & Lundeberg, J. (2004). A detailed picture of the origin of the Australian dingo, obtained from the study of mitochondrial DNA. *Proceedings of the National Academy of Sciences of the USA* **101**, 12387–12390.

Savolainen, P., Zhang, Y. P., Luo, J., Lundeberg, J. & Leitner, T. (2002). Genetic evidence for an East Asian origin of domestic dogs. *Science* **298**, 1610–1613.

Schmidt, K. A. (2003). Nest predation and population declines in Illinois songbirds: a case for mesopredator effects. *Conservation Biology* **17**, 1141–1150.

Seyfort, M. (2001). An emu vs. dingo fight. *Bird Observer (Nunawading)* **813**, 10.

Sharp, A., Norton, M., Marks, A. & Holmes, K. (2001). An evaluation of two indices of red fox (*Vulpes vulpes*) abundance in an arid environment. *Wildlife Research* **28**, 419–424.

Shepherd, N. C. (1981). Predation of red kangaroos, *Macropus rufus*, by the dingo, *Canis familiaris dingo* (Blumenbach), in northwestern New South Wales. *Australian Wildlife Research* **8**, 255–262.

Short, J (1985). The functional response of kangaroos, sheep and rabbits in an arid grazing system. *Journal of Applied Ecology* **22**, 435–447.

Short, J., Kinnear, J. E. & Robley, A. (2002). Surplus killing by introduced predators in Australia - evidence for ineffective anti-predator adaptations in native prey species? *Biological Conservation* **103**, 283–301.

Sinclair, A. R. E., Krebs, C. J., Fryxell, J. M., Turkington, R., Boutin, S., Boonstra, R., Seccombe-Hett, P., Lundberg, P. & Oksanen, L. (2000). Testing hypotheses of trophic level interactions: a boreal forest ecosystem. *Oikos* **89**, 313–328.

Sinclair, A. R. E., Mduma, S. & Brashares, J. S. (2003). Patterns of predation in a diverse predator-prey system. *Nature* **425**, 288–290.

Sinclair, A. R. E., Pech, R. P., Dickman, C. R., Hik, D., Mahon, P. & Newsome, A. E. (1998). Predicting effects of predation on conservation of endangered prey. *Conservation Biology* **12**, 564–575.

Smith, A. P. & Quin, D. G. (1996). Patterns and causes of extinction and decline in Australian conilurine rodents. *Biological Conservation* **77**, 243–267.

Smith, B. P. & Litchfield, C. A. (2009). A review of the relationship between Indigenous Australians, dingoes (*Canis dingo*) and domestic dogs (*Canis familiaris*). *Anthrozoos* **22**, 111–128.

Smith, N. (1999). The howl and the pussy: feral cats and wild dogs in the Australian imagination. *Australian Journal of Anthropology* **10**, 288–305.

Smith, P. J., Pressey, R. L. & Smith, J. E. (1994). Birds of particular conservation concern in the Western Division of New South Wales. *Biological Conservation* **69**, 315–338.

Soulé, M. E., Estes, J. A., Berger, J. & Del Rio, C. M. (2003). Ecological effectiveness: conservation goals for interactive species. *Conservation Biology* **17**, 1238–1250.

Soulé, M. E., Estes, J. A., Miller, B. & Honnold, D. L. (2005). Strongly interacting species: conservation policy, management, and ethics. *BioScience* **55**, 168–176.

Southgate, R., Paltridge, R., Masters, P. & Carthew, S. (2007a). Bilby distribution and fire: a test of alternative models of habitat suitability in the Tanami Desert, Australia. *Ecography* **30**, 759–776.

Southgate, R., Paltridge, R., Masters, P. & Ostendorf, B. (2007b). Modelling introduced predator and herbivore distributions in the Tanami Desert, Australia. *Journal of Arid Environments* **68**, 438–464.

Spencer, R. J. & Thompson, M. B. (2005). Experimental analysis of the impact of foxes on freshwater turtle populations. *Conservation Biology* **19**, 845–854.

Switalski, T. A. (2003). Coyote foraging ecology and vigilance in response to gray wolf reintroduction in Yellowstone National Park. *Canadian Journal of Zoology* **81**, 985–993.

Tench, W. (1788). *A narrative of the expedition to Botany Bay and a complete account of the settlement at Port Jackson*. Text Publishing, Melbourne.

Terborgh, J., Lopez, L., Nunez, P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G. H., Lambert, T. D. & Balbas, L. (2001). Ecological meltdown in predator-free forest fragments. *Science* **294**, 1923–1926.

Thompson, C. M. & Gese, E. M. (2007). Food webs and intraguild predation: community interactions of a native mesocarnivore. *Ecology* **88**, 334–346.

Thompson, M. B. (1983). Populations of the Murray River tortoise, *Emydura* (Chelodina): the effect of egg predation by the red fox, *Vulpes vulpes*. *Australian Wildlife Research* **10**, 363–371.

Thomson, P. C. (1992). The behavioural ecology of dingoes in north-western Australia. III. Hunting and feeding behaviour, and diet. *Wildlife Research* **19**, 531–541.

Thomson, P. C., Rose, K. & Kok, N. E. (1992). The behavioural ecology of dingoes in north-western Australia. V. Population dynamics and variation in the social system. *Wildlife Research* **19**, 565–584.

TREVES, A. & KARANTH, K. U. (2003). Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology* **17**, 1491–1499.

TREWBY, I. D., WILSON, G. J., DELAHAY, R. J., WALKER, N., YOUNG, R., DAVISON, J., CHEESEMAN, C., ROBERTSON, P. A., GORMAN, M. L. & MCDONALD, R. A. (2008). Experimental evidence of competitive release in sympatric carnivores. *Biology Letters* **4**, 170–172.

TRIGGER, D., MULCOCK, J., GAYNOR, A. & TOUSSAINT, Y. (2008). Ecological restoration, cultural preferences and the negotiation of 'nativeness' in Australia. *Geoforum* **39**, 1273–1283.

TRIGGS, B., BRUNNER, H. & CULLEN, J. M. (1984). The food of the fox, dog and cat in Croajingalong National Park, south-eastern Australia. *Australian Wildlife Research* **11**, 491–499.

VAN BOMMEL, L. (2010). *Guardian dogs: best practice manual for the use of livestock guardian dogs.* Invasive Animals Cooperative Research Centre, Canberra.

VANAK, A. T. & GOMPPER, M. E. (2009). Dogs *Canis familiaris* as carnivores: their role and function in intraguild competition. *Mammal Review* **39**, 265–283.

VERARDI, A., LUCCHINI, V. & RANDI, E. (2006). Detecting introgressive hybridization between free-ranging domestic dogs and wild wolves (*Canis lupus*) by admixture linkage disequilibrium analysis. *Molecular Ecology* **15**, 2845–2855.

VERNES, K., DENNIS, A. & WINTER, J. (2001). Mammalian diet and broad hunting strategy of the dingo (*Canis familiaris dingo*) in the wet tropical rain forests of northeastern Australia. *Biotropica* **33**, 339–345.

VILÀ, C., WALKER, C., SUNDQVIST, A. K., FLAGSTAD, Ø., ANDERSONE, Z., CASULLI, A., KOJOLA, I., VALDMANN, H., HALVERSON, J. & ELLEGREN, H. (2003). Combined use of maternal, paternal and bi-parental genetic markers for the identification of wolf-dog hybrids. *Heredity* **90**, 17–24.

VISSER, R. L., WATSON, J. E. M., DICKMAN, C. R., SOUTHGATE, R., JENKINS, D. & JOHNSON, C. N. (2009). A national framework for research on trophic regulation by the dingo in Australia. *Pacific Conservation Biology* **15**, 209–216.

VONHOLDT, B. M., POLLINGER, J. P., LOHMUELLER, K. E., HAN, E., PARKER, H. G., QUIGNON, P., DEGENHARDT, J. D., BOYKO, A. R., EARL, D. A., AUTON, A., REYNOLDS, A., BRYC, K., BRISBIN, A., KNOWLES, J. C., MOSHER, D. S., SPADY, T. C., ELKAHLOUN, A., GEFFEN, E., PILOT, M., JEDRZEJEWSKI, W., GRECO, C., RANDI, E., BANNASCH, D., WILTON, A., SHEARMAN, J., MUSIANI, M., CARGILL, M., JONES, P. G., QIAN, Z., HUANG, W., DING, Z.-L., ZHANG, Y.-p., BUSTAMANTE, C. D., OSTRANDER, E. A., NOVEMBRE, J. & WAYNE, R. K. (2010). Genome-wide SNP and haplotype analyses reveal a rich history underlying dog domestication. *Nature* **464**, 898–902.

WAGNER, K. K., SCHMIDT, R. H. & CONOVER, M. R. (1997). Compensation programs for wildlife damage in North America. *Wildlife Society Bulletin* **25**, 312–319.

WALLACH, A. D., JOHNSON, C. N., RITCHIE, E. G. & O'NEILL, A. J. (2010). Predator control promotes invasive dominated ecological states. *Ecology Letters* **13**, 1008–1018.

WALLACH, A. D. & O'NEILL, A. J. (2009a). Artificial water points: hotspots of extinction or biodiversity? *Biological Conservation* **142**, 1253–1254.

WALLACH, A. D. & O'NEILL, A. J. (2009b). Threatened species indicate hot-spots of top-down regulation. *Animal Biodiversity and Conservation* **32**, 127–133.

WALLACH, A. D., RITCHIE, E. G., READ, J. & O'NEILL, A. J. (2009). More than mere numbers: the impact of lethal control on the social stability of a top-order predator. *PLoS ONE* **4**, e6861.

WAYNE, R. K. & JENKS, S. M. (1991). Mitochondrial DNA analysis implying extensive hybridization of the endangered red wolf *Canis rufus*. *Nature* **351**, 565–568.

WEBB, J. K. (1996). Observation of three dingoes killing a large lace monitor (*Varanus varius*). *Australian Mammalogy* **19**, 55–56.

WHITE, P. J. & GARROTT, R. A. (2005). Yellowstone's ungulates after wolves - expectations, realizations, and predictions. *Biological Conservation* **125**, 141–152.

WHITEHOUSE, S. J. O. (1977). The diet of the dingo in Western Australia. *Australian Wildlife Research* **4**, 145–150.

WHITING, S. D., LONG, J. L., HADDEN, K. M., LAUDER, A. D. K. & KOCH, A. U. (2007). Insights into size, seasonality and biology of a nesting population of the olive ridley turtle in northern Australia. *Wildlife Research* **34**, 200–210.

WILSON, G., DEXTER, N., O'BRIEN, P. & BOMFORD, M. (1992). *Pest animals in Australia: a survey of introduced wild mammals.* Kangaroo Press, Kenthurst, Sydney.

WILSON, G. J. & DELAHAY, R. J. (2001). A review of methods to estimate the abundance of terrestrial carnivores using field signs and observation. *Wildlife Research* **28**, 151–164.

WOINARSKI, J. C. Z., MACKEY, B., NIX, H. & TRAILL, B. (2007). *The nature of northern Australia.* Australian National University Electronic Press, Canberra.

WOODALL, P. F. (1983). Distribution and population dynamics of dingoes (*Canis familiaris*) and feral pigs (*Sus scrofa*) in Queensland, 1945–1976. *Journal of Applied Ecology* **20**, 85–95.

WOOD JONES, F. (1921). The status of the dingo. *Transactions and Proceedings of the Royal Society of South Australia* **45**, 254–263.

WROE, S., ARGOT, C. & DICKMAN, C. (2004). On the rarity of big fierce carnivores and primacy of isolation and area: tracking large mammalian carnivore diversity on two isolated continents. *Proceedings of the Royal Society B: Biological Sciences* **271**, 1203–1211.